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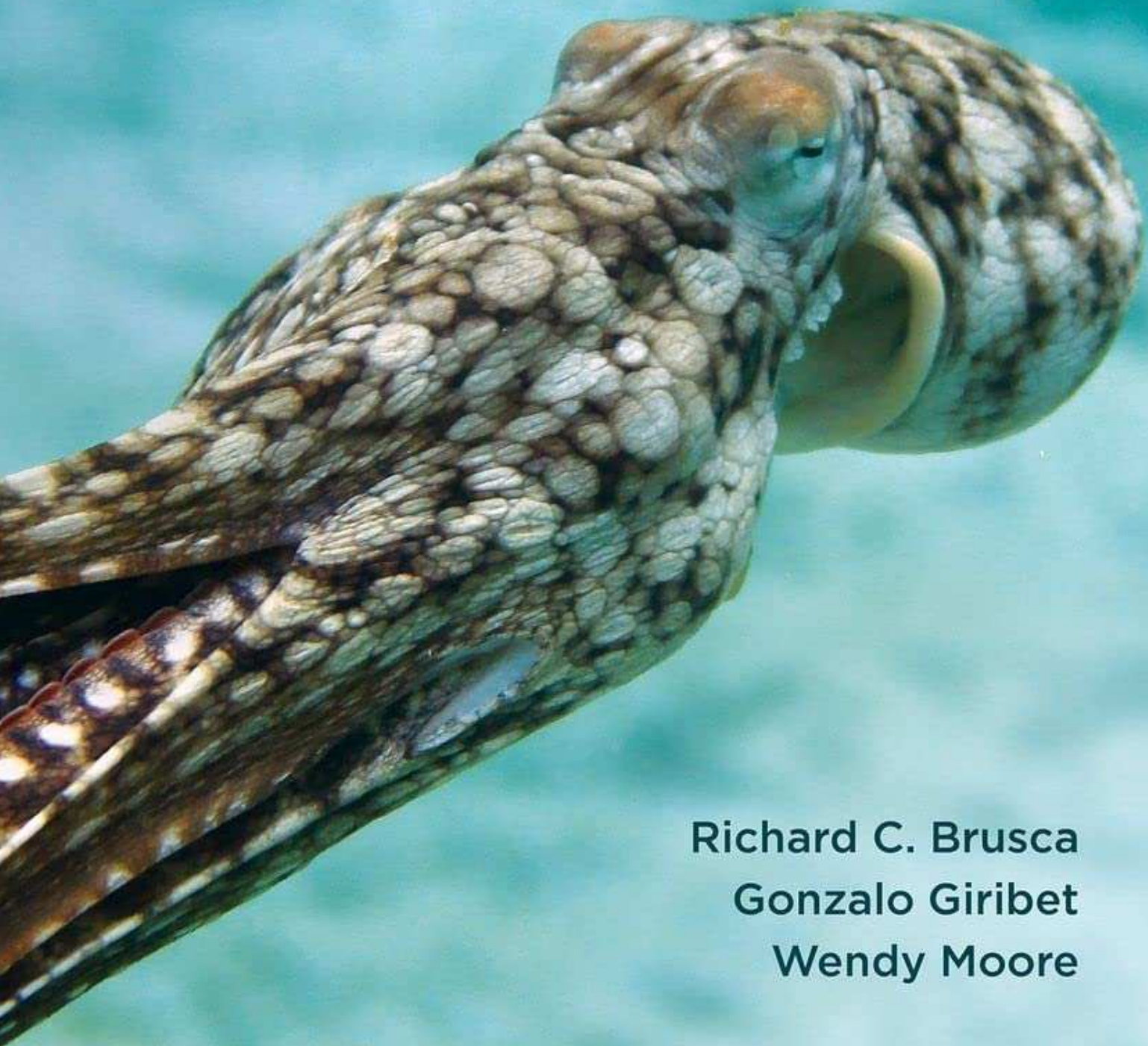

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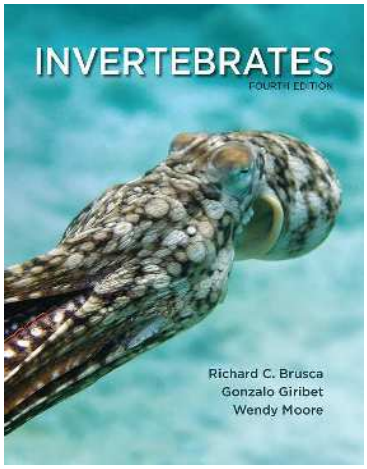

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About the cover

Day Octopus (*Octopus cyanea*). Found throughout the tropical Indo-Pacific, this is the most commonly seen octopus in Hawai'i. Hidden in a lair on the reef floor by night, the octopus will reach out with tentacles to gather coral rubble to protect the entrance. When at rest in its lair, it is a uniformly dark reddish-brown but during the day when hunting crabs on the reef bottom, it displays a spectacular array of color patterns and textures to match the varied landscape it crosses. An ink cloud released during escape contains mucus, melanin, dopamine, and tyrosinase, and is thought to confuse a fish predator and to depress its olfactory ability.

Larry Jon Friesen, PhD, completed his graduate research at the University of California, Santa Barbara, in Animal Communication. Dr. Friesen is a Professor of Biological Sciences at Santa Barbara City College, teaching Natural History, Evolution and Animal Diversity and continuing his life-long passion for nature photography.

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We dedicate this book to all our fellow teachers
and students of invertebrate zoology around the world.

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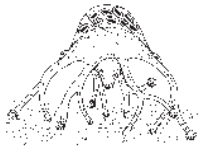
Foreword

Humans are well aware of the crushing tragedy of species loss among the grand mammals—the rhinoceroses, elephants, and even among our closest relatives, the primates—as well as among the birds, reptiles, fish, and amphibians. But meanwhile, though less often in the news, the invertebrate species and communities of the world have also been suffering. Insect populations are reduced globally to a fraction of former levels, many invertebrates are shifting their historical ranges, and invasive species are decimating indigenous ones, especially on islands and in freshwater environments. And we have barely begun to appreciate or document the impacts on marine invertebrates of global ocean warming and acidification and disruption of oceanic circulation patterns. The losses of these non-vertebrate species are already being felt and will become catastrophic in the not too distant future as insect-pollinated crops fail, soil ecosystems collapse, and marine food chains are disrupted.

Most humans think of invertebrates (when they think of them at all) as annoying pests or something to be afraid of, or, in the case of lobsters and prawns or oysters and mussels, as succulent mouthfuls. This book invites us, as it has for over three decades, to explore more deeply into the beautiful and fascinating diversity of our own family tree—our invertebrate cousins that dominate planet Earth. With this new, fourth edition, the account of the world of invertebrates is brought up to date with respect to the rapidly growing fields of molecular phylogenetics and evo-devo. New figures and color photographs add further appeal to this new edition, especially as they reflect some of the latest discoveries in invertebrates and the most up-to-date imaging techniques to capture the beauty of their whole bodies or their anatomy. The ever-useful, detailed classifications are updated to reflect the latest consensus in the field, with excellent synopses of the higher taxa making the book an enormously useful reference for any zoologist—not just students. And as with past editions, complicated ideas are presented accurately, clearly, and understandably.

Invertebrates has long been prestigious among invertebrate zoology texts, a reputation well earned. For coverage of some groups, such as the meiofaunal taxa, there is simply nothing comparable. Successive editions of this textbook have added newly discovered phyla. First, Loricifera (first edition), then Cycliophora (second edition), living on the mouthparts of lobsters, and finally Micrognathozoa (third edition), originally found at Disko Island, in Greenland but now known from several localities around the world. These discoveries should make us realize how much there remains to learn, as cycliophorans were discovered only relatively recently despite being ectocommensals on some of the most preferred foods of Europe and North America, the Norway lobster and the American and European lobsters of the genera *Nephrops* and *Homarus.* If we had only paid more attention to them before tossing them into the pot to be boiled! So, curl up in your favorite reading chair and enjoy a few pages when you're in the mood; you'll be surprised at how readable and fascinating the lives of invertebrates are.



Vicki Buchsbaum Pearse
Coauthor of *Animals Without Backbones* and *Living Invertebrates*, founding editor of *Invertebrate Biology*.

Reinhardt Møbjerg Kristensen
University of Copenhagen, Denmark.

Preface

This project began in 1980, when two California brothers who taught invertebrate biology courses at Humboldt State University and the University of Southern California sat down in front of their typewriters determined to write a "different invert textbook" in two or three years. It took them ten years. By the second edition personal computers were widely available, and in the early 1990s email further increased the efficiency and pace of the project. The success of the first edition led to the second (2003) being full color—a game changer. For the third edition (2016) Wendy Moore and Stephen Shuster joined the team, and a number of contributing specialists kindly agreed to revise or edit various sections of the book. For this fourth edition of *Invertebrates*, Gonzalo Giribet and Wendy Moore join as co-authors. In addition, 19 other specialists graciously agreed to revise selected chapters or chapter sections and we are deeply indebted to them (please see Guest Chapter Revisers). We have also had the good fortune to continue working with the highly professional team at Sinauer Associates, now an imprint of Oxford University Press. It truly does take a village.

The information explosion has continued since the third edition of this book, especially in the fields of molecular biology and phylogenetics. A fairly solid framework of the "new metazoan phylogeny" has emerged although some big questions still linger, such as the relationships of the four basal metazoan phyla and the internal relationships among the Platytrochozoa. Although the legacy names Protostomia and Deuterostomia (the later now with only three phyla) are retained, the composition and nature of these two animal clades has changed significantly since the first edition of this book. The enigmatic phylum Xenacoelomorpha remains supported as the sister group of the remaining Bilateria (aka the Nephrozoa). Protostomia comprises two well-supported clades, Spiralia and Ecdysozoa. There is support for the Ecdysozoa having three subclades—Nematoida, Panarthropoda, and Scalidophora—although the latter lacks strong molecular support. The sister group of Ecdysozoa, Spiralia (with 15 phyla), still remains only partly resolved, although the clades Gnathifera, Platytrochozoa, Rouphozoa and Lophotrochozoa have strong support. The Platyhelminthes, once thought to be primitive bilaterians, have been shown to be high up in the spiralian tree of life as a sister group to the hairy-bellied worms, Gastrotricha (together constituting the clade Rouphozoa). The sister group of Arthropoda is Onychophora, not Tardigrada as once thought. Among the Crustacea, the long-bodied forms (e.g., Cephalocarida, Branchiopoda, Remipedia) are no longer viewed as the most primitive living crustaceans, but rather form a clade called Allotriocarida that arises higher in the tree and that includes Hexapoda. Indeed, the sister group of the remipedes appears to be Hexapoda (insects and their kin). The two spiralian phyla Annelida and Mollusca are in the midst of major phylogenetic re-evaluation and for now their internal classification, while striving for monophyly, has many provisional rankings (the overall composition of Mollusca has been stable for decades, but that of Annelida continues to add taxonomic groups, the latest being the former phylum Orthonectida). As a result of recent molecular phylogenetic studies, some long-standing taxa have been abandoned (e.g., the phyla Sipuncula, Echiura and Orthonectida are now known to be clades of highly modified annelids), and other annelid and mollusc groups have been radically redefined (e.g., Polychaeta, Heterobranchia).

In addition to the revised phylogenetic trees and classifications, other major changes in this fourth edition include new summary boxes for each chapter, a revised and updated discussion of phylogenetic systematics (Chapter 2), and a shortening of the book's length. The chapter on protists has been deleted simply because surveys show they are not taught in any university courses that use this textbook (and protists are, of course, not invertebrates). As in previous editions, important new terms are printed in boldface when first defined (and these are noted in the Index). Specific gene names, like species names, are italicized, though note that their products (proteins) are not (nor are names for classes of genes, e.g., Hox and ParaHox genes).

Much of the art for this edition is new or has been updated. However, we continue to include diagrams that will be useful to students in the laboratory,

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including for animal dissections. We also continue to provide detailed classifications and taxonomic synopses within each phylum, and these have been thoroughly updated. We don't expect these to read in the same way as the rest of the chapter, but rather to be used as a reference to look up taxonomic names, understand the traits that distinguish groups, and get an overall sense of the scope of the higher taxa in each animal phylum.

We are delighted and honored that Vicki Buchsbaum Pearse and Reinhardt Møbjerg Kristensen wanted to write a Foreword for this edition of *Invertebrates*. Vicki, of course, has coauthored two very popular books on invertebrates herself, was a founding editor for the fine journal *Invertebrate Biology*, and has published extensively on everything from sponges to echinoderms (and is one of the few world experts on Placozoa). Reinhardt is a world expert on tardigrades and other meiofauna and microfauna, and he holds the distinguished honor of having discovered more animal phyla than any other modern biologist, three—Loricifera, Cycliophora, and Micrognathozoa! He has also been a leading expert in Arctic biology for the past forty years.

To say this book is a "labor of love" would be an understatement. Without a deep passion for invertebrates on the part of all the contributors it would not have been possible. Hopefully this book elevates in its readers their own passion and enthusiasm for that 95% of the animal kingdom that has so successfully flourished without backbones.

R.C.B., G.G., W.M.
March 2022

Acknowledgments

This edition of *Invertebrates* has again benefitted greatly from conscientious reviews provided by many specialists, and we extend to those wonderful professionals and friends our utmost gratitude. Special thanks to Judie Bronstein for discussions on symbiosis in its many forms. In addition, 19 specialists in various taxa generously agreed to revise chapters or sections of the book (see Guest Chapter Revisers). Thanks also to those guest revisers of the third edition who did not participate in this edition: S. Patricia Stock, C. Sarah Cohen, Joel W. Martin, Fernando Pardos, and Jesús Benito.

The highly talented staff at Sinauer Associates has always been a joy to work with, and for this edition we had the skills of their many professionals assisting us, including: Tracy Marton (Production Editor), Martha Lorantos (Lead Production Editor), Cailen Swain (Permissions Supervisor), Lou Doucette (Copyeditor), Sarah D'Arienzo (Editorial Assistant), Mark Siddall (Photo Researcher), Joan Gemme (Production Manager/Art Director), Meg Britton Clark (Production Specialist & Book Designer), Michele Ruschhaupt (freelance page layout assistance), Linda Hallinger (Indexer), and Jason Noe (Senior Acquisitions Editor, Oxford University Press). Most of the original artwork in this text was done from our own sketches or from other sources by the award-winning scientific illustrator Nancy Haver, supported by our publisher, Sinauer Associates. Thank you one and all; your technical skills are matched only by your patience and good humor. We are fortunate to have many of Larry Jon Friesen's splendid photographs once again adorning this edition of *Invertebrates*, including the cover photo.

Invertebrates is in four languages and enjoys a broad readership, notably in Europe and Latin America. Many students and professionals have written over the years expressing their support and encouragement and sending photographs or other material. To those loyal supporters of this long-standing project, we offer our most sincere thanks.

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Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA

Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA

Nephrozoa

PROTOSTOMIA

Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)

GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA

PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA

Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*

LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA

Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES

Ecdysozoa

SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA

NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA

PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA

MANDIBULATA
SUBPHYLUM MYRIAPODA

PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA

DEUTEROSTOMIA
PHYLUM CHORDATA

AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida

** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent

*** Paraphyletic (excludes Hexapoda)

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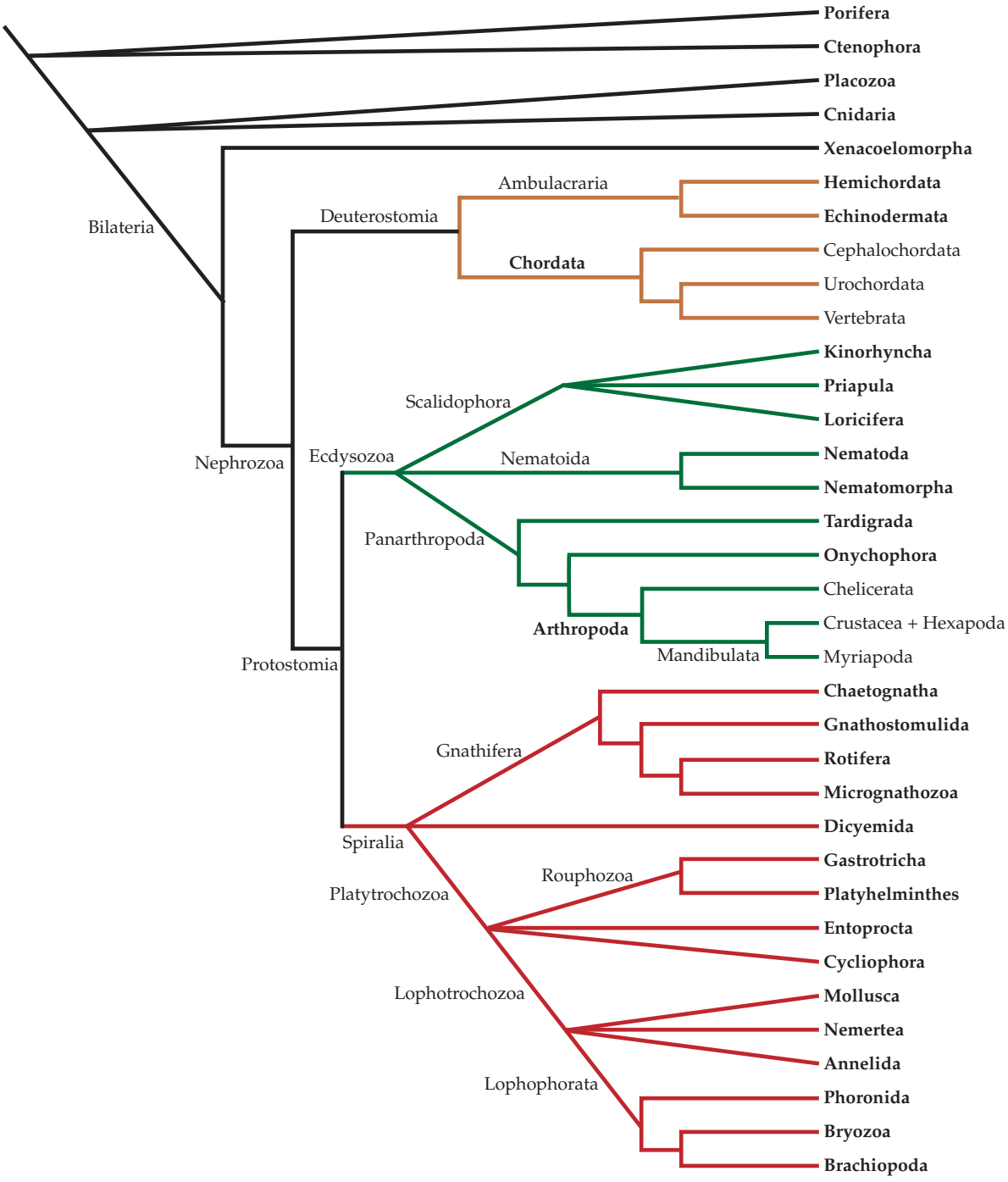

A phylogeny of Metazoa. This tree reflects a consensus view based primarily on recent molecular phylogenetic analyses. The 31 animal phyla are in boldface, whereas subphyla and other clades are in lightface. Spiralian lineages are in red, ecdysozoan lineages are in green, deuterostome lineages are in tan. Uncertainty still exists in several regions, and these are depicted as polytomies ("starbursts"). Thus, for example, the branching sequence for Placozoa, Cnidaria, and Bilateria is not yet resolved, so it is shown as an unresolved trichotomy. Similarly, two large polytomies exist among the Platytrochozoa, and the relationships of the three ecdysozoan clades are still unresolved, as are those of the three scalidophoran phyla. Due to uncertainty, Dicyemida is depicted in an unresolved trichotomy with Gnathifera and Platytrochozoa. See Chapter 28 for additional details.

Geologic Time Scale			
ERA	PERIOD	EPOCH	TIME (BEGINNING)
Cenozoic	**Quaternary**	Holocene	11,700 ybp
		Pleistocene	2.58 mya
	Neogene	Pliocene	5.33 mya
		Miocene	23.03 mya
	Paleogene	Oligocene	33.9 mya
		Eocene	56 mya
		Paleocene	66 mya
Mesozoic	**Cretaceous**		145 mya
	Jurassic		201.3 mya
	Triassic		251.9 mya
Paleozoic	**Permian**		298.9 mya
	Carboniferous	Pennsylvanian	323.2 mya
		Mississippian	358.9 mya
	Devonian		419.2 mya
	Silurian		443.8 mya
	Ordovician		485.4 mya
	Cambrian		541 mya
Precambrian	**Ediacaran**		635 mya
			4.6 bya

ybp = years before present; mya = million years ago; bya = billion years ago
Based on www.stratigraphy.org

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CHAPTER 1

Introduction

The incredible diversity of extant (= living) invertebrates on Earth is the outcome of more than half a billion years of evolution. Indirect evidence of the first life on Earth, prokaryotic organisms, has been found in some of the oldest sedimentary rocks on the planet, suggesting that life first appeared in Earth's seas almost as soon as the planet cooled enough for life to exist. The Earth is 4.6 billion years old, and the oldest rocks found so far are about 4.3 billion years old. Although the precise date of the first appearance of life on Earth remains debatable, there are tantalizing 3.6- to 3.8-billion-year-old trace fossils from Australia that resemble prokaryotic cells—although these have been challenged, and opinion is now split on whether they are traces of early bacteria or simply mineral deposits. However, good evidence of prokaryotic life has been found in pillow lava that formed on the seabed 3.5 billion years ago, now exposed in South Africa. And 3.4-billion-year-old fossil cells (probably sulfur-oxidizing bacteria) have been found among cemented sand grains on an ancient beach in Australia.[1]

The next big step in biological evolution came about when prokaryotic cells began taking in guests. Around 2 to 2.5 billion years ago, one of these primitive prokaryotic cells took in a free-living bacterium that established permanent residency—giving rise to the cellular organelles we call mitochondria. And that was the origin of the eukaryotic cell. Mitochondria, you will recall from your introductory biology course, generate energy for their host cells by oxidizing sugars, and in this case they also equipped early life to survive in Earth's gradually increasing oxygen levels. Evidence suggests that mitochondria evolved just once, from a symbiotic α-proteobacterium, and then subsequently diversified broadly. Modern free-living relatives of this bacterium harbor about 2,000 genes across several million base pairs, but their mitochondrial descendants have far fewer, sometimes as few as three genes. And human mitochondrial DNA harbors only about 16,000 base pairs. On the other hand, some plants have greatly

[1]There are three popular theories on how life first evolved on Earth. The classic "primeval soup" theory, dating from Stanley Miller's work in the 1950s, proposes that self-replicating organic molecules first appeared in Earth's early atmosphere and were deposited by rainfall into the ocean, where they reacted further to make nucleic acids, proteins, and other molecules of life. More recently, the idea of the first synthesis of biological molecules by chemical and thermal activity at deep-sea hydrothermal vents has been suggested. Hydrothermal vents also spew out compounds that could have been incorporated into the first life forms. The third proposal is that organic molecules, or even prokaryotic life itself, first arrived on Earth from another planet (recently Mars has been at the forefront) or from deep space, on comets or meteorites. Meteorites that fall to Earth contain amino acids and organic carbon molecules such as formaldehyde. Clearly, raw materials were not the issue—the trick was assembling the organic compounds to create a living, reproducing system.

expanded their mitochondrial genome, the largest so far discovered in the genus *Silene*, with around 11 million base pairs. Another prokaryotic intracellular guest, a cyanobacterium, became the ancestor of chloroplasts through the same symbiogenic process; chloroplasts, of course, are the photosynthesizing organelles that made plants and algae possible. In some plant and algal lines, the original chloroplast was lost, and a new one was picked up when a host cell took in an alga and co-opted its chloroplast in another kind of symbiogenic event.

Controversial hydrocarbon biomarkers suggest that the first eukaryotic cells might have appeared as early as 2.7 billion years ago, late in the Archean, although the earliest fossils that have been proposed to be eukaryotes—based on cell surface features and their large size—are 1.6 to 1.8 billion years old (Paleoproterozoic). Multicelled algae (protists) date as far back as 1.2 billion years (in the Mesoproterozoic Era). Eukaryote-like microfossils have been described from 1-billion-year-old freshwater deposits, suggesting that the eukaryotes might have left the sea and invaded the terrestrial realm long ago. Even though the eukaryotic condition appeared early in Earth's history, it took a few hundred million more years for multicellular organisms to first evolve.

Molecular clock estimates put the origin of Metazoa at 875 to 650 million years ago. The oldest generally accepted metazoan fossils are from the Ediacaran Period (635–541 Ma), found in the Fermeuse Formation of Newfoundland (~560 Ma) and the Doushantuo Formation of southern China (600–580 Ma). A 560-million-year-old likely cnidarian (named *Haootia quadriformis*) has been described from Newfoundland, with quadraradial symmetry and clearly preserved bundled muscular fibers. *Haootia* appears to be a polyp nearly 6 cm long, or perhaps an attached medusa—it resembles modern species of Staurozoa. Cnidarians and other apparent diploblastic animals have been reported from the Doushantuo deposits, although these have been met with skepticism in some quarters. However, in 2015, a seemingly reliable 600-million-year-old fossil sponge (*Eocyathispongia qiania*) was described from the Doushantuo Formation. In 2009, Jun-Yuan Chen and colleagues reported on embryos of reputed bilaterians (triploblasts) in the Doushantuo deposits—32-cell-stage embryos with micromeres and macromeres, apparent anterior–posterior and dorsoventral patterning, and ectoderm-like cells around part of their periphery. This finding was challenged, and the fossils were variously declared prokaryotes or protists by other workers. However, further discoveries of additional embryos seemed to support the view that these were bilaterian embryos and, in some cases, perhaps diapause embryos ("resting eggs") of bilaterians. Good trace fossils (tracks) of a minute wormlike bilaterian animal, possibly with legs, have also been described from 585-million-year-old rocks in Uruguay. These fossils put the appearance of "higher metazoans" (i.e., bilaterians) millions of years before the beginning of the Cambrian period.

There is no argument that Metazoa are monophyletic (i.e., a clade), and the animal kingdom is defined by numerous apomorphies, including: gastrulation and embryonic germ layer formation; unique modes of oogenesis and spermatogenesis; a unique sperm structure; mitochondrial gene reduction; epidermal epithelia with septate junctions, tight junctions, or zonula adherens; striate myofibrils; actin-myosin contractile elements; type IV collagen; and the presence of a basal lamina/basement membrane beneath epidermal layers (of course, some of these features have been secondarily lost in some groups). In addition, there is a series of molecular apomorphies unique to metazoans, including signaling, adhesion, and transcriptional regulation factors (e.g., *Wnt*, *Frizzled*, *Hedgehog*, *EGFR*, classical cadherin, Hox, and others). Evidence is strong that Metazoa arose out of the protist group Choanoflagellata, or a common ancestor, and the two comprise sister groups in almost all recent analyses. They are, in turn, part of a larger clade known as Opisthokonta that also includes the Fungi and several small protist groups.

The three great lineages of life on Earth—Bacteria, Archaea, Eukaryota—are very different from one another. Bacteria and Archaea have their DNA dispersed throughout the cell, whereas in Eukaryota the DNA is enclosed within a membrane-bound nucleus. The cell lineages that gave rise to the Eukaryota are still unknown. The many millennia between the origin of Eukaryota and the explosive radiation that apparently began in the Ediacaran is sometimes called the "boring billion years," but the fossil record is fairly sparse for that time period, so we're not sure how "boring" it actually was. One popular hypothesis suggests that oxygen levels were too low during that time for larger organisms to evolve.

It seems likely that a significant portion of Earth's biodiversity, at the level of both genes and species, resides in the "invisible" prokaryotic world, and we have come to realize how little we know about this hidden world. About 10,300 species of prokaryotes have been described, but there are an estimated 10 million (or up to ~1 trillion) undescribed prokaryote species on Earth. Today, there are an estimated 2,064,967 described and named eukaryote species: about 200,000 protists, 375,000 plants (300,000 seed plants), 100,000 fungi, and 1,453,163 animals (Metazoa). And 15,000 to 20,000 new species are described every year. An estimated 135,000 more plant species remain to be described. Overall, estimates of undescribed eukaryotes range from lows of 3–8 million to highs of 100 million or more. Of the 1,453,163 described species of living animals, around 58,000 are vertebrates (4%), more than half of which are fishes,

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and 1,395,163 (96%) are invertebrates (Table 1.1). This book attempts the audacious task of teaching you about those 1.4 million spineless wonders.

Keeping Track of Life

How can we possibly keep track of all these species names and information about each of them, and how do we organize them in a meaningful way? We do so with classifications. **Classifications** are lists of species, ranked in a subordinated fashion that reflects their evolutionary relationships and phylogenetic history. Classifications summarize the overarching aspects of the tree of life. At the highest level of classification, we can recognize two superkingdoms: Prokaryota (containing the kingdoms Archaea and Bacteria) and Eukaryota (containing the kingdoms Protista, Fungi, Plantae, and Animalia/Metazoa). Because "Protista" is not a monophyletic group, the protists are sometimes broken up into several kingdoms, or other classificatory ranks, but the relationships among some protist groups are still being debated.

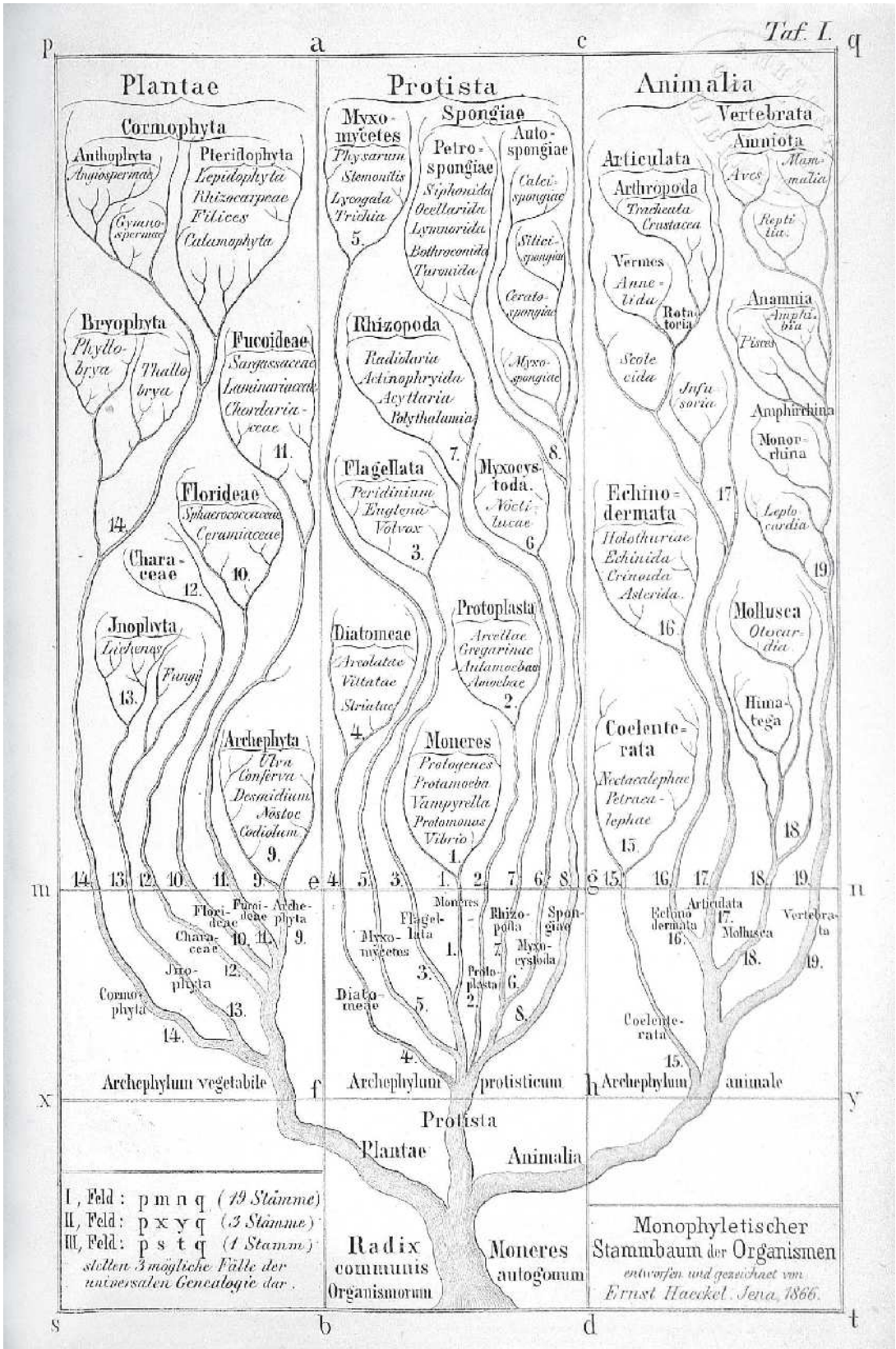
One of the earliest and best-known evolutionary trees of life published from a Darwinian (genealogical) perspective was by Ernst Haeckel in 1866 (Figure 1.1). Haeckel coined the term "phylogeny," and his famous trees codified what became a tradition of depicting phylogenetic hypotheses as branching diagrams, a tradition that has persisted since that time. However, a hand-drawn sketch in Charles Darwin's field notebook (1837) clearly depicts his view of South American mammal evolution in a branching tree of extant and fossil species. And in his book *On the Origin of Species* (1859), Darwin presented an abstract branching diagram of a theoretical tree of species as a way of illustrating his concept of descent with modification. The famous French zoologist Jean Baptiste P. A. de Lamarck probably presented the first historical trees of animals in his *Philosophie Zoologique* in 1809, and the French botanist Augustin Augier published a tree showing the relationships among plants in 1801 (perhaps the first evolutionary tree ever published)—even

TABLE 1.1 Numbers of Described Living Species in the 31 Animal Phyla, 1,453,163 total[a,b]

Taxon	Number of Described and Valid Living Species	Percent of Total Described Animal Species
Phylum Porifera	9,300	0.67
Phylum Placozoa	4	0.0003
Phylum Ctenophora	130	0.009
Phylum Cnidaria	13,300	0.95
Phylum Xenacoelomorpha	400	0.028
Phylum Dicyemida (=Rhombozoa)	120	0.009
Phylum Gnathostomulida	100	0.007
Phylum Rotifera	3,350	0.23
Phylum Micrognathozoa	1	0.00007
Phylum Chaetognatha	130	0.009
Phylum Entoprocta	200	0.014
Phylum Cycliophora	2	0.0001
Phylum Mollusca	73,000	5.02
Phylum Nemertea	1,300	0.09
Phylum Annelida	20,000	1.38
Phylum Phoronida	15	0.001
Phylum Bryozoa (= Ectoprocta)	6,300	0.43
Phylum Brachiopoda	440	0.03
Phylum Gastrotricha	860	0.06
Phylum Platyhelminthes	30,000	2.06
Phylum Kinorhyncha	300	0.02
Phylum Priapula	22	0.0016
Phylum Loricifera	38	0.0027
Phylum Nematoda	27,000	1.86
Phylum Nematomorpha	365	0.026
Phylum Tardigrada	1,300	0.09
Phylum Onychophora	200	0.014
Phylum Arthropoda (TOTAL)	**1,196,521**	**82.3**
Subphylum Chelicerata	113,000	7.8
Subphylum Myriapoda	16,000	1.10
Subphylum Crustacea	72,000	5.00
Subphylum Hexapoda	995,521	68.51
Phylum Chordata (TOTAL)	**61,035**	**4.20**
Subphylum Cephalochordata	35	0.003
Subphylum Urochordata	3,000	0.21
Subphylum Vertebrata	58,000	4.0
Phylum Hemichordata	130	0.009
Phylum Echinodermata	7,300	0.5

[a]1,395,163 (96%) are invertebrates. 82% of all known animals belong to just one phylum, Arthropoda; 87% belong to two phyla (Arthropoda + Mollusca); 92% belong to three phyla (Arthropoda + Mollusca + Chordata). 25 phyla each contain fewer than 1% of the known animal species, including some that may seem quite diverse to the casual seashore visitor, such as sponges, cnidarians, bryozoans, and echinoderms.

[b]Estimated numbers of other described (living) species: Prokaryota = 10,300; Protista = 200,000; Plantae = 315,000; Fungi = 100,000.



From E. H. P. A. Haeckel.1866. *Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von C. Darwin reformirte Decendenz-Theorie.* Georg Reimer, Berlin

FIGURE 1.1 **Haeckel's Tree of Life (1866).**

though both Lamarck's and Augier's trees were produced before the modern concept of evolution had been clearly articulated. We discuss various ways in which phylogenetic trees are developed in Chapter 2.

Since Haeckel's day, many names have been coined for the branches that sprout from these trees, and in recent years a glut of new names has been introduced to label various new clades nested within the tree of

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life, many of which have been proposed based on molecular data. We will not burden you with all of these names, but a few of them need to be defined here before we launch into our study of the invertebrates. Most of these names refer to groups of organisms that are thought to be natural phylogenetic lineages (i.e., groups that include all the descendants of a stem species, known as **monophyletic** groups, or **clades**). Examples of such natural, or monophyletic, groups are the superkingdom Eukaryota, kingdom Metazoa (the animals), and kingdom Plantae (the lower and higher plants).[2] All three of these large groupings are thought to have had a single origin, and they each include all of the species descended from that original ancestor. Some other named groups are natural, having a single evolutionary origin, but the group *does not contain all of the members* of the lineage. Such groups are said to be **paraphyletic**, and they are often the basal or deep lineages of a much larger clade. Paraphyletic groups comprise some, but not all, descendants of a stem species. The Protista are paraphyletic because the grouping excludes three large multicelled lineages that evolved out of it (e.g., Metazoa, Plantae, Fungi). Another well-known paraphyletic group is Crustacea (which excludes the Hexapoda/Insecta, a clade that evolved from a crustacean ancestor). The clade that includes both Crustacea and Hexapoda is called Pancrustacea. Classifications of life are ideally derived from evolutionary or phylogenetic trees and thus generally include only monophyletic groups. However, sometimes paraphyletic taxa are also used because they had been recognized historically and, if they are unambiguous, they can be important in facilitating meaningful communication among scientists and between the scientific community and society (e.g., Protista and Crustacea).

Some names refer to unnatural, or composite, groupings of organisms, such as "microbes" (i.e., all organisms that are microscopic in size, such as bacteria, archaeans, yeasts, unicellular fungi, and some protists). These unnatural groups are **polyphyletic**. For example, yeasts are unicellular fungi that evolved several times independently from multicellular filamentous ancestors; today they are assigned to one of three higher fungal phyla, so the concept of "yeast" represents a polyphyletic, or unnatural, grouping. The name "slugs" (or "sea slugs") also refers to a group of animals that do not share a single ancestry (the slug form has evolved many times among gastropod molluscs), so slugs are polyphyletic. We explore these concepts more fully in Chapter 2.

We know approximately how many genes are in organisms from yeast (about 6,000 genes) to humans (about 25,000 genes), but we don't know how many living species inhabit our planet, and the range in estimates is surprisingly broad. How many undescribed species are lingering out there, waiting for names and descriptions? However derived, predictions of global species diversity rely on extrapolations from existing real data. Methods of estimation have included rates of past species descriptions, expert opinion, the fraction of undescribed species in samples collected, and ratios between taxa in the taxonomic hierarchy. Each method has its limitations. Two recent estimates of undescribed marine animals (Mora et al. 2011 and Appeltans et al. 2012) concluded that 91% or 33%–67% (respectively) of the world's eukaryotic marine fauna is still undescribed. More recently, a large research program sampling the Western Australian upper continental slope for Crustacea and Polychaeta found 95% of the species to be undescribed (with the rate of new species obtained by the sampling program not even leveling off). Given the vast extent of the poorly sampled world's continental slopes, not to mention the deep sea, rain forests, and other little-sampled habitats, these data suggest that estimates that over 90% of eukaryotes on Earth are undescribed are not unreasonable.

Our great uncertainty about how many species of living organisms exist on Earth is unsettling. At our current rate of species descriptions, it might take us 10,000 years or more to describe just the rest of Earth's eukaryotic life forms. Not all of the species remaining to be described are invertebrates—between 1990 and 2002 alone, 38 new primate species were discovered and named. And if prokaryotes are thrown into this mix, the numbers become even larger. Recent gene-sequence surveys of the world's oceans (based largely on DNA "barcodes"—16S ribosomal RNA gene sequences for Bacteria and Archaea, 18S ribosomal RNA gene sequences for eukaryotes) have revealed a massive undescribed biota of microbes in the sea. Similar discoveries have been made with genetic searches for soil microbes, and a handful of soil can contain more than 5,000 species of prokaryotes and eukaryotes combined. For example, there are about 30,000 formally named bacterial varieties that are in pure culture, but estimates of undescribed species range from 10 million to a billion or more! And thousands of bacterial species inhabit the human body, almost all of which are not yet even named and described. Viruses still lack a universal molecular identifier, and the world scope of viral biodiversity is essentially unknown, despite the impact many of these undiscovered viruses may have on us.

[2] For decades, taxonomists have debated the boundary between protists and Plantae. We accept the view that it should be placed just prior to the evolutionary origin of chloroplasts and that Plantae should comprise all eukaryotes with plastids directly descending from the initially enslaved cyanobacterium, i.e., Rhodophyta (red algae), Glaucophyta (glaucophyte algae), and Viridiplantae ("green plants"), but exclude those like chromists that obtained their chloroplasts from plants secondarily by subsequent eukaryote-to-eukaryote lateral transfers. The structure of plastid genomes and the derived chloroplast protein-import machinery support a single origin of these closely related groups. Thus, Plantae is a monophyletic group containing two subkingdoms, Biliphyta (phyla Glaucophyta and Rhodophyta) and Viridiplantae (the phyla Chlorophyta, Charophyta, Anthocerotophyta, Bryophyta, Marchantiophyta, and Tracheophyta). In the past, some workers have restricted Plantae to land plants (embryophytes, or higher plants) and included the other Viridiplantae with the Protista in a larger group called Protoctista (which also included the lower fungi).

There are currently several attempts to compile a list of all *known* species on Earth. The United States Geological Survey (USGS) has hosted ITIS—the Integrated Taxonomic Information System. The goal of ITIS is to create an easily accessible database with reliable information on species names and their classification. Recently, ITIS and several other initiatives turned their data over to the Catalogue of Life (CoL) project, which is building the species list and maintaining a "consensus classification" of all life (see www.catalogueoflife.org and Ruggiero et al. 2015). The Encyclopedia of Life (EOL) project is building a website that offers not just species names, but also ecological information about each species; it currently contains more than 200,000 vetted species pages. WoRMS (the World Register of Marine Species) is an open-access online database with the goal of listing all described eukaryotic species, including their higher taxonomy.

However, at our current rate of anthropogenically driven extinction, a majority of Earth's species will go extinct long before they are ever described. In the United States alone, at least 5,000 named species are threatened with extinction, and an estimated 500 known species have already gone extinct since people first arrived in North America. Globally, the United Nations Environment Programme estimates that by 2030 nearly 25% of the world's mammals could go extinct, and recent counts indicate over 325 vertebrate species have already become extinct since 1500. Some workers now refer to the time since the start of the Industrial Revolution as the Anthropocene—a geologic period marked by humanity's profound global transformation of the environment. More than half of Earth's terrestrial surface is now plowed, pastured, fertilized, irrigated, drained, bulldozed, compacted, eroded, reconstructed, mined, logged, or otherwise converted to new uses. Human-driven deforestation removes 15 billion trees per year. E. O. Wilson once estimated that about 25,000 species are going extinct annually on Earth (we just don't know what they are!).

Even though invertebrates make up 95% of the described animal kingdom (Table 1.1), they account for only 38% of the 500 or so species now under protection by the U.S. Endangered Species Act. NatureServe has argued that more than 1,800 invertebrate species need protection, while the IUCN Red List of Threatened Species documents the extinction risk of nearly 50,000 species of animals and plants. In 2002, the U.N. Convention on Biological Diversity committed nations to significantly reduce rates of biodiversity loss by 2010, and in 2010 this call was renewed with a set of specific targets for 2020. However, several recent studies have shown that the convention has so far failed dismally and rates of biodiversity loss do not appear to be slowing at all; in fact, they are likely accelerating.

The single greatest threat to species survival for the past 200 years has been habitat loss, although over the past 75 years or so, loss of keystone predators has also been a major perturbation to ecosystems (including in the sea, where only 7% of the world's ocean has any form of protection, and only 2.5% is highly protected). More recently, invasive species are becoming an increasing threat, especially in the time of globalization. We hear mostly about deforestation, but as much as 50% of the Earth's coastal environments have also been degraded during past decades, at rates exceeding those of tropical forest loss. And, it is now clear that the damaging effects of habitat loss will be escalated by anthropogenically driven global climate change. The concentration of carbon dioxide (CO_2) in Earth's atmosphere has risen by about 40% since the start of the industrial era, as a result of fossil fuel burning and land use change, and nearly a third of all the CO_2 emitted through human activities has been absorbed by the ocean, resulting in acidification of surface waters, although much of this carbon is eventually transported to the isolated deep sea as plankton and nekton die and sink. In fact, the oceans overall are now about 30% more acidic than they were 100 years ago. This drastic drop in ocean pH is creating hardships on animals with calcium carbonate skeletons, and damage has been documented in everything from corals to sea butterflies (pteropod molluscs). In May 2019, the concentration of CO_2 in the atmosphere reached 415 ppm, the highest it has been over the past 2 million years (since well before our species evolved). One recent study suggests that the same amount of CO_2 may be emitted over the twenty-first century as was released in pulses of volcanic eruptions during the end-Triassic mass extinction event 200 million years ago, which is enough to warm the planet by around 2°C. Rising concentrations of greenhouse gases in the atmosphere are leading to increasing global temperatures and changes in precipitation regimes, and these changes are impacting the distribution of biota across the planet. Globally, average air temperatures have risen about 0.8°C since 1880, mean land surface temperature has warmed 0.27°C per decade since 1979, and projections from global climate models predict global atmospheric temperatures to increase by about 4°C by the end of this century.

The global human population is 7.6 billion and expected to rise to 10 billion by the middle of this century. Humans now constitute 36% of the mammalian biomass, and livestock another 60%, leaving just 4% for the more than 5,000 species of wild mammals. Climate warming is leading to marine "heat waves" that result in mass killings of shallow-water animals and not-too-gradual shifts in species ranges. These are also compromising the health of or even outright destroying the world's kelp forests, the most productive ecosystems on the planet, rich in invertebrate diversity. Melting polar ice and glaciers, combined with expansion of warming ocean waters, are driving up sea level, which is expected to be as much as 2 m higher by the

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end of this century. Even the accumulation of plastics has become a major threat to animals in the sea, where massive concentrations of large plastics occur on the surface and microplastics are entering marine food webs and even accumulating on the seafloor of the deep ocean. An estimated 311 million tons of plastic are produced annually worldwide, 90% of these being derived from petrol (and less than 15% being recycled). And growth of coastal cities, sewage discharge, and agriculture are leading to massive increases in nitrogen and phosphorus being delivered to coastal waters. These are stimulating rapid increases in primary production and, in warm, stratified, and/or poorly mixed waters, resulting in hypoxia—depletion of dissolved oxygen—and acidification, both of which individually can have adverse effects on sea life. Industrial fishing occurs in over 55% of the ocean's area and has a spatial extent more than four times that of agriculture. On land, increasing frequency of unusually hot days is creating stress on many insects, as is decreasing precipitation and the use of pesticides. Reports of insect declines, best documented in Europe and North America, suggest that as much as 40% of insect species in temperate countries may face extinction over the next few decades. Recent studies suggest a 30% drop in the number of North American birds since 1970.

Prokaryotes and Eukaryotes

The discovery that organisms with a cell nucleus constitute a natural (monophyletic) group divided the living world neatly into two categories, the **prokaryotes** (Archaea and Bacteria: those organisms lacking membrane-enclosed organelles and a nucleus, and without linear chromosomes) and the **eukaryotes** (those organisms that do possess membrane-bound organelles, a nucleus, and linear chromosomes). Investigations by Carl Woese and others, beginning in the 1970s, led to the discovery that the prokaryotes themselves comprise two distinct groups, called **Bacteria** (= Eubacteria) and **Archaea** (= Archaebacteria), both quite distinct from eukaryotes (Box 1A). Bacteria correspond more or less to our traditional understanding of bacteria. Archaea strongly resemble Bacteria, but they have genetic and metabolic characteristics that make them quite unique. For example, Archaea differ from both Bacteria and Eukaryota in the composition of their ribosomes, in the construction of their cell walls, and in the kinds of lipids in their cell membranes. Some Bacteria conduct chlorophyll-based photosynthesis, a trait that is never present in Archaea (photosynthesis is the harvesting of light to produce energy/sugars and oxygen). Current thinking favors the view that prokaryotes ruled Earth for about a billion years before the eukaryotic cell appeared.

As the prokaryotes evolved, they adapted to colonize every conceivable environment on Earth. During their early evolution, Earth's air had almost no oxygen, consisting primarily of CO_2, methane, and nitrogen. The metabolism of the earliest prokaryotes relied on hydrogen, methane, and sulfur and did not produce oxygen as a by-product. It was the appearance of the first oceanic photosynthesizing prokaryotes that led to increased atmospheric oxygen concentrations, setting the stage for the evolution of complex multicellular life. And aquatic species were probably able to colonize land only because the oxygen helped create the ozone layer that shields against the sun's ultraviolet radiation. Just *when* oxygen-producing photosynthesis began is still being debated, but when it happened, most of the early chemoautotrophic prokaryotes were likely poisoned by the "new gas" in the environment. A large body of evidence points to a sharp rise in the concentration of atmospheric oxygen between 2.45 and 2.32 billion years ago (this is sometimes called the "great oxidation event"), around the same time the eukaryotic cell first appeared. This evidence includes red beds or layers tinged by oxidized iron (i.e., rust) and oil biomarkers that may be the remains of Cyanobacteria (photosynthetic true Bacteria). However, in western Australia, thick shale deposits that are 3.2 billion years old have bacterial remains that hint at oxygen-producing photosynthesis. These ancient oxygen levels might have reached around 40% of present atmospheric levels. There is also evidence in the geological record that atmospheric oxygen did not steadily increase, but fluctuated wildly, dropping at times to a mere 0.1% of current levels. It may not have been until around 800 million years ago that high oxygen levels stabilized, and it might have been around then, in the Neoproterozoic, that multicelled animals made their first appearance.

Terrestrial photosynthesis has little effect on atmospheric O_2 because it is nearly balanced by the reverse processes of respiration and decay. By contrast, marine photosynthesis is a net source of O_2 because a small fraction (~0.1%) of the organic matter synthesized in the oceans is buried in sediments. It is this small "leak" in the marine organic carbon cycle that is responsible for most of our accumulated atmospheric O_2. Cyanobacteria are thought to have been largely responsible for the initial rise of atmospheric O_2 on Earth, and even today *Prochlorococcus* can be the numerically dominant phytoplankton in tropical and subtropical oceans, accounting for 20% to 48% of the photosynthetic biomass and production in some regions. Overall, this cyanobacterium may be responsible for about 5% of global photosynthesis, and it thrives from the sunlit sea surface to a depth of 200 m, where light is minimal. Today most marine photosynthesis is performed by Cyanobacteria and single-celled protists, such as diatoms and coccolithophores. Cyanobacteria are nearly unique among the prokaryotes in performing oxygenic photosynthesis, often together with nitrogen fixation, and thus they are major primary producers in both marine and terrestrial ecosystems.

BOX 1A The Six Kingdoms of Life*

PROKARYOTES (Superkingdom Prokaryota)*

Kingdom Bacteria (= Eubacteria)
The "true" bacteria, including Cyanobacteria (blue-green algae), Proteobacteria, Spirochaetae, and numerous other phyla; never with membrane-enclosed organelles or nuclei, or a cytoskeleton; none are methanogens; some use chlorophyll-based photosynthesis; with peptidoglycan in cell wall; with a single known RNA polymerase.

Kingdom Archaea (= Archaebacteria)
Anaerobic or aerobic, largely methane-producing microorganisms; never with membrane-enclosed organelles or nuclei, or a cytoskeleton; none use chlorophyll-based photosynthesis; without peptidoglycan in cell wall; with several RNA polymerases.

EUKARYOTES (Superkingdom Eukaryota)

Cells with a variety of membrane-enclosed organelles (e.g., mitochondria, lysosomes, peroxisomes) and with a membrane-enclosed nucleus. Cells gain structural support from an internal network of fibrous proteins called a cytoskeleton.

Kingdom Protista
Largely unicellular eukaryotes that do not undergo tissue formation through the process of embryological layering. A paraphyletic grouping of many phyla, including euglenids, diatoms and some other brown algae, ciliates, dinoflagellates, foraminiferans, amebas, and others (Chapter 3). Protists descended from bacteria by the acquisition of a nucleus, endomembrane, cytoskeleton, and mitochondria. The 200,000 or so described living species probably represent about 10% of the actual protist diversity on Earth today.

Kingdom Fungi
The fungi. Probably a monophyletic group that includes molds, mushrooms, yeasts, and others. Saprobic, heterotrophic, multicellular organisms. We view the demarcation between Protista and Fungi as lying immediately before the origin of the chitinous wall around vegetative fungal cells and the associated loss of phagotrophy. The earliest fossil records of fungi are from the Middle Ordovician, about 460 million years ago. The 100,000 described species are thought to represent only a small percentage of the actual diversity, and estimates of total fungal biodiversity range from 3 to 10 million. The detection of fungal species by molecular soil surveys has suggested that only 1% to 17% of soil fungi have so far been described and named.

Kingdom Plantae (= Archaeplastida)
Unicellular and multicellular, photosynthetic, chlorophyll-bearing eukaryotes with plastids directly descended from an initially enslaved cyanobacterium. About 400,000 named living species. Includes Glaucophyta (glaucophyte algae), Rhodophyta (red algae), and Viridiplantae (green plants). Viridiplantae includes the phyla Chlorophyta (green algae), Charophyta (freshwater green algae), Anthocerotophyta (hornworts and their kin), Marchantiophyta (liverworts), Bryophyta (other nonvascular plants), and Tracheophyta (the vascular plants, about 260,000 of which are flowering plants). Tracheophytes develop through embryonic tissue layering, in a manner analogous to animal embryogeny. The described species of Plantae are thought to represent about half of Earth's actual plant diversity.

Kingdom Animalia (= Metazoa)
The multicellular animals. A monophyletic taxon, containing 31 phyla of ingestive, heterotrophic, multicellular organisms that develop by tissue layering during embryogenesis. About 1,398,696 species of living metazoans have been described; estimates of the number of undescribed animal species range from lows of 3–8 million to highs of over 100 million.

*Portions of the old "kingdom Monera" are now included in the Bacteria (Eubacteria) and the Archaea. Viruses (about 5,000 described "species") and subviral parasites such as viroids and prions, which are all regarded as laterally transmissible parasitic genetic elements, are not included in this classification. Prions are infectious proteins, devoid of a nucleic acid genome but subject to mutation and thus evolution. Viruses comprise an ancient, polyphyletic group of stripped-down parasitic genetic fragments. Recent work suggests that they might have played important roles in major evolutionary transitions, such as the emergence of DNA and DNA replication mechanisms, the formation of the major "superkingdoms" of life, and perhaps even the origin of the eukaryotic nucleus. Viral classification is standardized by the ICTV (International Committee on Taxonomy of Viruses).

Many Archaea live in extreme environments, and this pattern is often interpreted as a refugial lifestyle—in other words, such creatures tend to live in places where they have been able to survive without confronting dangerous environments or competition from more highly derived life forms. Many of these "extremophiles" are anaerobic chemoautotrophs, and they have been found in a variety of habitats, such as deep-sea hydrothermal vents, benthic marine cold seeps, hot springs, saline lakes, sewage treatment ponds, subglacial lakes beneath the ice of Antarctica (where the water is liquid due to a combination of geothermal heating and pressure), and the guts of humans and other animals. Hydrothermal vents on the seafloor and hydrothermal pools (geothermal hot springs on land) have both been implicated in the origin of life on the planet, and today both harbor extensive mats of microbial life. But one of the most astonishing discoveries of the 1980s was that extremophile Archaea (and some fungi) are widespread in the deep rocks of Earth's crust. Since then, a community

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of hydrogen-eating Archaea has been found living in a geothermal hot spring in Idaho, 600 feet beneath Earth's surface, relying on neither sunshine nor organic carbon. Archaea are known to grow at temperatures up to 121°C in deep-sea hydrothermal vents. Archaea have been found at depths as great as 2.8 km, living in igneous rocks with temperatures as high as 75°C. Recently, a diverse microbial biota (Bacteria, Archaea, and even eukaryotes) has been found to live as deep as 2.5 km beneath the seafloor, in ancient buried sediments, and is remarkably abundant in coal bed layers. And in the early part of this century, thanks to new high-throughput sequencing technologies, it was discovered that there are massively more species of prokaryotes in the environment than had been thought. Even deep within sediments, at least 800 m below the seafloor, huge populations of prokaryotes have been discovered.

We are now realizing that the 10,000 or so described species of Bacteria and Archaea are barely the tip of the iceberg. Extremophiles include **halophiles** (which grow in the presence of high salt concentrations, in some cases as high as 35% salt); **thermophiles** and **psychrophiles** (which live at very high or very low temperatures); **acidophiles** and **alkaliphiles** (which are optimally adapted to acidic or alkaline pH environments); and **barophiles** (which grow best under pressure). Molecular phylogenetic studies now suggest that some of these extremophiles, particularly the thermophiles, might be very similar to the "universal ancestor" of all life on Earth.[3]

The vast majority of species that have been described are animals. The kingdom Animalia, or **Metazoa**, is usually defined as the ingestive, heterotrophic, sexual, multicellular eukaryotes that undergo embryonic tissue formation.[4] The process of embryonic tissue formation takes place through a major reorganization and differentiation process called **gastrulation**. However, metazoans possess other unique attributes as well, such as an acetylcholine/cholinesterase-based nervous system, special types of cell–cell junctions, and a unique family of connective tissue proteins called collagens. Metazoans have also been shown to possess a distinctive set of insertions and deletions in genes coding for proteins in the mitochondrial genome. Among the Metazoa are some species that possess a backbone (or vertebral column), but most do not. Those that possess a backbone constitute the subphylum Vertebrata of the phylum Chordata, and they account for only about 4% (about 58,000 species) of all described animals. Those that do not possess a backbone (the remainder of the phylum Chordata, plus 30 additional animal phyla) constitute the invertebrates. Thus, we see that the division of animals into invertebrates and vertebrates is based more on tradition and convenience, reflecting a dichotomy of interests among zoologists, than it is on the recognition of natural biological groupings. About 15,000 to 20,000 new species are named and described by biologists each year, most of them invertebrates (especially insects).

Not only are invertebrates diverse and numerous, they span over six orders of magnitude in size. Many species are microscopic (even though they may have thousands of cells in their bodies). Some of the smallest are cycliophorans (350 μm, or 0.35 mm), loriciferans (as small as 85 μm, or 0.085 mm), and the coral reef nematode *Greeffiella minutum*, which is only 80 μm (0.08 mm) long. However, species with bodies smaller than 1 mm occur in many other phyla. Invertebrates can also be quite large. Some jellyfish reach 25 m including the tentacles, the giant squid (*Architeuthis dux*) reaches 13 m including the tentacles, a sperm whale nematode parasite (*Placentonema gigantisima*) can exceed 8 m, and some earthworms can reach 3 m in length. There is a record of a nemertean reaching 60 m, but this lacks reliable verification. Giant clams (*Tridacna*) can exceed 400 kg in weight, and the terrestrial coconut crab (*Birgus latro*) can exceed 4 kg—perhaps the heaviest land invertebrate.

Where Did Invertebrates Come From?

Evolutionary analyses confirm that the ancestors of plants and animals (and fungi) were protists, and the phenomenon of multicellularity arose independently in these three groups, although in different ways. Genetic and developmental data confirm that the basic mechanisms of pattern formation and cell–cell communication during development were independently derived in animals and in plants. In animals, segmental identity is established by the spatially specific transcriptional activation of an overlapping series of master regulatory genes, the homeobox (Hox) genes. The master regulatory genes of plants are not members of the homeobox gene family, but members

[3]One of the most striking examples of a thermophile is *Pyrolobus fumarii*, a chemolithotrophic archaean that lives in oceanic hydrothermal vents at temperatures of 90°C–113°C. (Chemolithotrophs are organisms that use inorganic compounds as energy sources.) On the other hand, *Polaromonas vacuolata* grows optimally at 4°C. *Picrophilus oshimae* is an acidophile whose growth optimum is pH 0.7. (*P. oshimae* is also a thermophile, preferring temperatures of 60°C.) The alkaliphile *Natronobacterium gregoryi* lives in soda lakes where the pH can rise as high as 12. Halophilic microorganisms abound in hypersaline lakes such as the Dead Sea and Great Salt Lake and in solar salt evaporation ponds, and the green alga *Dunaliella salina* lives in the Dead Sea at salinities of 23% salt. Hypersaline lakes are often colored red by dense microbial communities (e.g., *Halobacterium*). *Halobacterium salinarum* lives in the salt pans of San Francisco Bay and colors them red. Barophiles have been found living at all depths in the sea, and one unnamed species from the Mariana Trench (the deepest part of the ocean) has been shown to require at least 500 atmospheres of pressure in order to grow.

[4]Heterotrophic organisms are those that derive their nutritional requirements from complex organic substances (i.e., by consuming other organisms or organic materials as food). In contrast, autotrophs are able to form nutritional organic substances from simple inorganic matter such as carbon dioxide (e.g., plants).

of the MADS-box family of transcription factor genes. There is no evidence that the animal homeobox and MADS-box transcription factor genes are homologous.

Although the fossil record is rich with the history of many early animal lineages, many others have left few or no fossils. Many ancient animals were very small, many were soft-bodied and did not fossilize well, and others lived where conditions were not suitable for the formation of fossils. However, highly fossilizable groups such as the echinoderms (starfish, urchins), molluscs (clams, snails), arthropods (crustaceans, insects), corals, bryozoans, brachiopods, and vertebrates have left a rich fossil record. In fact, for some groups (e.g., echinoderms, brachiopods, bryozoans, molluscs), the number of extinct species known from fossils exceeds the number of known living forms. Of course, this makes sense given the long history of animal life on Earth and that representatives of about 60% the extant animal phyla were present in the Cambrian Period. Life on land, however, did not appear until later, and terrestrial radiations probably began only about 470 million years ago. The following account briefly summarizes the early history of life and the rise of the invertebrates.

The Dawn of Life

It used to be thought that the Proterozoic Eon, 2.5 billion to 541 million years ago, was a time of only a few simple kinds of life; hence the name. However, recent discoveries have shown that life on Earth began early and had a very long history throughout the Proterozoic. As noted above, some of the oldest rocks known on Earth have markings suspected to represent anaerobic sulfur-reducing prokaryotes and perhaps even cyanobacterial stromatolites, which may be Earth's first photosynthetic organisms. Undisputed cyanobacterial fossils 3.5 billion years of age are known, and older ones have been suggested. The first actual traces of eukaryotic life (benthic algae) are 1.6 to 1.8 billion years old, whereas the first certain eukaryotic fossils (phytoplankton) are 1.2 billion years old. Together, these prokaryotes and protists appear to have formed diverse communities in shallow marine habitats throughout the Proterozoic. Living stromatolites (compact layered colonies of Cyanobacteria and mud) are still with us and can be found in certain high-evaporation/high-salinity coastal environments in places such as Shark Bay (Western Australia), Scammon's Lagoon (Baja California), salt ponds on islands in the Sea of Cortez, the Persian Gulf, the Paracas coast of Peru, the Bahamas, and Antarctica. Living stromatolites also occur in some isolated inland waters, such as the famous Cuatro Ciénegas Oasis, Coahuila, Mexico.

In the end era of the Proterozoic (the Neoproterozoic Era, 1 billion years ago to 541 Ma) the world was different from what it is today. Atmospheric oxygen levels were much lower. The deep ocean was especially oxygen poor. Three ice-covered Earth events are hypothesized to have occurred during the Neoproterozoic Era, based on the occurrence of multiple glaciations at sea level in low latitudes in the geological record. These "Snowball Earth" events, which might have lasted up to 10 million years each, are thought to have been interrupted by periods of rapid warming and global greenhouse conditions. The causes of these wide climatic swings during the Neoproterozoic are still unclear, although there is evidence that the world oceans lacked the $CaCO_3$-based carbon stabilization chemistry we have today. Indeed, major carbon precipitators such as foraminiferans and coccolithophores had probably not yet evolved in the world's oceans. It seems likely that buildup of atmospheric CO_2 generated by massive volcanic eruption periods drove the warming events. All these changes were taking place during the breakup of a supercontinent known as Rodinia (about 750 Ma)—the supercontinent that preceded Pangaea. It was against this backdrop that the Metazoa first arose, perhaps 875 to 650 million years ago. Around 800 million years ago, atmospheric oxygen seems to have stabilized at a relatively high level, setting the stage for the rapid evolution of eukaryotes. Oxygen, of course, was critical to the diversification of large and metabolically active, complex life.

The prevailing view is that Metazoa arose in the Neoproterozoic (latest Precambrian), began to diversify, and then radiated rapidly in the Cambrian—the "Cambrian Explosion"—when there was a rapid increase in animal diversity and abundance, as manifest in the fossil record, between around 541 and 520 million years ago. However, during the Neoproterozoic these early animal lineages must have survived some extreme climate swings on Earth, including profound changes in ocean and atmospheric chemistry and widespread global glacial events.

The Ediacaran Period and the Origin of Animals

One of the most perplexing unsolved mysteries in biology is the origin and early radiation of Metazoa (the animal kingdom). Fossil evidence suggests that by the end-Proterozoic Ediacaran Period a worldwide marine invertebrate fauna was already well established, and this coincides roughly with molecular estimates for the origin of animals. Although the animals that existed during this time left few records, the fauna of the Ediacaran (635–541 Ma) contains the first evidence of many, possibly modern phyla. Living phyla thought to be represented among the Ediacaran fauna include Porifera, Cnidaria, Mollusca, possibly Annelida, and others. Some authors have even suggested the presence of Onychophora, Arthropoda, and Echinodermata, although these are more controversial. The Ediacaran *Dickinsonia* has been said to represent a "placozoan-grade" or "Cnidarian-grade animal," *Kimberella* may be a mollusc, *Eoandromeda* a ctenophore, and

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Thectardis a sponge (although all of these classifications are debatable). Over 100 Ediacaran animal genera have been described from around the world. However, most Ediacaran animals cannot be unambiguously assigned to any living phylum, and these animals may represent phyla or other high-level taxa that went extinct at the Proterozoic–Cambrian transition.

Early reports of Ediacaran fossils are from sites in Newfoundland and Namibia, but the name is derived from the superb assemblages of these fossils discovered at Ediacara in the Flinders Ranges of South Australia. Most of the Ediacaran organisms were preserved as shallow-water impressions on sandstone beds, but some of the 25 or so worldwide sites probably represent deep-water and continental slope communities. The Ediacaran fauna was mostly soft bodied, and there have been no heavily shelled creatures reported from these deposits. Even the alleged molluscs and arthropod-like creatures from this fauna are thought to have had soft (unmineralized or lightly mineralized) skeletons. A few chitinous structures probably developed during this time, such as the sabellid-like tubes of worms and the radulae of early molluscs.[5] Siliceous spicules of hexactinellid sponges have been reported from Australian and Chinese Ediacaran deposits. In 2014, Ediacaran-age metazoan reefs were discovered in Namibia that were built by skeletonized creatures named *Cloudina*. Resembling cnidarians, these are the oldest known structural reef-building animals although their phylogenetic affinities are uncertain.

Many of these Ediacaran animals appear to have lacked complex internal organ structures, and none have yet shown clear evidence of having a mouth or anus. Many were small and possessed radial symmetry. However, at least by late in the Ediacaran Period, large animals with bilateral symmetry seem to have appeared, such as the segmented, sheetlike *Dickinsonia* (which reached 1 m in length; Figure 1.2), which led some workers to infer they might have had internal organs. Some workers have questioned whether or not Ediacaran life even included any animals, suggesting that it might be represented only by protists, algae, fungi, lichens, and microbial colonies and mats. However, some Ediacaran fossils seem to be unmistakably Porifera and Cnidaria, and others (e.g., *Kimberella*) show strong similarity to molluscs. *Kimberella* has been associated with scratch marks reminiscent of radula scrapings. Still others are thought to possess bilateral symmetry, an idea once controversial but now gaining traction. Among the bilaterian fossils are *Kimberella*, the "small shelly fossils" (e.g., the enigmatic *Cloudina*), and embryos of probable bilaterian origin from the Doushantuo Formation of south China, although these bilaterian records have their detractors. Other evidence of bilaterians in these deposits includes what appear to be predatory bore holes in the small shelly fossils, and a variety of horizontal and vertical burrows that were perhaps made by motile animals.

The beginning of the Ediacaran Period coincides with the end of the last "Snowball Earth" event of the Precambrian, when most of Earth's land, and perhaps much of its ocean, was frozen over. And at the end of the Ediacaran many living creatures seem to have gone extinct.[6] The Ediacaran Period was followed by the Cambrian Period (541–485 Ma) and the great "explosion" of skeletonized metazoan life associated with that time. Life quickly got very interesting and very complicated in the Cambrian! Why large, skeletonized animals appeared at that particular time, and in such great profusion, remains a mystery, but the fossil record clearly informs us that by the early Cambrian a good number of the major animal phyla we recognize today had come into being. Certainly, great changes were occurring at the end of the Precambrian and the start of the early Cambrian—the breakup of the supercontinents, rising sea levels, fluctuations in atmospheric composition (including oxygen and CO_2 levels), changes in ocean chemistry—and these likely played a role in the demise of the Ediacaran fauna and the rise of Cambrian life.

The Paleozoic Era (541–251.9 Ma)

The Phanerozoic Eon (the time of abundant life on Earth that encompasses the Paleozoic, Mesozoic and Cenozoic Eras) was ushered in with the almost simultaneous appearance in the early Cambrian of well-developed, large, calcareous body skeletons in numerous groups, such as archaeocyathans (coral-like organisms that may have been early sponges), molluscs, bryozoans, brachiopods, crustaceans, chaetognaths (represented by fossils long called protoconodonts), and trilobites. It used to be that the first appearance of these well-mineralized animal skeletons was used to define the beginning of the Cambrian. However, the dating of the Precambrian-Cambrian boundary has changed considerably in the past decades. In the 1970s, with the discovery of small shelly fossils *below* the oldest Cambrian trilobites—a fauna composed of spicules, sclerites,

[5]Chitin is a cellulose-like family of compounds that is widely distributed in nature, especially in invertebrates, fungi, and many protists, but it is apparently uncommon in deuterostome animals and higher plants, perhaps due to the absence of the chitin synthase enzyme.

[6]The largest mass extinctions recorded in the fossil record occurred at the ends of the Precambrian (the Ediacaran–Cambrian transition), Ordovician, Devonian, and Permian and in the Early Triassic, Late Triassic, and end-Cretaceous. Most of these extinction events were experienced by both marine and terrestrial organisms. The Triassic events and the end-Devonian event have recently been shown to be less severe extinction events than once thought. And a relatively little-studied mass extinction event in the Late Permian, about 260 million years ago, has recently begun to emerge as a much larger extinction event than previously thought, with perhaps 56% of plant species and 58% of marine invertebrate genera disappearing. Earth is today entering a sixth great mass extinction, driven entirely by humans.

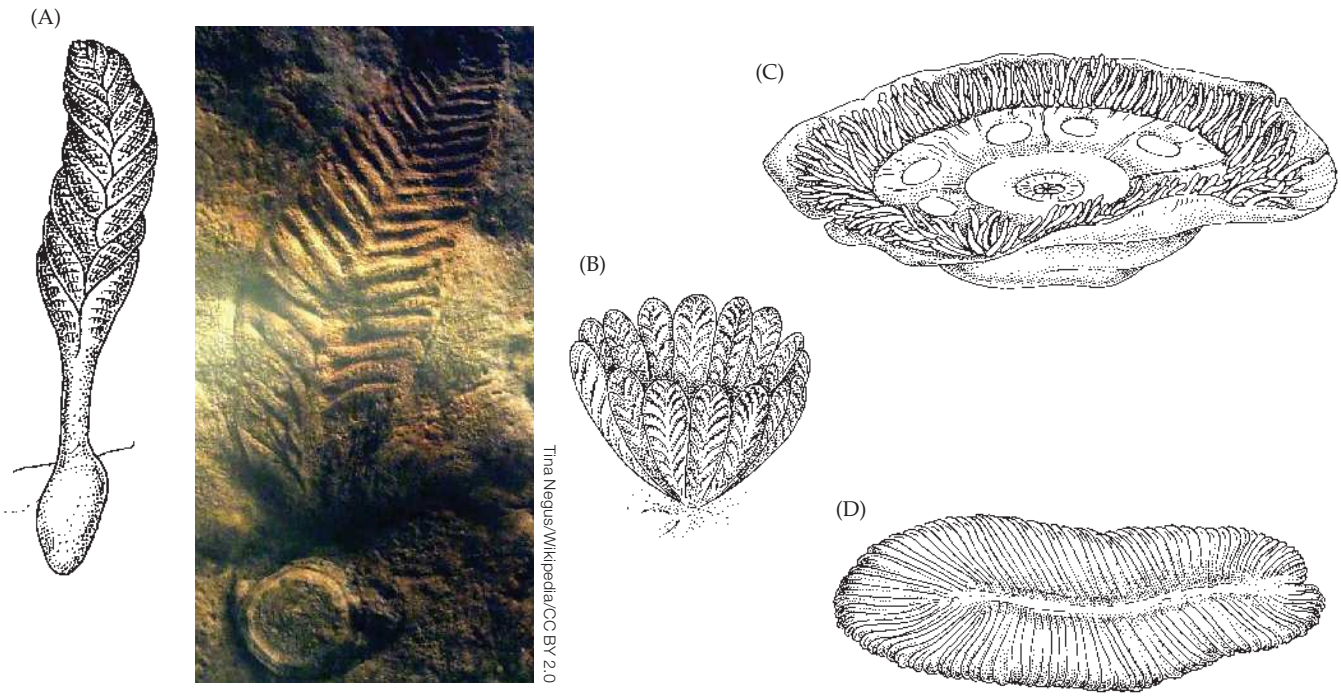

FIGURE 1.2 Some Ediacaran (Late Proterozoic) animals. (A) *Charnia* and *Charniodiscus*, two animals resembling modern sea pens (Anthozoa, Pennatulacea). (B) A bushlike fossil of uncertain affinity (suggestive of a cnidarian). (C) *Ediacara*, a cnidarian medusa. (D) The enigmatic *Dickinsonia*. (E) One of the many soft-bodied trilobite-like creatures known from the Ediacaran Period. (some of which also occurred in the Early Cambrian). (After R. J. F. Jenkins 1992. In J. H. Lipps and P. W. Signor [Eds.], *Origin and Early Evolution of the Metazoa*, pp. 131–178. Plenum, New York. https://link.springer.com/chapter/10.1007/978-1-4899-2427-8_5)

and ossicles of animals plausibly interpreted as sponges, molluscs (including extinct scleritome-bearing groups such as halkieriids), stem-group brachiopods, and so on—the base of the Cambrian was revised. Today, the Precambrian-Cambrian boundary is defined by the first occurrence of the trace fossil *Treptichnus pedum* (Figure 1.3), one of the first putative, penetrative animal burrows, suggesting a metazoan capable of causing a good deal of bioturbation that oxygenated and mixed the sediment at depths not previously attained. This sediment mixing is sometimes called the "agronomic revolution," and it provides one of the possible ecological explanations for the Cambrian "explosion" of animal life. The nature of the animal that left the *T. pedum* trace fossil has been a matter of speculation, but it must have been relatively large, based on the size of the burrows. Comparisons with the feeding traces of extant priapulans are consistent with *T. pedum*. The burrow traces of *T. pedum* have also been associated with the presence of some sort of hydrostatic skeleton, such as a coelomic or a large pseudocoelomic cavity that allowed the animals to burrow. In an event, the newly skeletonized animals of the Paleozoic radiated quickly and filled a multitude of ecological roles in shallow-water marine environments, and by the early Cambrian most living phyla possessing hard parts had appeared. The earliest land plants appeared about 470 million years ago.

Evidence suggests that in the Early Cambrian the world ocean increased its calcium content dramatically, which coincided with the proliferation of skeletonized animals. Climates were warm, and shallow epicontinental seas covered broad regions of Paleozoic continents. The explosion of bilaterally symmetrical animals, the Bilateria, also began around the Proterozoic–Cambrian transition. Seed ferns and other gymnosperms also arose during the Paleozoic, perhaps a bit more than 400 million years ago, whereas angiosperms may have arisen around 200 million years ago, as suggested by molecular data (although the oldest undisputed angiosperm fossils are from about 175 Ma).

Did all the metazoan lineages arise quickly, during the first 10 million years or so of the Cambrian? Or

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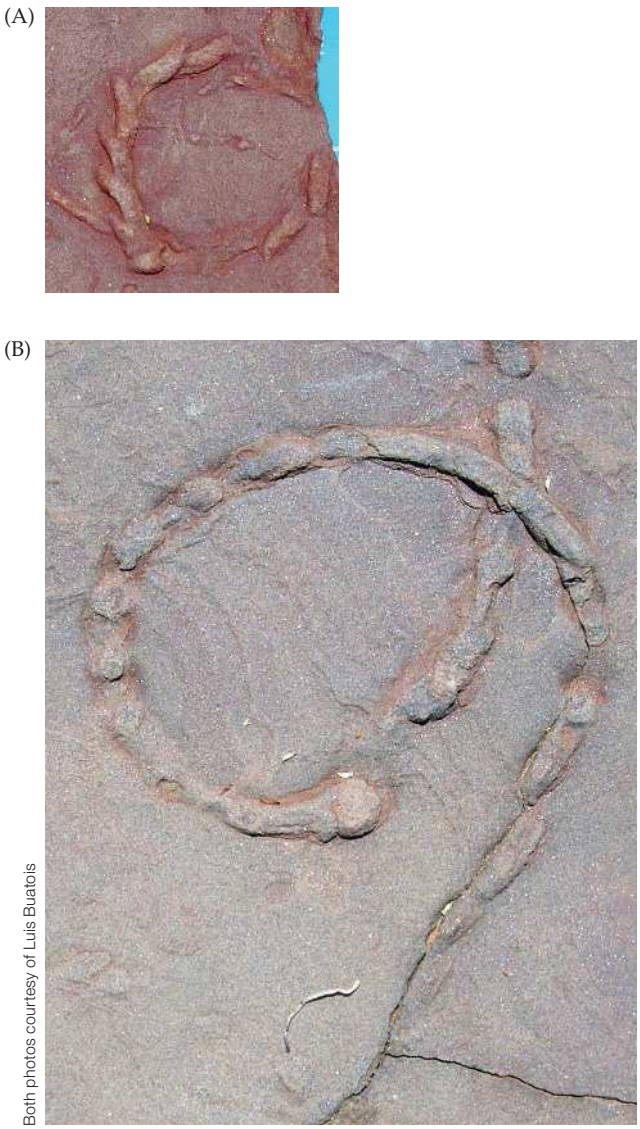

FIGURE 1.3 ***Treptichnus pedum*, trace fossils from the Vanrhynsdorp Group (Klipbak Formation) of South Africa.** (A) Specimen showing classic branching burrow pattern of this ichnotaxon. (B) Specimen showing looping pattern.

were many (or most) of them already getting established in the Ediacaran but we have yet to find evidence of this, perhaps because they lacked hard skeletons or were very small? This latter idea, sometimes called the "phylogenetic fuse" hypothesis, is supported by the discovery of undisputed and modern-appearing crustaceans in the earliest Cambrian, as well as many creatures from the Ediacaran that resemble modern phyla (or their embryos). Given that advanced phyla like arthropods were already well established in the earliest Cambrian, it seems likely that earlier-derived phyla of ecdysozoans must have been alive and thriving in the Ediacaran. Indeed, apparent phosphatized bilaterian animal embryos from the Ediacaran provide evidence of the cryptic roots of Metazoa and the likelihood that the evolutionary fuse of modern animal phyla was lit well before the Cambrian began.

Geological evidence tells us that Earth's earliest atmosphere lacked free oxygen, and the radiation of the animal kingdom could not have begun under those conditions. Free oxygen probably accumulated over many millions of years as a by-product of photosynthetic activity in the oceans, particularly by the cyanobacterial stromatolites and planktonic species. A long-standing hypothesis suggests that the beginning of an oxygenated atmosphere was around 2.4 billion years ago, and it was then that "modern life" began to evolve (at the beginning of the Proterozoic). However, evidence for free oxygen levels in the Proterozoic is still unclear, and there are some data that suggest an oxygenated atmosphere might have evolved even earlier than that. Proterozoic seas might have been oxic near the surface, but anoxic in deep waters and on the bottom. Some workers suggest that the absence of metazoan life in the early fossil record is due to the simple fact that the first animals were small, lacked skeletons, and did not fossilize well. The discovery of highly diverse communities of metazoan meiofauna in the Proterozoic strata of south China and in deposits from the middle and upper Cambrian (e.g., the Swedish Orsten fauna) lends support to the idea that many of the first animals were microscopic.[7] However, large animals also are not uncommon among the Ediacaran and early Cambrian faunas.

It has also been proposed that the advent of predatory lifestyles, early in the Cambrian, was the key that favored the first appearance of animal skeletons (as defensive structures), leading to the Cambrian Explosion. The rapid appearance and spread of diverse metazoan skeletons in the early Cambrian certainly heralded the beginning of the Phanerozoic Eon (i.e., all time after the Precambrian). The Ediacaran fauna seems to have included primarily passive suspension and detritus feeders; very few of these animals appear to have been active carnivores or herbivores. Early Cambrian animal communities, on the other hand, included most of the trophic roles found in modern marine communities, including giant predatory arthropods.

Much of what we know about earliest Cambrian life comes from the early Cambrian Chengjiang fossil deposits of the Yunnan Province in southern China and similarly aged (although less well preserved) deposits spread across China and the Siberian Platform. The Chengjiang deposits are the oldest Cambrian occurrences of well-preserved soft-bodied and hard-bodied animals, and although they are dominated

[7] Orsten-type preservation entails the phosphatization of cuticles with almost no deformation. It preserves the finest details of organisms, including setae, and such deposits have yielded three-dimensional fossils at the scale of 0.1–2.0 mm. First discovered in Sweden, Orsten-type deposits are now known from several continents, from the early Cambrian (520 Ma) to the middle Cretaceous (100 Ma). Most of the earliest "Orsten fossils" are undisputed arthropods.

by arthropods, they also include a rich assemblage of exquisitely preserved lobopodians, medusae (Cnidaria), and brachiopods, many of which appear closely related to Ediacaran species.

In the middle Cambrian fossil record (e.g., the 508 Ma Burgess Shale fauna of western Canada, 518 Ma Qingjiang biota of China, and similar deposits elsewhere; Figure 1.4), cnidarians, annelids, and tardigrades make their first positive appearance and the first complete echinoderm skeletons appear. Twelve million years younger than the Chengjiang fauna, the Burgess Shale material is also dominated by arthropods (and their allies), including the infamous *Opabinia* and *Anomalocaris*. Most of the Burgess Shale fauna can also be assigned to living phyla. There are numerous other (less famous) Cambrian fossil sites, such as the Sirius Passet fauna in Greenland, the Emu Bay Shale in Australia, the Sinsk biota in Russia, and the Kaili and Guanshan biotas in China. In the upper Cambrian fossil record (e.g., the Orsten deposits of southern Sweden and similar strata), the first pentastomid Crustacea and the first agnathan fishes make their appearances. By the end of the Cambrian, nearly all of the major, modern animal phyla had appeared. The Burgess Shale–like assemblage in Lower Ordovician rocks of Morocco tells us that many of the Cambrian lineages survived for tens of millions of years (Figure 1.4).

The driving force for this Cambrian explosion has perplexed scientists since Darwin's day. In fact, it has been referred to as "Darwin's dilemma," because he could not reconcile such rapid origination and diversification of major animal groups with his view of gradual evolution driven only by natural selection. Some analyses have suggested that rates of phenotypic and genomic evolution might have been many times faster during the Cambrian than in the rest of the Paleozoic. One popular notion is that atmospheric oxygen reached a critical level around 580 million years ago, in the Ediacaran, and it allowed for larger animals and skeletonized animals to begin to evolve. This might have led to the appearance of large carnivores, which rely on oxygen for high-energy pursuits. Once the carnivores proliferated, a predator-prey arms race ensued,

Courtesy of Carel Brest von Kempen. Fauna of the Burgess Shale. Acrylic on illustration board

FIGURE 1.4 Fauna of the Burgess Shale, Carel Brest von Kempen. Acrylic on illustration board. Depicted are stromatolites, *Leptomitus*, *Vauxia*, *Billingsella*, *Hallucigenia*, *Aysheaia*, *Anomalocaris*, *Opabinia*, *Lejopyge*, *Olenoides*, *Asaphiscus*, *Elrathia*, *Modocia*, *Naraoia*, *Habellia*, *Burgessia*, *Plenocaris*, *Sarotrocercus*, *Odaraia*, *Pseudoarctolepis*, *Canadaspis*, *Marrella*, *Branchiocaris*, *Ottoia*, *Hyolithes*, *Canadia*, *Gogia*, *Pikaia*, *Wiwaxia*, *Dinomischus*, and *Amiskwia*.

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driving the rapid evolution of never-ending new body forms. However, some other evidence suggests that high oxygen levels existed well before that date.

In addition to the agronomic revolution mentioned previously, another explanation for the explosive radiation of Metazoa in the Cambrian is a rapid increase in nutrient supplies to the world's oceans, especially phosphorus (P) and potassium (K). This is hypothesized to have occurred as the Earth cooled enough for subducting mantle to hydrate with seawater about 600 million years ago, thus moving water from the oceans into the lower mantle and lowering sea level, which in turn exposed great swaths of new landmasses that underwent erosion of P and K, which in turn were transported to the sea as fertilizers. In addition, massive uplift of mountains and plume-driven doming of landmasses also might have added new nutrient-erosion sources around the Precambrian–Cambrian transition.

The early Paleozoic also saw the first xiphosurans, eurypterids, and teleost fishes (in the Ordovician). The first land animals (arachnids, myriapods) appeared in the upper Silurian. By the Devonian Period, life on land had begun to proliferate. Forest ecosystems became established and began reducing atmospheric CO_2 levels (eventually terminating an earlier Paleozoic greenhouse environment). The first insects also appeared in the early Paleozoic (see Chapter 22). Insects probably developed flight in the Lower Devonian (~406 Ma), and they began their long history of coevolution with plants shortly thereafter (at least by the mid-Carboniferous, when tree fern galls first appeared in the fossil record).[8] During the Carboniferous Period, global climates were generally warm and humid, and extensive coal-producing swamps existed.

The late Paleozoic witnessed the formation of Earth's most recent supercontinent Pangaea, in the Permian Period (about 270 Ma). The end of the Paleozoic Era/Permian Period (251.9 Ma) was marked by the largest mass extinction known, in which an estimated 90% of Earth's marine species (and 70% of the terrestrial vertebrate genera) were lost over a brief span of a few million years. The Paleozoic reef corals (Rugosa and Tabulata) went extinct, as did the once-dominant trilobites, never to be seen again. The driving force of the massive Permian extinction is a hotly debated subject, and hypotheses range from rapid global warming to rapid global cooling! Either might have been driven by a huge asteroid impact, perhaps coupled with massive Earth volcanism, and perhaps also degassing of methane from stagnant ocean basins. Some evidence suggests that toxic waters decimated shallow bottom marine communities at that time. All of these might have created a large and rapid global warming (or cooling) event, depending on how things played out. The trillions of tons of carbon released into the atmosphere and oceans from enormous volcanism events likely also led to ocean acidification and a drop in dissolved oxygen in the oceans, further possible causes of oceanic extinction events. A volcanism event at this time was likely the one that created the massive flood basalts known as the Siberian Traps in Asia. Volcanism at this time could have led to atmospheric "pollution" in the form of dust and sulfur particles that cooled Earth's surface and/or massive gas emissions that led to a prolonged greenhouse warming and ocean acidification.

[8]Coevolution is the reciprocal adaptation that occurs over time between closely interacting species. One classic example is plants and their pollinators, which have evolved in lockstep since the late Paleozoic to form remarkably finely tuned anatomies, physiologies, and behaviors, among willing (or unwilling) partners.

The Mesozoic Era (251.9–66 Ma)

The Mesozoic Era is divided into three broad periods: Triassic, Jurassic, and Cretaceous. The Triassic began with the continents joined together as Pangaea. The land was high, and few shallow seas existed. Global climates were warm, and deserts were extensive. Although the Triassic is perhaps best known for the emergence of the dinosaurs, vertebrate diversity in general exploded during this period, as the first land mammals made their appearance. In Triassic seas, modern-looking scleractinian corals appeared, and the diversity of predatory invertebrates and fishes increased dramatically, although the paleogeological data suggest that deeper marine waters might have been too low in oxygen to harbor much multicellular life. The end of the Triassic witnessed a global extinction event that resulted in the disappearance of around half of all the living species. This was perhaps driven by the combination of asteroid impact and widespread volcanism that created the Central Atlantic Magmatic Province of northeastern South America 200 million years ago, although there is considerable disagreement about the extent and cause of this extinction event. Recent studies suggest elevated atmospheric CO_2 was the culprit behind the end-Triassic extinction event, possibly caused by high rates of magmatic CO_2 degassing. Certainly, it's possible that all these events took place.

The Jurassic saw a continuation of warm, stable climates, perhaps with little latitudinal or seasonal variation and probably little mixing between shallow and deep oceanic waters. Pangaea split into two large landmasses, a northern Laurasia and southern Gondwana, separated by a circumglobal tropical seaway known as the **Tethys Sea**. Many tropical marine families and genera today are thought to be direct descendants of lineages inhabiting that pantropical Tethys Sea. On land, modern genera of many gymnosperms and advanced angiosperms appeared, and the first birds begin to evolve (e.g., *Archaeopteryx*, ~150 Ma). Leaf-mining insects (lepidopterans) appeared by the Upper Jurassic (150 Ma), and other leaf-mining orders appeared through the Cretaceous, coincident with the radiation of the vascular plants.

In the Cretaceous, large-scale fragmentation of Gondwana and Laurasia took place, resulting in the formation of the Atlantic and Southern Oceans. During this period, landmasses subsided and sea levels were high; the oceans sent their waters far inland, and great epicontinental seas and coastal swamps developed. As land masses fragmented and new oceans formed, global climates began to cool and oceanic mixing began to move oxygenated waters to greater depths in the sea.

The end of the Cretaceous, 66 million years ago, was marked by the Cretaceous-Paleocene mass extinction, in which an estimated 75% of Earth's species were lost, including the (nonavian) dinosaurs and all of the sea's rich Mesozoic ammonite diversity. There is strong evidence that this extinction event was driven by a combination of two factors: massive Earth volcanism associated with the great flood basalts of western India known as the Deccan Traps, combined with a major meteor impact (documented by the Chicxulub Crater in the Yucatán region of modern Mexico). The Deccan Traps flood basalts, a result of two different deep mantle hotspots joining forces, comprise an almost unimaginable 1.3 million cubic kilometers of erupted lava, 3,000 m thick in some places. The main eruptions were initiated about 250,000 years before the Cretaceous-Paleocene boundary, and overall the lava might have flowed for over 750,000 years. However, an estimated 90% of the eruptive flow took place rapidly, coincident with the Cretaceous-Paleocene boundary. The sulfur dioxide gas injected into the atmosphere from this massive volcanic event would have converted to sulfate aerosols that caused climate cooling, and when these aerosols washed out (as acid rain), they would have acidified the oceans. The scale of biological turnover between the Cretaceous and Paleocene is nearly unprecedented in Earth history. All the nonavian dinosaurs, marine reptiles, ammonites, and reef-forming rudistid clams went extinct. Planktonic foraminiferans and land plants were devastated. There is recent evidence suggesting that the full strength of the end-Cretaceous mass extinctions might not have kicked in until about 300,000 years after the Chicxulub impact. If comet impacts are beginning to sound like a recurring theme in the history of life on Earth, it's because so many large impact craters have been found (at least 70 that are larger than 6 km in diameter), and many of these coincide with major transitions in the fossil record.

The Cenozoic Era (66 Ma–present)

The Cenozoic Era dawned with a continuing worldwide cooling trend. As South America decoupled from Antarctica, the Drake Passage opened to initiate the circum-Antarctic current, which eventually drove the formation of the Antarctic ice cap, which in turn led to our modern cold ocean bottom conditions (in the Miocene). India moved north from Antarctica and collided with southern Asia (in the early Oligocene). Africa collided with western Asia (late Oligocene/early Miocene), separating the Mediterranean Sea from the Indian Ocean and breaking up the circumtropical Tethys Sea. Around 56 million years ago, the Earth warmed rapidly as greenhouse gasses spiked in the atmosphere and global oceans warmed all the way down to the deep sea. The cause of this Paleocene–Eocene Thermal Maximum is uncertain, but massive volcanic eruptions that could have cooked CO_2 out of organic seafloor sediments have been suggested, as have wildfires burning through Paleocene peat deposits, and another meteor impact (that could have released large deposits of methane hydrate from the seafloor). Relatively recently (in the Pliocene), the Arctic ice cap formed, and the Isthmus of Panama rose, separating the Caribbean Sea from the Pacific and breaking up the last remnant of the ancient Tethys Seaway, probably about 3 million years ago. Modern coral reefs (scleractinian-based reefs) appeared early in the Cenozoic, reestablishing the niche once held by the rugose and tabulate corals of the Paleozoic.

This textbook focuses primarily on invertebrate life at the very end of the Cenozoic, in the Quaternary Period (Pleistocene + Holocene). However, evaluation of the present-day success of animal groups also involves consideration of the deeper history of modern lineages, the diversity of life over time (numbers of species and higher taxa), and the abundance of life in various environments. The predominance of certain kinds of invertebrates today is unquestionable. For example, of the estimated 1,398,696 named and described species of living animals (1,340,696 of which are invertebrates), 82% are arthropods (and 82% of arthropods are insects). It would be hard to argue that insects are not the most successful group of animals on Earth today. And the fossil record tells us that arthropods have always been key players in the biosphere, even before the appearance of the insects. Table 1.1 conveys a general idea of the levels of diversity among the animal phyla today. Note that 82% of all known animals belong to just one phylum, Arthropoda; 87% belong to two phyla (Arthropoda + Mollusca); 91% belong to three phyla (Arthropoda + Mollusca + Chordata). Also, 25 phyla each contain fewer than 1% of the known animal species, including some that may seem quite diverse to the casual seashore visitor, such as sponges, cnidarians, bryozoans, and echinoderms.

Where Do Invertebrates Live?

Marine Habitats

The global ocean is Earth's largest biome. In fact, it is fair to say Earth is a marine planet—salt water covers 71% of its surface. And the vast three-dimensional

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world of the seas contains 99% of Earth's inhabited space. Life almost certainly evolved in the sea. The major events, described in the "Where Did Invertebrates Come From?" section, that led to the diversification of invertebrates occurred in late Proterozoic and early Cambrian shallow seas. Many aspects of the marine world minimize physical and chemical stresses on organisms. The challenge of evolving gas exchange and osmotic regulatory structures that can function in freshwater and terrestrial environments are formidable, and relatively few lineages were able to do so and fully escape their marine origin. Thus, it is not surprising to find that the marine environment continues to harbor the greatest diversity of higher taxa and major body plans—13 of the 31 living animal phyla are strictly marine (e.g., Placozoa, Ctenophora, Chaetognatha, Dicyemida, Cycliophora, Gnathostomulida, Phoronida, Brachiopoda, Kinorhyncha, Priapula, Loricifera, Echinodermata, Hemichordata), and many others have barely penetrated the terrestrial or freshwater realm. Productivity in the world's oceans is very high (representing about half of global primary production), and this also contributes to the high diversity of animal life in the sea. The total primary productivity of the seas is about 48.7×10^9 metric tons of carbon per year. Perhaps the most significant factor, however, is the special nature of seawater itself.

Water is a very efficient thermal buffer. Because of its high heat capacity, it is slow to heat up or cool down. Large bodies of water, such as oceans, absorb and lose great amounts of heat with little change in actual water temperature. In fact, the oceans store over 90% of the excess heat accumulating in the world's atmospheric climate system today. Thus, oceanic temperatures are very stable in comparison with those of freshwater and terrestrial environments. Short-term temperature extremes occur only in intertidal and estuarine habitats, and invertebrates living in such areas must possess behavioral and physiological adaptations that allow them to survive these temperature changes, which are often combined with aerial exposure during low tide periods.

The saltiness, or salinity, of seawater averages about 3.5% (often expressed as parts per thousand, 35‰). This property, too, is quite stable, especially in areas away from shore and the influence of rivers. The salinity of seawater gives it a high density, which enhances buoyancy, thereby minimizing energy expenditures for flotation. Furthermore, the various ions that contribute to the total salinity occur in fairly constant proportions. These qualities result in a total ionic concentration in seawater that is similar to that in the body fluids of most animals, minimizing the problems of osmotic and ionic regulation (see Chapter 3). The pH of seawater is also quite stable throughout most of the ocean. Naturally occurring carbonate compounds participate in a series of chemical reactions that buffer seawater at about pH 7.5–8.5. However, today's anthropogenic-driven increase in atmospheric CO_2 threatens to alter the carbonate buffering capacity of the world's seas. A large fraction (over 25%) of the CO_2 added to the atmosphere by burning of fossil fuels enters the ocean. Seawater reacts with CO_2 to form carbonic acid, decreasing the pH of ocean surface waters. The lowering of sea surface pH disrupts formation of calcium carbonate skeletons in both animals and protists.

In shallow and nearshore waters CO_2, various nutrients, and sunlight are generally available in quantities sufficient to allow high levels of photosynthesis, either seasonally or continuously (depending on latitude and other factors). Dissolved oxygen levels rarely drop below those required for normal respiration, except in stagnant waters, such as might occur in certain estuarine or ocean basin habitats, or where anthropogenic activities have created eutrophic conditions that can result in oxygen minimum zones (OMZs), hypoxic regions, or even anoxic seafloor conditions. Hypoxia occurs when dissolved oxygen falls below 2 ml of O_2/liter. The size and number of OMZs, defined by O_2 concentrations below 20 μM and sometimes called "dead zones," in the world oceans have been growing rapidly in recent decades as a result of humans releasing huge quantities of organic waste and fertilizers into the sea. Deep-sea ecosystems contain the largest hypoxic and anoxic regions of the biosphere. Permanently anoxic conditions in the oceans are present in certain seafloor locations and, among other areas, in the interior of the Black Sea[9] and in the deep (>3,000 m) hypersaline anoxic basins of the Mediterranean Sea, where it has long been thought that no metazoans could live. However, recently several species of Loricifera were discovered living in the anoxic Mediterranean basins (perhaps the only animals able to live permanently in anoxic conditions).

Because the marine realm is home to most of the animals discussed in this book, some terms that describe the subdivisions of that environment and the categories of animals that inhabit them will be useful. Figure 1.5 illustrates a generalized cross section through an ocean. The shoreline marks the littoral region, where sea, air, and land meet and interact (Figure 1.6A). Obviously, this region is affected by the rise and fall of the tides, and we can subdivide it into zones or shore elevations relative to the tides. The **supralittoral zone**, or splash zone, is rarely covered by water, even at high tide, but it is subjected to storm surges and spray from waves. The **eulittoral zone**, or true intertidal zone, lies between the levels of the highest and lowest tides. It can be subdivided by its flora and fauna, and by mean monthly hours of aerial exposure, into high, mid, and low intertidal zones. The **sublittoral zone**, or subtidal

[9]Despite its large surface area (423,500 km2), the Black Sea has only a thin surface layer that supports eukaryotic life. The water mass below about 175 m is devoid of dissolved oxygen, making this the largest anoxic body of water in the world.

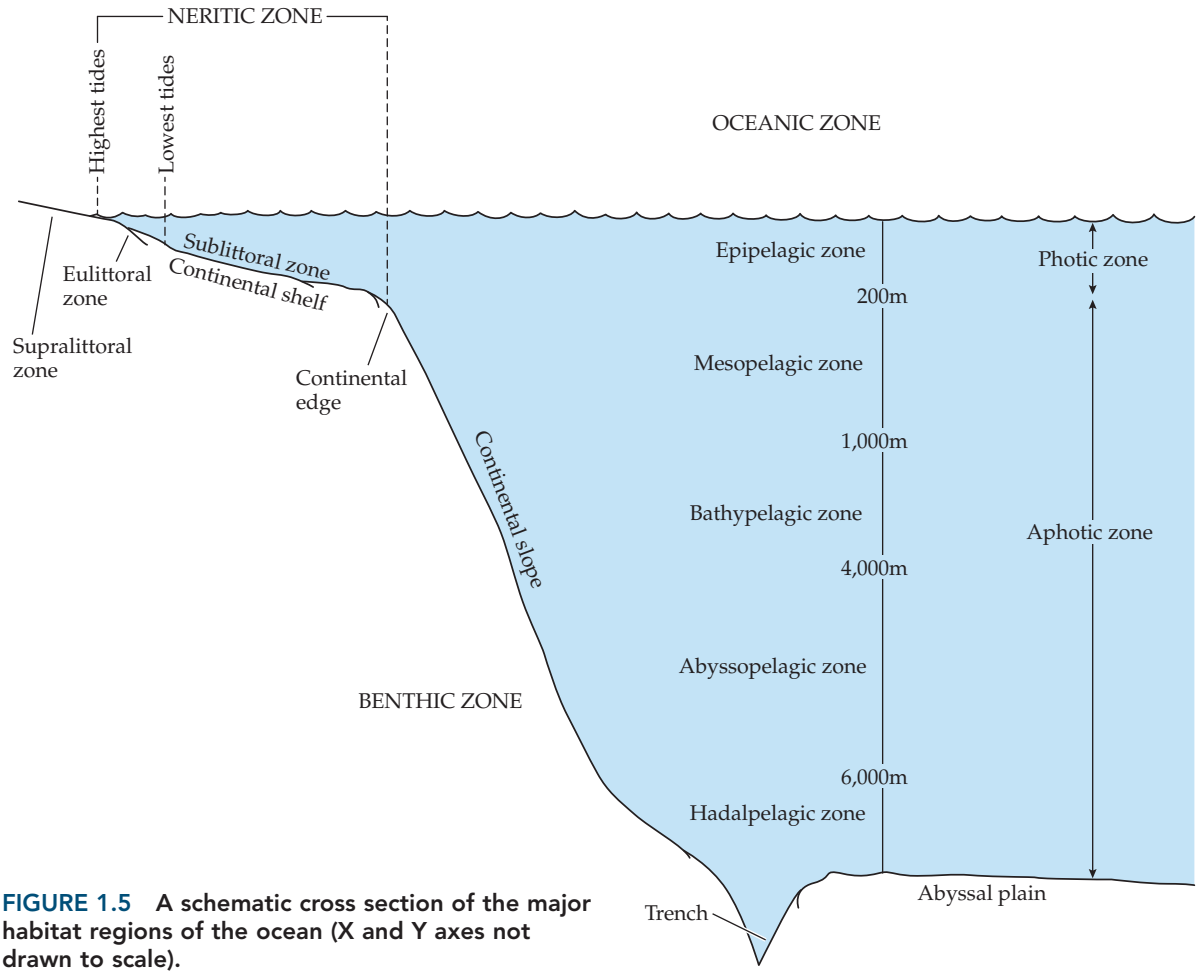

FIGURE 1.5 **A schematic cross section of the major habitat regions of the ocean (X and Y axes not drawn to scale).**

zone, is never uncovered, even at very low tides, but it is influenced by tidal action (e.g., by changes in turbulence, turbidity, and light penetration).

Organisms that inhabit the world's littoral regions are subjected to dynamic and often demanding conditions, and yet these areas commonly are home to exceptionally high numbers of species. Most animals and plants are more or less restricted to particular elevations along the shore, a condition resulting in the phenomenon of zonation. Such zones are visible as distinct bands or communities of organisms along the shoreline. The upper elevational limit of an intertidal organism is commonly established by its ability to tolerate conditions of exposure to air (e.g., desiccation, temperature fluctuations), whereas its lower elevational limit is often determined by biological factors (competition with or predation by other species). There are, of course, many exceptions to these generalizations.

Extending seaward from the shoreline is the **continental shelf**, a feature of most large landmasses. The continental shelf may be only a few kilometers wide, or it may extend up to 1,000 km from shore (50 to 100 km is average for most areas). It usually reaches a depth of 150–200 m. These nearshore shelf areas are among the most productive environments of the ocean, being rich in nutrients and shallow enough to permit photosynthesis from surface to seafloor.

The outer limit of the continental shelf—called the **continental edge**—is indicated by a relatively sudden increase in the steepness of the bottom contour. The "steep" parts of the ocean floor, the **continental slopes**, actually have slopes of only 4%–6% (although the slope is much steeper around volcanic islands). The continental slope continues from the continental edge to the deep ocean floor, which forms the expansive, relatively flat **abyssal plain**. The abyssal plain is an average of about 4 km below the sea's surface, but it is interrupted by a variety of ridges, seamounts, mountain ranges, trenches, and other formations. The bottom of some deep-sea trenches exceed 10 km in depth.

Organisms that inhabit the water column are known as **pelagic** organisms, whereas those living on the sea bottom anywhere along the entire contour shown in Figure 1.5 are referred to as **benthic** organisms. Organisms living in the water *near* the seafloor are **demersal**. Both the variety and the abundance of life tend to decrease with increasing depth, from the rich littoral and continental shelf environments to the deep abyssal plain. However, an overgeneralization of this relationship can be misleading. For example, although pelagic biomass

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FIGURE 1.6 A few of Earth's major ecosystems. (A) Exposed rocks and algae in the intertidal zone, northern California. (B) A tidal flat in a salt marsh, New York. (C) A mangrove forest at low tide, in Mexico. (D) A freshwater stream in a tropical wet forest ("rain forest"), Costa Rica. (E) Flowering trees in a tropical dry forest, Costa Rica. (F) The Sonoran Desert in Arizona. Fully a third of the land on our planet is desert or semidesert, and this ecosystem is predicted to grow with global warming.

declines exponentially with depth, both diversity and biomass increase again near the bottom, in a thick layer of resuspended sediments called the **benthic boundary layer**. Also, shelf and slope habitats in temperate regions are often characterized by low animal density but high species diversity. In many areas, benthic diversity increases abruptly below the continental edge (100–300 m depth), peaks at 1,000 to 2,000 m depth, and

then decreases gradually. Species diversity in the benthic abyssal region itself may be surprisingly high. The first impression of early marine scientists—that the deep seabed was an environment able to sustain only a few species in impoverished simple communities—was long ago shown to be incorrect, and it is now known that deep-sea biodiversity in some regions is quite high, in some areas even rivaling tropical rain forests. Much of the discovery of high deep-sea biodiversity can be traced back to the pioneering work of Howard Sanders (1921–2001), of Woods Hole Oceanographic Institution. Additionally, the deep ocean covers more than half the planet!

Benthic animals may live on the surface of the substratum (**epifauna**, or **epibenthic** forms, such as most sea anemones, sponges, many snails, and barnacles) or burrow within soft substrata (**infauna**). Infaunal forms include many relatively large invertebrates, such as clams and various crustaceans and worms, as well as some specialized, very tiny forms that inhabit the spaces between sand grains, termed **interstitial** organisms (the smallest of which are **meiofauna**, usually defined as animals smaller than 0.5 mm). Five phyla of metazoans are exclusively meiofaunal (the first four being found only in the sea): Gastrotricha, Gnathostomulida, Kinorhyncha, Loricifera, Micrognathozoa. Benthic animals may also be categorized by their locomotor capabilities. Animals that are generally quite motile and active are described as being **errant** (e.g., crabs, many worms), whereas those that are firmly attached to the substratum are called **sessile** (e.g., sponges, corals, barnacles). Others are unattached or weakly attached but generally do not move around much (e.g., crinoids, solitary anemones, most clams); these animals are said to be **sedentary**.

The region of water extending from the surface to near the bottom of the sea is called the **pelagic zone**. The pelagic region over the continental shelf is called the **neritic zone**, and that over the continental slope and beyond is called the **oceanic zone**. The pelagic region can also be subdivided into increments on the basis of water depth (Figure 1.5) or the depth to which light penetrates. The latter factor is, of course, of paramount biological importance. Only within the **photic zone** does enough sunlight penetrate that photosynthesis can occur, and (except in a few special circumstances) all life in the deeper, **aphotic zone** depends ultimately upon organic input from the overlying sunlit layers of the sea. Notable exceptions are the restricted deep-sea hydrothermal vent and benthic cold seep communities in which sulfur-fixing microorganisms serve as the basis of the food chain.[10] The photic zone can be up to 200 m deep in the clear waters of the open ocean, decreasing to about 40 m over continental shelves and to as little as 20 m in some coastal waters. Phytoplankton in the photic zone of the world's oceans account for about half the production of organic matter on Earth. Note that some oceanographers restrict the term "aphotic zone" to mean depths below 1,000 m, where absolutely no sunlight penetrates; the region between this depth and the photic zone is then called the **disphotic, twilight, or mesopelagic zone**. Nearly 64% of the surface of planet Earth—over 200 million km^2—lies in the sea below the photic zone (below 200 m depth), and in this region it is estimated that 16 gigatons of carbon fixed by phytoplankton sink to the ocean interior ever year as the only food source for the majority of organisms in the deep sea (1 gigaton is 1 billion tons).

Organisms that inhabit the pelagic zone are often described in terms of their relative powers of locomotion. Pelagic animals that are strong swimmers, such as fishes and squids, constitute the **nekton**. Those pelagic forms that simply float and drift, or generally are at the mercy of water movements, are collectively called **plankton**. Many planktonic animals (e.g., small crustaceans) actually swim very well, but they are so small that they are swept along by prevailing currents in spite of their swimming movements, even though those movements may serve to assist them in feeding or escaping predators. Both photosynthetic organisms (**phytoplankton**) and animals (**zooplankton**) are included among the plankton, the latter being represented by invertebrates such as jellyfish, comb jellies, arrow worms, many small crustaceans, and the pelagic larvae of many benthic adults. Planktonic animals that spend their entire lives in the pelagic realm are called **holoplanktonic** animals; those whose adult stage is benthic are called **meroplanktonic** animals.

The oceans hold some unique habitats. Perhaps the most well known are coral reefs, which comprise one of the world's most diverse ecosystems. In 1997, Marjorie Reaka-Kudla estimated there were about 93,000 described animal species living in the world ocean's coral reefs but that this was only 10% of the actual diversity (due to all of the undescribed species). Since then, some workers have suggested the number of coral reef animals might be three times, or more, than Reaka-Kudla estimated.

Another well-known ocean ecosystem comprises the hydrothermal vent communities. These are abundant in the world's oceans and tend to occur in areas where tectonic plates are moving apart and near plate hotspots (the land equivalents are geysers, fumaroles, and hot springs). Oceanic hydrothermal vents have in common an abundance of reduced chemicals, such as sulfides and methane. Chemosynthetic bacteria and archaeans form the base of the food chain in these ecosystems. One of the signature animals of hydrothermal vents is the tubeworm annelid *Riftia pachyptila*, which has no mouth, gut, or anus and cannot feed by normal means (see Chapter

[10] In addition to deep-sea hydrothermal vents, nonphotosynthetic chemoautotroph-based communities have recently been discovered in a cave, Movile Cave in Romania. The base of the food chain in this unique cave ecosystem is autotrophic microorganisms (bacteria and fungi) thriving in thin mats in and near-geothermal waters that contain high levels of hydrogen sulfide. This community sustains dozens of microbial and invertebrate species. It is thought that the hydrogen sulfide originates from a deep magmatic source, similar to that seen in deep-sea vents.

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14). Instead, *Riftia* depends on intracellular chemoautotrophic symbionts—which fill a large internal organ called the trophosome—for nutrition. The symbionts are Proteobacteria, which are functionally analogous to plant chloroplasts in that they generate organic carbon as a food source for their worm hosts.

Another unique marine habitat consists of large vertebrate carcasses that sink to the bottom in deep waters, especially cetaceans (whales, dolphins, and porpoises). Unlike in shallower waters, where a large carcass will be consumed by scavengers over a relatively short period of time, these "whale falls" can last for several years and allow for the establishment of an entire food web, characterized by a specific assemblage of species, especially crustaceans, annelids, bivalve molluscs, and fishes. Some of the more famous members of the whale fall community are species of *Osedax*, the so-called zombie worms, which consume the bones of dead cetaceans in these communities (see Chapter 15).

One of the most unusual marine environments inhabited by invertebrates are the pockets of concentrated brines that are encased in the ice matrix of Earth's polar regions (brines are generally considered to be 5% or more dissolved salts; ocean water is 3.4%–3.5% salt). At very low temperatures (to –20°C) and light levels, a food web in miniature exists, including photosynthetic bacteria and protists (especially diatoms), heterotrophic protists, flatworms, small crustaceans, etc. These are highly adapted, normally planktonic species that get trapped, and survive, when winter sea ice forms.

Estuaries and Coastal Wetlands

Estuaries usually occur along low-lying coasts and are created by the interaction of fresh and marine waters, typically where rivers meet the sea. Here one finds an unstable blending of freshwater and saltwater conditions, moving water, tidal influences, and drastic seasonal fluctuations. Estuaries usually receive high concentrations of nutrients from terrestrial runoff in their freshwater sources and are typically highly productive environments. Temperature and salinity vary greatly with tidal activity and with season. Depending on tides and turbulence, the waters of estuaries may be relatively well mixed and more or less homogeneously brackish, or they may be distinctly stratified, with fresh water floating on the denser salt water below.

The amount of dissolved oxygen in an estuary may also change markedly throughout a 24-hour cycle as a function of temperature and the metabolism of photosynthetic organisms. In many cases, hypoxic (very low oxygen) conditions may occur on a daily basis, especially in the early morning hours. Animals inhabiting these areas must be capable of migrating to regions of higher oxygen levels, be able to store oxygen bound to certain body fluid pigments, or be able to switch temporarily to metabolic processes that do not require oxygen-based respiration. Furthermore, vast amounts of silt borne by freshwater runoff are carried into the waters of estuaries; most of this silt settles out and creates extensive tidal flats or deltaic regions (Figure 1.6B). In addition to the natural stresses common to estuarine existence, the inhabitants of estuaries are also subject to stresses resulting from human activity—pollution, thermal additions from power plants, dredging and filling operations, excessive siltation resulting from coastal and upland deforestation and development, and storm drain discharges are some examples.

Most coastal wetlands and estuaries, such as salt marshes and mangrove forests, are characterized by stands of halophytes (flowering plants that flourish in saline conditions; Figure 1.6B,C). Salt marshes and mangrove swamps are alternately flooded and uncovered by tidal action within the estuary and are thus subjected to the fluctuating conditions just described. The dense halophyte stands and the mixing of waters of different salinities create an efficient nutrient trap. Instead of being swept out to sea, most dissolved nutrients entering an estuary (or generated within it) are utilized there, yielding some of the most productive regions in the world. This great productivity does eventually enter the sea in two principal ways: as plant detritus (mainly from halophyte debris), and via the nektonic animals that move into and out of the estuary. The contribution of estuaries to general coastal productivity can hardly be exaggerated. The organic matter produced by plants of the Florida Everglades, for example, forms the base of a major detritus food web that culminates in the rich fisheries of Florida Bay. Furthermore, 60%–80% of the world's commercial marine fishes rely on estuaries directly, either as homes for migrating adults or as protective nurseries for the young. Estuaries and other coastal wetlands are also of prime importance to both resident and migratory populations of water birds.

A large number of invertebrates have adapted to life in these dynamic environments. In general, animals have but two alternatives when encountering stressful conditions: either they migrate to more favorable environments, or they remain and tolerate (accommodate to) the changing conditions. Many animals migrate into estuaries to spend only a portion of their life cycle, whereas others move in and out on a daily basis with the tides. Other species remain in estuaries throughout their lives, and these species show a remarkable range of physiological adaptations to the environmental conditions with which they must cope (see Chapter 3).

Freshwater Habitats

Most of the world's unfrozen fresh water is stored beneath the land surface. It is groundwater, stored in aquifers and out of sight. Although the world's aquifers are environmentally stable, humans are depleting more than half of them at an alarming rate. Because surface bodies of fresh water are so much smaller than both aquifers and the oceans, surface water is much

more readily and drastically influenced by extrinsic environmental factors and thus is a relatively unstable environment (Figure 1.6D). Changes in temperature and other conditions in ponds, streams, and lakes may occur quickly and be of a magnitude never experienced in most marine environments. Seasonal changes are even more extreme and may include complete freezing during the winter and complete drying in the summer. Ponds that hold water for only a few weeks during and after rainy seasons are called **ephemeral pools** (or vernal pools). They typically contain a unique and highly specialized invertebrate fauna capable of producing resting, or diapause, stages (usually eggs or embryos) that can survive for months or even years without water. As stressful as this sounds, ephemeral pools contain rich communities of plant and animal life, especially endemic species of crustaceans. **Diapause** is a form of dormancy in which invertebrates in any stage of development before the adult, including the egg stage, cease their growth and development. Diapause is genetically determined. Some species are programmed to enter diapause when certain environmental conditions provide the proper cues (often a combination of temperature and length of daylight). Hibernation and aestivation are two other types of dormancy, but they are not genetically programmed and may occur irregularly, or not at all, during any stage of an animal's development. **Hibernation** is a temporary response to cold, while **aestivation** is a temporary response to high temperatures and arid conditions.

Because the internal milieu of animals is typically close to that of sea water, the very low salinity of fresh water (rarely more than 1‰) and the lack of constant relative ion concentrations subject freshwater inhabitants to severe ionic and osmotic stresses. These conditions, along with other factors such as reduced buoyancy, less stable pH, and rapid nutrient input and depletion, produce environments that support far less biological diversity than the ocean does. Nonetheless, many different invertebrates do live in fresh water and have solved the problems associated with this environment. Special adaptations to life in fresh water are summarized in Chapter 3, and they are discussed in later chapters in relation to the groups of invertebrates that have such adaptations.

Stygobionts are aquatic obligates in subterranean ground waters, including streams and underground lakes that often connect to the sea. Aquatic creatures that inhabit subterranean alluvial waters and karst ecosystems also fall into this category, and many have been shown to be highly endemic and vulnerable to changing environmental conditions.

Freshwater habitats (including wetlands) are some of the most threatened environments on Earth. Throughout the United States, people destroy 100,000 acres of wetlands annually. Rare aquatic habitats such as ephemeral pools and subterranean rivers are disappearing faster than they can be studied. Underground, or hypogean, habitats are often aquatic, and these habitats are quickly being destroyed by pollution and groundwater overdraft. In California, 96% of the historic wetlands have been lost to agriculture and development, and globally wetland loss is three times as high as forest loss. The 2018 Living Planet Index (www.livingplanetindex.org) showed that populations of freshwater species had declined by an average of 83% since 1970, a far steeper drop than for terrestrial or marine species.

Terrestrial Habitats

Life on land is in many ways even more rigorous than life in fresh water. Temperature extremes are usually encountered on a daily basis, water balance is a critical problem, and just physically supporting the body requires major expenditures of energy. Water provides a medium for support; for dispersing gametes, larvae, and adults; and for diluting waste products and is a source of dissolved materials needed by animals. Animals living in terrestrial environments do not enjoy those benefits of water, and they must pay the price. The hottest terrestrial habitat on Earth may be the Lut Desert in southeast Iran, where soil surface temperatures can reach nearly 71°C (160°F). But even this desert has a vibrant ecosystem, supported in part by bird carcasses and a "hidden sea"—a surprising shallow layer of salty groundwater.

Relatively few phyla have successfully invaded the terrestrial world. Invertebrate success on land is exemplified by the arthropods, notably the terrestrial isopods, insects, and spiders, mites, scorpions, and other arachnids. These arthropod groups include truly terrestrial species that have invaded even the most arid environments (Figure 1.6F). Except for some snails and nematodes, all other land-dwelling invertebrates, including such familiar animals as earthworms, are largely restricted to relatively moist areas.

Terrestrial environments are commonly described in terms of moisture availability. **Xeric** habitats are dry, **mesic** environments have a moderate amount of moisture, and **hydric** habitats are very wet. Adaptations of terrestrial invertebrates to these various conditions are described in Chapter 3 and, for individual taxa, in subsequent chapters.

A Special Type of Environment: Symbiosis

Many invertebrates live in intimate association with other animals or plants. And, of course all Metazoa (and the eukaryotes in general) share an ancient genetic relationship with prokaryotes. An intimate association between two different species is termed a symbiotic relationship, or **symbiosis**. Symbiosis was first defined in 1879 by German mycologist H. A. DeBary as "unlike organisms living together." In most symbiotic

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relationships, a larger organism (called the host) provides an environment (its body, burrow, nest, etc.) on or within which a smaller organism (the symbiont) lives. Some symbiotic relationships are rather transient—for example, the relationship between ticks or lice and their vertebrate host—whereas others are more or less permanent. Some symbionts are opportunistic (**facultative**), whereas others cannot survive without their host (**obligatory**). And, importantly, some symbioses evolve such intimacy that, over time, genes of the smaller symbiont may get incorporated into the genome of the "host."

Symbiotic relationships can be subdivided into several categories based on the nature of the interaction between the symbiont and its host (although in many cases the exact nature of the relationship is unknown). Perhaps the most familiar type of symbiotic relationship is **parasitism**, in which the symbiont (a parasite) receives benefits at the host's expense. Parasites may be external (**ectoparasites**), such as lice, ticks, and leeches; or they may be internal (**endoparasites**), such as liver flukes, some roundworms, and tapeworms. Other parasites may be neither strictly internal nor strictly external; rather, they may live in a body cavity or area of the host that communicates with the environment, such as the gill chamber of a fish or the mouth or anus of a host animal (**mesoparasites**). Some parasites live their entire adult lives in association with their hosts and are permanent parasites, whereas temporary, or intermittent, parasites such as bedbugs feed on the host and then leave it. There are even nest parasites, such as ant-nest beetles (Carabidae: Paussini) that inhabit the nests of host ants and feed on them, apparently by tricking the ants into thinking they are one of them. In some of these cases, the line between parasitism and predation becomes blurred. Temporary parasites, such as mosquitoes and aegiid isopods, are often referred to as **micropredators**, in recognition of the fact that they usually "prey" on several different host individuals (that happen to be much larger than themselves).

Parasites that parasitize other parasites are **hyperparasitic**. **Parasitoids** are insects, usually flies or wasps, whose immature stages feed on the bodies of their hosts, usually other insects, and ultimately kill the host. A **definitive host** is one in which the parasite reaches reproductive maturity. An **intermediate host** is one that is required for a parasite's development but in which the parasite does not reach reproductive maturity. Multiple hosts are more common than not in the world of parasites. Even most human pathogens circulate in other animals (or else originated in nonhuman hosts); influenza, plague, and trypanosomiasis all transmit from animals to humans. Over half of all human pathogens are **zoonotic** (have animal hosts, other than humans, in their life cycle). Every species probably serves as host to several (or many) parasites. It has been suggested that parasitism is the most popular lifestyle on Earth! Since insects are the most diverse group of organisms on Earth, and since all insects harbor numerous parasites, it is fair to say that the most common mode of life on Earth is that of an insect parasite. Most parasites have yet to be described, and as species go extinct, so, often, do their parasites (when the passenger pigeon was eliminated in 1914, it took two species of parasitic lice with it).

A few groups of invertebrates are predominantly or exclusively parasitic. Many texts and courses on parasitology pay particular attention to the effects of these animals on humans, crops, and livestock. Here we also try to focus on parasitism from "the parasite's point of view," that is, as a particular lifestyle suited to a specific environment, requiring certain adaptations and conferring certain advantages.

The term **mutualism** was introduced into biology in 1873 by Pierre van Beneden to recognize "mutual aid" between species. Mutualism is generally defined as cooperation between species, an association in which both host and symbiont benefit. Such relationships may be extremely intimate and important for the survival of both parties; for example, the bacteria in our own large intestine are important in the production of certain vitamins and in processing material in our gut. In fact, beneficial associations with specific bacterial symbionts characterize many, if not all, animal species, although most of these relationships have not been well studied. Another example is the relationship between termites and certain protists that inhabit their digestive tracts and are responsible for the breakdown of cellulose into compounds that can be assimilated by the insect hosts. In nature, 90% of land plants are mycorrhizal, and virtually all mammalian and insect herbivores would starve without their cellulose-digesting symbionts. Other mutualistic relationships may be less binding on the organisms involved. Cleaner shrimps, for example, inhabit coral reef environments, where they establish "cleaning stations" that are visited regularly by reef-dwelling fishes that present themselves to the shrimps for the removal of parasites. Obviously, even this rather loose association results in benefits for the shrimps (a meal) as well as for the fishes (removal of parasites). The mutualistic relationships between flowering plants (which have been around for over 100 million years) and their pollinators are essential to the survival of the plants and their insect partners (and, in some cases, their nectar-feeding bird or bat partners).

There are many types of mutualism, and Bronstein (2015) has categorized them as **transportation mutualism** (e.g., pollination, fig–fig wasp, yucca–yucca moth, seed dispersal), **protection mutualism** (e.g., ant-plant, bioluminescence, cleaning), and **nutritional mutualism** (e.g., legume-rhizobium, mycorrhizal, fungus-growing ants, bark beetle–fungus, coral-algae symbioses, gut microbiomes). Mutualistic relationships may be extremely intimate and important for the survival of both parties. Mutualism can be

obligate (neither population, or species, can survive without the other, such as fig pollination mutualism or yucca pollination mutualism), or it can be **facultative** (under certain conditions, the populations, or species, can survive without the other although they may not perform as well as when partnered). Some workers have noted that not all mutualisms are necessarily symbiotic, and thus the more specific term "symbiotic mutualism" can be used to describe those in which there is prolonged physical intimacy between partner species. Another form of interaction is known as "facilitation"—an interaction in which the presence of one species alters the environment in a way that enhances the growth, survival, or reproduction of a second, neighboring species (although the two may not share physical intimacy). In cases where each species facilitates the other, the interaction is a mutualism, usually a nonsymbiotic mutualism.

Mutualisms are some of the most threatened ecological relationships on Earth. For example, as we lose pollinator species, the plants they rely on suffer and begin to decline. In some cases, plants rely on single species for pollination. For example, each of the 900 or so species of giant fig trees of the tropics (*Ficus* is the most widespread plant genus in the tropics) is pollinated by a single variety of wasp. Imagine what would happen to the trees if they lost their very specific pollinators. Imagine what would happen to the rest of the community. Of immediate concern is colony collapse disorder (CCD), a syndrome that is killing honeybees worldwide. Bees pollinate 71% of the crops that provide 90% of human food; but since 2006, U.S. beekeepers have seen honeybee colony loss rates increase to 35% per year. The causes for CCD have yet to be fully elucidated, but overuse of pesticides in the environment appears to play a key role. In the European Union, about 500 active substances used in pesticides are approved.

A third type of symbiosis is called **commensalism**. This category is something of a catchall for associations in which neither significant harm nor mutual benefit is obvious. Commensalism is usually described as an association that is advantageous to one party (the symbiont) but leaves the other (the host) unaffected. For instance, among invertebrates there are numerous examples of one species inhabiting the tube or burrow of another (**inquilism**); the former obtains protection, food, or both with little or no apparent effect on the latter. A special type of commensalism is **phoresis**, wherein the two symbionts "travel together," but there is no physiological or biochemical dependency on the part of either participant. Usually one phoront is smaller than the other and is mechanically carried about by its larger companion.

There is a good deal of overlap among the categories of symbiosis just described, and many animal relationships have elements of two or even of all the categories, depending on life history stage or environmental conditions. Taken in its broad sense, the concept of symbiosis has profound implications for understanding Earth's biodiversity.

Changing Views of Invertebrate Phylogeny

Significant changes in our view of animal phylogeny have come about over the past three decades, primarily from the rapidly expanding field of molecular phylogenetics and also from new paleontological work and new ultrastructural and embryological studies. Broadly speaking, the 31 phyla of Metazoa are now classified into four basal, nonbilaterian phyla (the diploblastic phyla: Porifera, Cnidaria, Ctenophora, Placozoa) and the Bilateria (the 27 triploblastic phyla). The Bilateria comprise two long-recognized clades, Protostomia and Deuterostomia, but four phyla once regarded as deuterostomes are now recognized as protostomes (Chaetognatha, Phoronida, Bryozoa, Brachiopoda), leaving only three phyla of Deuterostomia—Echinodermata, Hemichordata, and Chordata. The newly created phylum Xenacoelomorpha, housing taxa formerly allied with the Platyhelminthes (Acoela, Nemertodermatida, and *Xenoturbella*), remains somewhat enigmatic, but most analyses place this phylum as sister group to Nephrozoa—the remaining bilaterians.

Among the protostomes, molecular phylogenetic research identifies two major clades, Ecdysozoa and Spiralia. However, despite great efforts to date, the specific relationships of the phyla within Ecdysozoa and Spiralia also remain somewhat elusive, although some strongly supported internal clades have been identified. These ideas are more fully discussed in Chapter 8. Among the deuterostomes, Echinodermata and Hemichordata form a well-supported clade (Ambulacraria), and this is the sister group to Chordata. Within Chordata, the long-standing idea that lancelets (Cephalochordata) are the sister group to the Vertebrata (Craniata) has been overturned, and strong evidence now supports the tunicates (Urochordata) as the sister group to the vertebrates. A summary classification and geologic time scale are provided on the front inside cover of this book.

Teasing apart the evolutionary relationships of the metazoan phyla has been challenging because of their ancient roots, and it has required finding informative phylogenetic markers for groups that are hundreds of millions of years old. One challenge has been that different regions of the genome have experienced different evolutionary histories, thus producing conflicting phylogenetic signals. Not only has this required using multiple genes, and even genome-level analyses, it has also led to the development of sophisticated algorithms that model the evolution of individual amino

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acids. Those phyla still stubbornly resisting phylogenetic understanding will probably require new and even more sophisticated analysis protocols. One of the important things that has been revealed over the past couple of decades through the work of molecular phylogenetics and developmental biology is that there is far more homoplasy in the animal world than we suspected, even in such complex features as segmentation and nervous systems. For example, one surprising discovery of the early days of molecular systematics is that Annelida (considered spiralians) and Panarthropoda (Onychophora, Tardigrada, Arthropoda—placed within Ecdysozoa) are far more distantly related than was previously thought. And another, only distantly related phylum, the Kinorhyncha, also show segmentation. We still have much to learn about these new twists in animal phylogeny. Even spiral cleavage, once thought to be a largely immutable aspect of animal development (due to "developmental constraints"), has been shown to be flexible—to the point of being greatly altered or even lost in some lineages. Further, we now know that many genes once thought to be specific to particular innovations actually appeared in the tree of life much earlier than did the features themselves; so we can no longer necessarily expect to find novel genes associated with novel morphological or developmental features. For example, cellular adhesion and transcriptional regulation genes essential to animal multicellularity also occur in the protistan ancestral line leading to Metazoa. And we now know that many genes once thought to be specific to vertebrates can be found as far down the tree of life as Cnidaria (but have been lost in many lineages in between). Many novel phenotypes have arisen by way of modification of gene function and by interactions between existing genes.

Legacy Names

As you might have guessed by now, some of the names in use today for higher taxa were created before biologists achieved their current understanding of animal phylogeny, and due to more recent reassignments of phyla, these names are no longer fully descriptive. As noted, the two great clades of Bilateria have long been called Protostomia and Deuterostomia. The names were originally based on what was known at the time about early embryonic development, especially the fate of the blastopore. Deuterostomia were those animals in which the blastopore became the adult anus, the mouth thus forming de novo, secondarily. Hence the name: *deutero* = "second," *stome* = "mouth." In Protostomia (*proto* = "first"), on the other hand, the blastopore gave rise to the mouth, and the anus formed elsewhere. However, we now know that some members of the clade Protostomia have deuterostomous development (e.g., nematomorphs, priapulans), and in some Deuterostomia the anus does not originate from the blastopore. In fact, it seems that the blastopore, the mouth, and the anus have a degree of developmental independence. Similarly, the name Spiralia was created by Waldemar Schleip in 1929, after the stereotypical spiral cleavage seen in most member phyla, but even this name is not fully descriptive, because several phyla of Spiralia lack this developmental pattern (e.g., Bryozoa, Brachiopoda, Gastrotricha). These kinds of names for higher taxa, that are no longer fully descriptive based on their original intent, are **legacy names**. To fully appreciate them, one needs to understand a bit of their history; otherwise they can seem illogical. Again, these ideas are explored more fully in Chapter 8.

Phylogenetics and Classification Schemes

As noted previously, the rapidly growing number of molecular phylogenetic studies, especially genomic-scale phylogenetics, has changed many of our views on animal relationships and classifications. This work is also generating large and highly resolved phylogenetic trees, with detailed branching patterns depicting the history of life on Earth. Such detail creates challenges for biologists who strive to produce classifications that accurately reflect phylogeny, because the traditional Linnean hierarchical ranks are too few in number to capture the great depth and detail of these trees. Many of the new trees have scores of branching points, or even hundreds of branches that appear as long comblike topologies. But the standard Linnean ranks number only 30 or so. There are a few solutions to this dilemma, such as using unranked classifications, but none of the solutions is perfect. We briefly discuss these in Chapter 2. In this book, we mostly use ranked classifications that mirror, or at least do not conflict with, the phylogeny of the groups in question. In a few instances, we have had to use fully or partly unranked subordinated classifications (e.g., annelids and molluscs). Again, this is all explained in more detail in Chapter 2. But the upshot is, things are changing and the "traditional" classification schemes many students are used to seeing are beginning to look rather different these days.

A Final Introductory Message to the Reader

Because of our comparative approach, it is important that you become familiar with Chapters 1 through 4 before attempting to study and comprehend the sections dealing with individual animal groups. These four chapters are designed to accomplish several goals: (1) to define some basic terminology, (2) to introduce a number of important concepts, and (3) to describe in detail the themes that we use throughout the rest of the book. They also offer students a bit of a "refresher course" in general biology.

The fundamental theme of this book is evolution, and we approach invertebrate evolution primarily through the field of comparative biology. In Chapter 2 we provide an explanation of how biologists derive evolutionary schemes and classifications, how theories about the phylogeny of animal groups grow and change, and how the information presented in this text has been used to construct theories on how life evolved on Earth. In Chapters 3 and 4 we lay out the fundamental anatomical and morphological designs and developmental strategies of metazoans. Like all features of organisms, these designs and strategies are not random, but form patterns. Recognition and analysis of these patterns constitute the basic building blocks of this book. We then proceed in the "animal chapters" to explore the evolution of the invertebrates in light of various combinations of these basic functional body plans and lifestyles. With this background, you should be able to follow the evolutionary changes and branchings among the invertebrate phyla, their body systems, and their various pathways to success on Earth. Note that chapters treating large phyla (e.g., molluscs, annelids, the arthropods) have rather lengthy taxonomic synopsis sections. We don't expect students to read every word of these synopses; they are provided more as a reference source for readers to look up taxa within the context of our current state of knowledge for the groups.

Through our approach, we hope to add continuity to the massive subject of invertebrate zoology, which is often covered (in texts and lectures) by a sort of "flash card" method, in which the primary goal is to have the student memorize animal names and characteristics and keep them properly associated, at least until after the examination. Thus, we urge you to look back frequently at these first few chapters as you read ahead and explore how invertebrates are put together, how they live, and how they evolved.

Chapter Summary

Are you ready to join us on this journey through the diversity of animal life on planet Earth? Good! In this introductory chapter we provide you with some background material for what lies ahead. We start with a brief overview of the history of life on Earth, especially the large clade Metazoa (= Animalia). Although the oldest generally accepted animal fossils are from the Ediacaran Period (635–541 Ma), molecular clock estimates have suggested that Metazoa might have arisen much earlier (875–650 Ma). On land, however, animals may not have begun to radiate until around 470 million years ago. Approximately 2 million living eukaryote species, about 1.45 million of which are animals, have so far been described, but estimates of undescribed/unnamed eukaryote species range from 3 to 100 million (or more). Species are not evenly distributed among the 31 animal phyla (Table 1.1). Of the 1.4 million named living animal species, 1.2 million (82.3%) belong to one phylum, Arthropoda, and 1.33 million (92%) belong to just three phyla (Arthropoda, Mollusca, and Chordata). And seven animal phyla each contain fewer than 100 named species.

We organize our knowledge of these species through classifications, which are based upon our current understanding of the one great tree of life. Our understanding of the topology of that tree is always being refined as new data and new ways of analyzing our data appear. But our principal goal is always to recognize natural, or monophyletic, groups (which are also called clades); these are groups of species that have descended from a single common ancestor and that include all the descendants of that ancestor. In this way, our classifications reflect our understanding of the tree of life, the evolutionary history of life on Earth. However, many previously recognized taxa have been shown to be paraphyletic or polyphyletic, basically representing mistakes made by previous systematists that have been revealed in light of new information. In contrast to monophyletic groups, paraphyletic groups have a common ancestor, but they do not contain all of the descendants of that ancestor. An example of a paraphyletic group is Crustacea; while crustaceans are all descended from an immediate common ancestor, one group is traditionally excluded—the insects and their kin (Hexapoda). Polyphyletic groups contained species that are not all descended from an immediate common ancestor. An example of a polyphyletic group was Vermes, and old name used for many wormlike animals, that included representatives of many current animal phyla.

Significant changes in our view of animal phylogeny have come about over the past three decades, primarily from the rapidly expanding field of molecular phylogenetics, and also from new paleontological work and new ultrastructural and embryological studies. Broadly speaking, the 31 currently recognized phyla of Metazoa are today classified into four basal, nonbilaterian phyla (the diploblastic phyla: Porifera, Cnidaria, Ctenophora, Placozoa) and the Bilateria (the 27 triploblastic phyla).

Marine, freshwater, and terrestrial environments present different kinds of challenges for animals, especially in terms of water balance, excretion, reproduction, support, and locomotion; this is briefly reviewed in this chapter.

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CHAPTER 2

Systematics, Phylogeny, and Classifications

The affinities of all the beings of the same class have sometimes been represented by a great tree. . . . As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.

Charles Darwin, *The Origin of Species*, 1859

Systematics is the study of biological diversity and its origins. Systematists identify and distinguish species, describe and name new taxa, provide tools to aid others in identifying specimens, infer the evolutionary relationships among species and higher taxa, undertake biogeographic analyses, and produce classification systems that reflect evolutionary history. These stages in systematic research overlap and cycle back on themselves in a highly iterative fashion. In sum, the role of systematics is to document and understand Earth's biological diversity, to reconstruct the history of that biodiversity, and to develop natural (evolutionary) classifications of living and extinct organisms.

Just as your own family has grown through time and you are connected to your parents and your grandparents, all organisms that have ever lived on Earth are related to one another through genetic descent. **Phylogenetic trees** are diagrams comprising branches and nodes that depict this flow of genetic information over time to illustrate how organisms are related. Since all organisms are kin to one another, there is a single tree of life, whose branching pattern reflects the evolutionary relationships among all species on Earth (Darwin's "great Tree of Life"). However, because multicellular life has been evolving on Earth for hundreds of millions of years, and we cannot time travel, we don't know for certain how all of the branches of the tree are connected to one another. That is, there is not a universal record of the pattern of genetic decent since life began. But, there are *traces* of that pattern embedded in the anatomy and genomes of all of the organisms roaming the Earth today and even in some that are no longer among us (e.g., fossils can be studied anatomically, and ancient DNA allows us to study the genomes of some organisms that died more than one million years ago). Systematists seek to uncover those traces to generate hypotheses of how organisms and species are related to one another. They do this by creating and analyzing data matrices of homologous anatomical or genetic traits, formally called **characters**, among

The chapter opener photo shows representatives of two phyla that are only distantly related, deeply in time: sponges (Porifera) and crabs (Arthropoda). Both are ancient phyla that arose in Precambrian seas more than 550 million years ago.

organisms. As new data become available and are added to the analysis, trees are revised and updated. As we will see throughout this book, many long-held ideas about animal relationships have recently been altered (or even overturned) by analyses of DNA sequence data. In this chapter, we will present the underpinnings of phylogenetic analysis and the construction of classifications.

Phylogeny, Monophyly, Paraphyly, and Polyphyly

A **phylogenetic tree** is a branching diagram that depicts how organisms are related to one another (Figure 2.1). It is a graphical means of expressing relationships (or genetic connectivity) among species or other taxa and is, in fact, a nested set of clades. Understanding the concept of a clade (or monophyletic group) is critical to being able to read a tree correctly. A **monophyletic group, or clade,** is a group of species that includes a common ancestor and all of the descendants of that common ancestor—that is, it is a unique branch in the tree of life. Monophyletic groups can be separated from the rest of the tree of life by cutting a single branch once. If you were able to walk up to the tree of life and cut off one branch, any branch, and hold that trimming in your hand, you would be holding a monophyletic group (Figure 2.1). A monophyletic group is a group of taxa that are one another's closest relatives. You and your immediate family (you, your parents, and your siblings) is one example of a monophyletic group.

Most trees published in the literature (and in this text) are rooted, and rooted trees not only show a pattern of relationship but also indicate the direction in which time is moving along the branches—always from the root (oldest) to the tips (youngest) of the tree, no matter how the tree is drawn (Figure 2.2). Thus, rooted trees depict ancestor-descendant relationships.

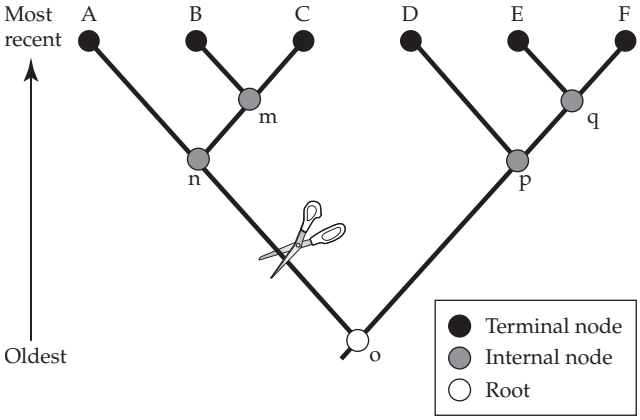

FIGURE 2.1 Learning to read trees. This phylogeny depicts the relationships among six taxa (A–F). Phylogenetic trees are always composed of nodes and branches, but the nodes are usually not indicated. In this tree, the terminal nodes are solid black circles (A–F), and they represent the extant species. The internal nodes are gray or open circles (m–q), and they represent the most recent common ancestors (MRCA) of their descendants. Node o is the root node; it indicates where this tree would attach to the rest of the tree of life, and it tells us the direction in which time moves along the branches of the tree (from bottom to top). Time always moves from the root node toward the terminal nodes, as indicated by the arrow to the left. A monophyletic group (or clade) is a group of taxa that includes the MRCA and the descendants of that ancestor. You could cut this tree along any single branch and hold the trimming in your hand, and that would be a monophyletic group. Trees are nested sets of monophyletic groups (or clades). Sister groups are two monophyletic groups that are more closely related to one another than they are to any other groups. Sister groups share a most recent common ancestor. The sister group of taxon A in this tree is m + B + C, and their MCRA is represented by node n. The sister group of the clade that includes A + B + C is the clade composed of p + q + D + E + F. These two clades share a MRCA depicted by node o.

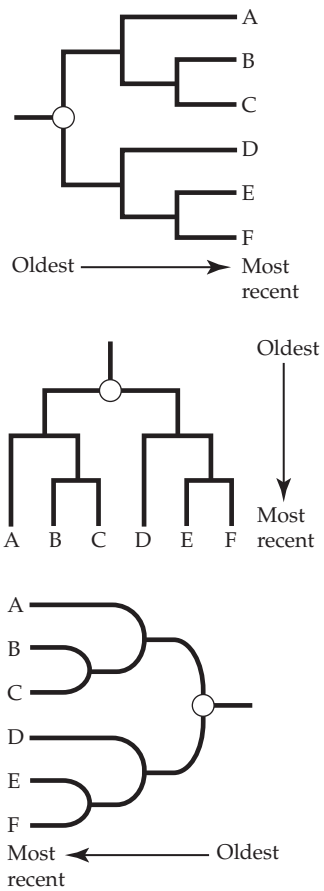

FIGURE 2.2. Trees, the root node, and direction of time. These three trees depict the same pattern of relationship between taxa A–F as the tree shows in Figure 2.1. In each tree the root node is indicated by a circle, and an arrow depicts the direction in which time moves along the branches, from the root node to the terminal nodes (sometimes called "leaves").

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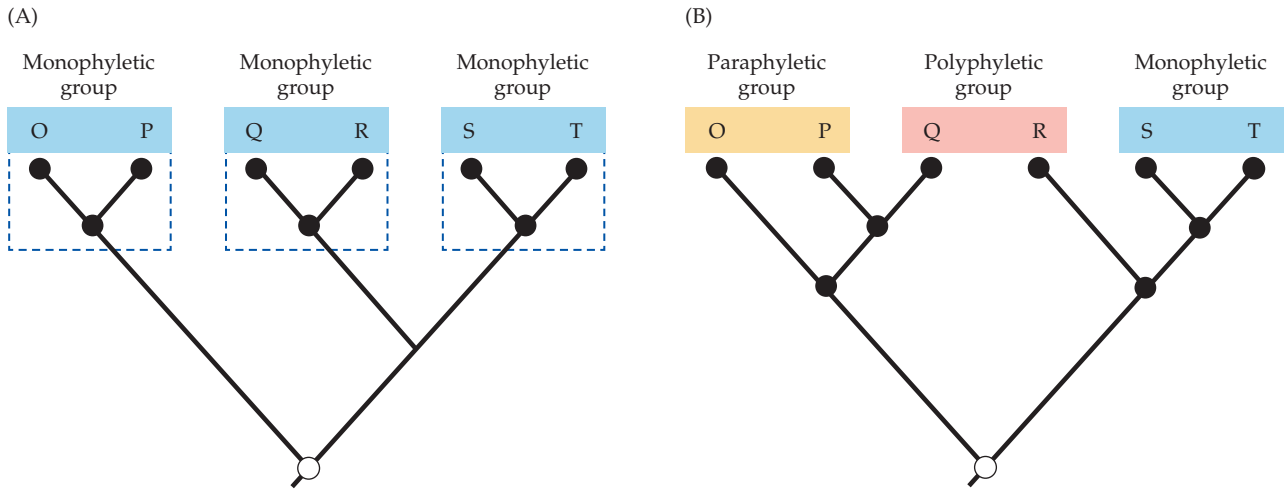

FIGURE 2.3. Monophyly, paraphyly, and polyphyly. Trees A and B depict two different, but potentially correct, phylogenies of six living species (O–T). In both scenarios a systematist proposed to classify the six extant species into three groups: O + P, Q + R, and S + T. If the evolutionary relationships among these taxa are correctly depicted in tree A, then all three groups the systematist erected are monophyletic. However, if the evolutionary relationships among these taxa are correctly depicted by tree B, then only S + T would be a monophyletic group. O + P would be a paraphyletic group since it excludes species Q, and Q + R would be a polyphyletic group because these two species evolved from more than one most recent common ancestor. If we knew the shape of the tree of life with certainty, systematists would erect only monophyletic groups. Paraphyletic and polyphyletic groups are erected due to a lack of knowledge of the evolutionary relationships among taxa (or the shape of the underlying tree).

If we knew for certain what the shape of the tree of life looked like, then systematists would erect only monophyletic groups (Figure 2.3A). But because we do not yet fully know the shape of the tree, sometimes systematists mistakenly create paraphyletic or polyphyletic groups. These kinds of nonmonophyletic taxa or species groups are illustrated in Figure 2.3B.

A group whose member species are all descendants of a common ancestor but that does *not* contain all the species descended from that ancestor is called a **paraphyletic group** (Figure 2.3B, O + P group). Paraphyly implies that for some reason one or more members of a natural group have been separated out and placed in a different group. As we will see, many paraphyletic groups exist within animal classifications today.[1]

A **polyphyletic group** is a group whose member species arose from two or more, different immediate ancestors. Such composite groups are proposed due to insufficient knowledge concerning how the taxa in question are related to other taxa (Figure 2.3B, Q + R group). Polyphyletic groups are usually established because the features or characters used to recognize and diagnose the group are not homologous but rather are the result of evolutionary convergence.[2] One of the principal goals of systematists is to discover such polyphyletic or "artificial" taxa and, through careful study, reclassify their members into appropriate monophyletic taxa.

Homology

As mentioned earlier, systematists infer phylogenies by comparing heritable traits, formally called **characters**, which they break down into **character states** to capture the variation in form of that character among the taxa they are studying. In practical usage, the terms "character" and "character state" are often used interchangeably. This practice can be a bit confusing. When the term "character" is used in a discussion of two or more homologues, it is typically being used in the same sense as "character state." Characters and character states

[1]Some biologists consider paraphyly a subset of monophyly, using the term "holophyly" to denote the strictly monophyletic groups. However, this alternative use of these terms is not common, and we do not use it in this book.

[2]There are many examples of previously established groups which are now known or suspected to be polyphyletic. For example, the old phylum Gephyrea contained species that we now classify into three distinct taxa that are only distantly related to one another—Sipuncula, Thalassematidae, and Priapula (the first two are now in the phylum Annelida but are not closely related). Another example is the old group Radiata, which included all animals possessing radial symmetry (e.g., Cnidaria, Ctenophora, and Echinodermata). Most recently, the group called Articulata, containing the Annelida and the Arthropoda (and their kin), has been shown by molecular phylogenetics to be polyphyletic. Polyphyletic taxa usually are established because the features or characters used to recognize and diagnose them are the results of evolutionary convergence in different lineages. Convergent evolution can often be understood only by careful comparative embryological or anatomical studies, sometimes requiring the efforts of several generations of specialists. The complex nature of the probable convergence between annelid and arthropod segmental development, for example, is yet to be fully worked out.

(A)

Characters	Crustacea	Springtails	Silverfish	Dragonflies	Crickets	Beetles	Butterflies
	Taxa						
1. Thorax of only 3 segments, each bearing one pair of legs	No	Yes	Yes	Yes	Yes	Yes	Yes
2. Mouthparts external, not embedded within head	No	No	Yes	Yes	Yes	Yes	Yes
3. Wings present	No	No	No	Yes	Yes	Yes	Yes
4. Wing base with 3rd auxiliary sclerite, allowing wings to fold flat over the abdomen	No	No	No	No	Yes	Yes	Yes
5. Pupal stage present	No	No	No	No	No	Yes	Yes

(B)

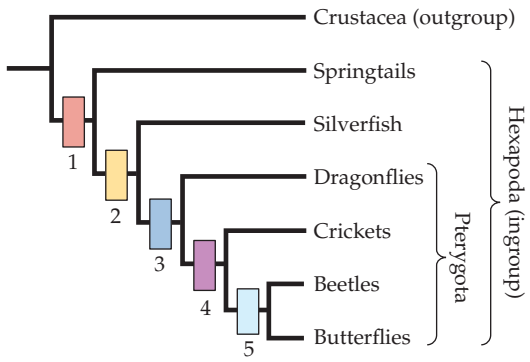

FIGURE 2.4. Example of a data matrix of five characters and seven taxa. The character states for each of the seven taxa are coded in the matrix. If the character is not present within a taxon, the matrix is coded with "no"; if it is present in that taxon, the matrix is coded with "yes" (systematists often use "absence" and "presence" instead of "no" and "yes," and these are represented in matrices as "0" and "1," but additional states may exist in the so-called multistate characters, as opposed to binary ones). These character states are plotted on the corresponding tree to the right along the branch where they change from no to yes. The place where the character state first appears represents an apomorphy for the corresponding ancestral node to the right, and that character state occurs in all the descendants of the ancestor. Among the descendants, manifestations of this character are called homologues, or homologous features. Homologues share a common developmental and evolutionary origin. For example, the presence of wings is an apomorphy of clade Pterygota (and wings are homologous throughout the Pterygota), but the presence of wings is a plesiomorphy of the clade containing only beetles and butterflies. The clade containing only beetles and butterflies is defined by the apomorphy of a pupal stage (representative of complete metamorphosis).

(which are usually either morphological or molecular) are assembled into data matrices (Figure 2.4) in which every character amounts to a hypothesis of homology.

Homologous characters have *shared ancestry.* That is, they are traits that are present in two or more taxa and inherited from their common ancestor. Homologous characters share an evolutionary history. The process of evolutionary descent with modification has produced a hierarchical pattern of homologies that can be traced through lineages of living organisms. It is this pattern that we use to reconstruct the history of life. The functions of homologous structures may be similar or different, but this has no bearing on the underlying homology of the structures involved. Our ability to recognize anatomical homologues often depends on developmental or embryological evidence and on the relative position of the anatomical structure or the nucleotide or amino acids in nucleotide or protein sequences.

Homology is a concept that is applicable to anatomical structures, to genes, and to developmental processes. However, homology at one of these levels does not necessarily indicate homology at another. Biologists should always be clear regarding the level at which they are inferring homology: genes, their expression patterns, their developmental roles, or the structures to which they give rise. Researchers sometimes assume similar patterns of regulatory gene expression are also evidence of homology among structures. This can result in mistakes because it ignores the evolutionary histories of the genes and of the structures in which they are expressed. The functions of homologous genes (orthologues or paralogues), just like those of homologous structures, can diverge from one another over evolutionary time. Similarly, the functions of nonhomologous genes can converge over time. Therefore, similarity of function is not a valid criterion for the determination of homology of either genes or structures. For example, the phenomenon of gene recruitment (co-option) can lead to situations in which truly orthologous genes are expressed in nonhomologous structures during development. Most regulatory genes play several distinct roles during development, and homologous genes can be independently recruited to superficially similar roles. A classic example is the regulatory gene *Distal-less*, which is expressed in the distal portion of appendages of many animals during their embryogeny (e.g., arthropods, echinoderms, chordates). Although the domains of *Distal-less* gene expression might reflect a homologous role in specifying proximodistal axes of appendages, the appendages themselves are clearly not homologous.

Characters are the attributes, or features, of organisms or groups of organisms (clades, taxa) that biologists rely on to indicate their relatedness to other similar organisms and to distinguish them from other groups.

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Characters are the observable features and expressions of the genotype, and they can be anything from the actual amino acid sequences of the genes themselves to the phenotypic expressions of the genotype. A character can be any genetically inherited trait that systematists can examine and measure; it can be a morphological, anatomical, developmental, or molecular feature of an organism, its chromosomal makeup (karyotype) or biochemical "fingerprint," or even a physiological, or ethological (behavioral), attribute—the webs of spiders are a classic example of behavioral traits relatively easy to document. A large number of biochemical, molecular, and bioinformatics techniques for measuring similarity and inferring relationships among organisms have been developed over the past few decades. Thus, a variety of kinds of data are available that provide systematists with homologous characters needed to define and compare species and infer phylogenies.

With the advent of technology for rapid amplification of DNA fragments and sequencing of the nucleic acids, the field of systematics has undergone dramatic change.[3] Questions of evolutionary relationship, which had traditionally been addressed only by comparative anatomy, can now be tested by an independent source of data. Since the 1990s, **molecular phylogenetics** has swept the literature with evolutionary trees built by analyses of gene sequences. Trees built from DNA sequence data have corroborated some relationships previously inferred by analyses of morphological traits, but they also provided support for novel relationships never predicted.[4] In molecular-based data matrices, every column in the aligned matrix represents a character, or a hypothesis of a homologous position in the alignment, and the character states are the specific nucleotides (A, adenine; T, thymine; C, cytosine; and G, guanine) or amino acids that occur in those taxa at those sites, or their inferred insertions or deletions.[5] Every character in a phylogenetic character matrix, whether built from anatomical or genetic data, is a hypothesis of homology.

[3]On February 12, 1988 (by appropriate coincidence, Charles Darwin's birthday), a paper published by Katherine Field, Rudy Raff, and others presented the first credible molecular analysis of metazoan phylogeny based on sequences from the small ribosomal subunit RNA gene (SSU or 18S rRNA). This work initiated a paradigm shift in phylogenetic analysis, and today the field of molecular phylogenetics is rooted in the methods pioneered in that important paper. In 1997, Anna Marie Aguinaldo and colleagues also published a revolutionary paper, proposing a radical new view of animal phylogeny—one that hypothesized the Protostomia to comprise two distinct clades, a "molting clade" (called Ecdysozoa) and a nonmolting clade (called Spiralia in this book).

The first molecular phylogenies were constructed from analyses of ribosomal genes, which code for RNA that forms the 3-D structure of ribosomes (the large ribosomal subunit or 28S rRNA, and the small subunit or 18S rRNA). However, the number of genes used to infer phylogenies increased quickly to include both nuclear and mitochondrial protein-coding genes. Whereas analyses of single genes were the standard only a few years ago, most molecular phylogenetic analyses today use multiple, preferably unlinked, genes concatenated together into one supermatrix. In fact, new and relatively inexpensive DNA sequencing technology, high-throughput sequencing, is allowing for molecular phylogenies to be constructed from larger portions of the genome, up to tens of thousands of genes. Specific regions of the genome can be targeted a priori through methods such as anchored hybrid enrichment or ultraconserved elements, or novel genes of phylogenetic significance can be discovered after shotgun sequencing of all DNA molecules (genomes) or RNA molecules (transcriptomes). No matter what type of genetic data are selected or how they are sequenced, these methods result in rich multigene data sets for phylogenetic inference. Resulting trees are therefore inferred from a larger portion of the genome than previous methods that relied on only a handful of genes, whose history may or may not precisely reflect the history of the taxa being analyzed.

[4]Equally exciting are techniques being developed to extract DNA from fossilized bone, tissue, or dung. In 2003, scientists managed to extract DNA from Siberian permafrost sediments and soils of caves in New Zealand. The Siberian sediments yielded the oldest reliable ancient DNA up to that time, from plants as much as 400,000 years old (angiosperms, gymnosperms, and mosses) as well as from numerous animals, including both living and extinct species up to 30,000 years old. In 2008, the entire genome of the extinct woolly mammoth (*Mammuthus primigenius*) from Siberia was sequenced, showing a sequence identity of over 98% with modern African elephants (the two diverged from one another about 6 million years ago). Also in 2008, DNA was sequenced from lice (Insecta: Phthiraptera: *Pediculus humanus*) preserved in the scalps of 1,000-year-old Peruvian mummies. The lice belonged to a subtype of head and body lice found all over the world, thus proving that human lice were in the New World well before Columbus. Since then, scientists have begun sequencing DNA from even older animals—the oldest so far is from two mammoths older than 1 million years, perhaps pushing the limits of how long DNA can actually survive. By extracting fragments of DNA from ancient soils and sediments (known as "environmental DNA") in North America, scientists have begun to reconstruct Pleistocene and early Holocene ecosystems. The extraction of DNA from 2,000- to 4,000-year-old cores from the Arctic region has yielded a variety of plants, bison, horses, bears, mammoths, and lemmings. Environmental DNA comes from urine, feces, hair, skin, eggshells, feathers, and even the saliva of animals, as well as from the decaying leaves and fine rootlets of plants. Ancient DNA analyses have led to the discovery of new types of ancient humans and revealed interbreeding between our ancestors and our archaic cousins, which left a genetic legacy that shapes who we are today. Much of the genome of Neanderthal has now been sequenced. As a result, we now know that modern *Homo sapiens* carry a remnant of Neanderthal DNA from interbreeding events that have been postulated to have occurred as humans migrated out of Africa and into Eurasia, at least 80,000 years ago.

[5]Not long after the first molecular-based trees were published, it was recognized that analyses of molecular sequence data are prone to predicting erroneous relationships under certain circumstances. Rapidly evolving lineages were inferred to be closely related, regardless of their true evolutionary relationships, due to a phenomenon known as long branch attraction (LBA). Since there are only four possible character states in molecular sequence data (the four nucleotides), when DNA substitution rates are high, there is a high probability that two lineages will *independently* evolve the same nucleotide at the same site by chance alone. In these circumstances, phylogenetic algorithms (especially parsimony methods) erroneously interpret these convergences to be signs of shared ancestry (synapomorphies) and therefore misinterpret taxa on long branches to be close relatives.

Using phylogenetic algorithms that incorporate models of evolution can minimize the LBA problem. These models include three components: (1) models of DNA substitution, which describe the rates at which one nucleotide replaces another over evolutionary time; (2) the relative nucleotide base frequency in a data set; and (3) the relative rates at which sites in an alignment evolve in a data set. Things get more complicated in analysis of data as amino acids, as typically done in many phylogenomic analyses, especially those using transcriptomes, and models become more complex and computationally intensive. Popular evolutionary-model-based algorithms include maximum likelihood and Bayesian methods of phylogenetic estimation.

Apomorphy and Plesiomorphy

Monophyletic groups (or clades) are defined only by apomorphies. **Apomorphies** are shared, derived character states, and they stand in opposition to **plesiomorphies**, which are relatively older states (or forms) of that character.[6] An apomorphy is only an apomorphy *at one specific place* in a phylogeny, along the branch in the tree in which the character state evolved. At the specific point on a phylogenetic tree where such a transformation takes place, the new (derived) character state is called an **apomorphy** and the former (ancestral) state is called a **plesiomorphy**. Character states can be apomorphic in one place in the tree and plesiomorphic in another. Within Arthropoda, for example, having just three thoracic segments, each bearing one pair of legs, is a derived character state whose evolutionary appearance marked the origin of the Hexapoda (thus distinguishing them from all other arthropods) (Figure 2.4). But for groups or lineages *within* the Hexapoda, such as the Pterygota, these same features represent retained ancestral features (plesiomorphies), whereas having wings is a shared, derived trait (or apomorphy) for the clade Pterygota. In the most general sense, so-called **primitive character states** are attributes of lineages that are relatively older and have been retained from some more distant ancestor; in other words, they have been around for a longer time relative to the apomorphic state, geologically or genealogically speaking.

In sum, systematists aim to document biodiversity by recognizing the boundaries of natural lineages and describing them by inferring the shape of the tree of life and building systems to classify species that reflect that evolutionary history. They do this by analyzing homologous characters to build a phylogeny, with each clade in that phylogeny defined by at least one apomorphy, or shared derived character state. It seems fairly straightforward, so why is this process so difficult? The answer to that question boils down to the fact that we cannot always recognize homologous characters, so there are many chances for error as we seek to obtain the shape of the one true tree of life.

Challenges of Phylogenetic Inference

Attempts to relate two taxa by comparing nonhomologous characters will result in errors. For example, the hands of chimpanzees and humans are homologous characters (i.e., homologues) because they have the same evolutionary and developmental origin; the wings of bats and insects, although similar in some ways, are not homologous characters because they have completely different origins. In a strict sense, the concept of homology has nothing to do with similarity or degree of resemblance. Some homologous features look very different in different taxa (e.g., the pectoral fins of whales and the arms of humans; the forewings of beetles and those of flies). Again, the concept of homology is related to the level of analysis being considered. The wings of bats and birds are homologous as tetrapod forelimbs, but they are not homologous as "wings," because wings evolved independently in these two groups (i.e., the wings of bats and birds do not share a common ancestral wing). Homology is a powerful concept, but it is important to remember that homologies are really hypotheses, open to testing and possible refutation.

Through **convergent evolution**, similar-appearing (but nonhomologous) structures may evolve in distantly related groups of organisms in quite different ways; that is, they have separate genetic and developmental origins. For example, early biologists were misled by the superficial similarities between the vertebrate eye and the cephalopod eye, the bivalve shells of molluscs and of brachiopods, and the sucking mouthparts of true bugs (Hemiptera) and of mosquitoes (Diptera). Structures such as these, which appear superficially similar but that have arisen independently and have separate genetic and phylogenetic origins, are called **convergent characters**. There are both ecological and genomic explanations for the evolution of morphological similarity. Through the phenomenon of convergent evolution, similar-appearing structures may arise independently, with separate genetic and developmental origins, in response to the same ecological factors. Convergent traits (among both animals and plants) have been recognized at nearly all levels of biological organization, ranging from molecules to morphology to behavior.

One of the most interesting cases of convergent evolution is the recently discovered analogies between voice and vocal learning in some mammals and birds (vocal learning is the ability to imitate sounds). Not only have the vocal regions of certain bird and mammal brains converged in their anatomy, but more than 50 genes have contributed to their convergent specialization—convergent behavior and neural circuits for vocal learning are accompanied by convergent molecular changes of multiple genes in species separated by millions of years from a common ancestor.

Convergence is often confused with **parallelism**. **Parallel characters** are similar features that have arisen more than once in different species but that share a common genetic and developmental basis. Parallel evolution is the result of "distant" or underlying homology; for parallel evolution to occur, the genetic potential for certain features must persist within a group, thus allowing the feature to appear and reappear in various related species or groups of species. Parallelism might be thought of as a kind of "evolutionary repeatedness."[7] Failure to

[6] Apomorphies that are shared by two or more taxa are sometimes referred to as synapomorphies; plesiomorphies shared by two or more taxa are sometimes referred to symplesiomorphies.

[7] Parallelism in this context is not to be confused with the evolution of species (or characters within species) "in parallel," that is, when two species (or characters) change more or less together over time. Host-parasite coevolution is an example of "evolution in parallel."

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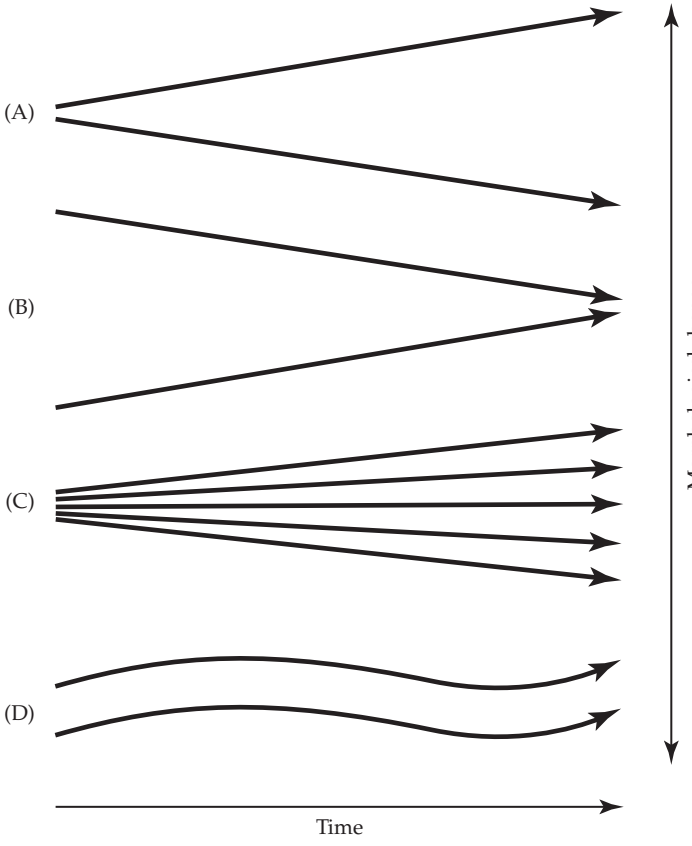

FIGURE 2.5 Common patterns of evolution displayed by independent lineages. (A) Divergence occurs when two or more lineages (or characters) evolve independently to become less similar. (B) Convergence occurs when two or more lineages (or characters) evolve independently toward a similar state. Convergence generally refers to very distantly related taxa and to characters sharing no common genetic (phylogenetic or ontogenetic) basis. (C) Radiations occur when a species gives rise to more than two descendant lineages. (D) Parallel evolution occurs when two or more species (or lineages) change similarly so that, despite evolutionary activity, they remain similar in some ways. Parallelism generally refers to closely related taxa, usually species, within which the characters or structures in question share a common genetic basis.

recognize convergences (and parallelisms) among different groups of organisms has led to the creation of "unnatural," or polyphyletic, taxa in the past (Figure 2.3). For example, the intracellular parasites known as Myxozoa were long thought to be protists, but they have recently been shown to be highly specialized parasitic cnidarians. These and some other groups (e.g., yeasts) mistakenly classified among the Protista made protists a polyphyletic group; removal of those nonprotistan taxa has left the Protista a paraphyletic group (a natural group, with a single origin, but from which animals, plants and fungi, which are nested within, are excluded). Parallelism is commonly encountered in characters of morphological "reduction," such as reduction in the number of segments, spines, fin rays, and so on or in the loss of vision and pigmentation in many different kinds of animals.

Another phenomenon complicating phylogenetic inference is **evolutionary reversal**, wherein a feature reverts back to a previous, ancestral condition. Together, these three evolutionary processes (convergence, parallelism, reversal) constitute the phenomenon known as **homoplasy**—the recurrence of similarity in evolution (Figure 2.5). As you might guess, for systematists, homoplasy can be both fascinating and frustrating!

When comparing homologues among species, one quickly sees that variation in the expression of a character is the rule, rather than the exception. A character may have only two contrasting character states, or it may have several different states. A simple example is hair color in humans; black, brown, red, and blond are all discrete states of the character "hair color" (to make things more complicated, we could treat the character as a "continuous character," with an infinite number of states reflecting all possible colors from white to black). Not only can characters vary within a species, they also typically have several states among groups of species within higher taxa, such as patterns of body hair among various primates or the spine patterns on the legs of crustaceans.

It is important to understand that what we designate a "character" is really a hypothesis that the attributes that appear different in different organisms are simply alternative states of the same feature (i.e., they are homologues). Note that convergences are not homologies, whereas parallelisms and reversals do represent an underlying genetic homology. In other words, some kinds of homoplastic characters are homologues, and others are not. The recognition and selection of proper characters is clearly of primary importance in systematics and phylogenetics, and a great deal has been written on this subject. Systematics is, to a great extent, a search for the homologues that define natural evolutionary lineages. Most recently, great efforts have been made to define homologous gene sequences that can serve as reliable characters to infer relationships among species.

Constructing Phylogenies

Our classifications will come to be, as far as they can be so made, genealogies.

Charles Darwin, *The Origin of Species*, 1859

From what you have read so far in this chapter, it should be evident that comparative biologists, particularly systematists, spend a great deal of their time seeking to identify and unambiguously define two natural entities: homologous characters and monophyletic groups (i.e., clades). Biologists may present their ideas on such matters of relationship in the form of trees, classifications, or narrative discussions (evolutionary scenarios). In all three contexts, these presentations represent sets of evolutionary hypotheses—hypotheses of common ancestry (or ancestor-descendant relationships).

Patterns of relatedness are usually displayed by biologists in branching diagrams called trees, and these are the least ambiguous (most testable) way to present evolutionary hypotheses, although it is now recognized that for some organisms networks may be better representations of relationships than trees, especially in organisms with rampant genome recombination. Once constructed, such trees can then be converted into classification schemes, which are dynamic ways of representing our understanding of the history of life on Earth. Thus, trees and classifications are actually hypotheses of the evolution of life and the natural order it has created. Although classification schemes are ultimately derived from phylogenetic trees, they do not always reflect precisely the arrangement of natural groups in the trees. Discrepancies between phylogenetic trees and classifications derived from them most commonly occur when biologists choose to establish or recognize paraphyletic taxa. Thus, to recognize the protists as a distinct taxon (the kingdom Protista) would be to recognize a paraphyletic group (because it excludes three large lineages that descended from it—animals, plants, and fungi). Whereas most systematists advocate that only monophyletic taxa be recognized in a formal classification, many paraphyletic taxa persist in animal classification, for convenience or tradition or because they are simply not yet known to be paraphyletic (there are probably thousands of taxa for which we do not yet know whether they are monophyletic or paraphyletic). For example, the long-recognized group Reptilia is paraphyletic because it excludes one of that group's most distinct lineages, the birds. The subphylum Crustacea is paraphyletic because it omits the Hexapoda (insects and their kin), which evolved from within the crustaceans long ago. And, of course, the group "Invertebrata" is a paraphyletic group—it is Metazoa excluding the vertebrates. Even Prokaryota is a paraphyletic group (the Eukaryota evolved out of it). In fact, taxonomic groups at all levels are likely to have been derived from within other taxonomic groups, leaving the latter paraphyletic, and we are beginning to discover that paraphyly abounds in the Linnean hierarchy of life that has been built over the past centuries. The issue of how to deal with such long-standing, well-known paraphyletic taxa in classification schemes is still being debated. One way of doing this might be to indicate their paraphyletic status by a code in the classification scheme (e.g., some type of notation beside the name). This code would inform readers that to view the precise phylogenetic relationships of such taxa, they must look to the phylogenetic tree.

Biologists today use a method known as **phylogenetic systematics** (or **cladistics**) when inferring patterns of evolutionary relationships. Phylogenetic systematics had its origin in 1950 in a book by the German biologist Willi Hennig; the English translation (with revisions) appeared in 1966. Its popularity has grown steadily since that time. Through the years, **phylogenetic systematics** has evolved well beyond the framework Hennig originally proposed. Its detailed methodology has been formalized and expanded and will certainly continue to be elaborated for some time to come. The goal of phylogenetic systematics is to produce explicit and testable hypotheses of genealogical relationships among monophyletic groups of organisms. As a systematic methodology, it is based entirely on recency of common descent (i.e., genealogy). The trees used by phylogenetic systematists are constructed to depict only genealogy, or ancestor-descendant relationships. The term **cladogenesis** refers to splitting; in the case of biology, this means the splitting of one species (or one lineage) into two or more species (or lineages). It is this splitting process that produces genealogical (ancestor-descendant) relationships.

Phylogenetic inference can be a time-consuming process. The number of mathematically possible trees (of all branching patterns) for more than a few species is enormous—for three taxa there are only four possible rooted trees, but for ten taxa there are 34 million possible rooted trees. Needless to say, such analyses are not possible without the aid of computers. Algorithms for computer-assisted tree construction began appearing in the late 1970s, and today the development of such programs comprises an entire field of research.

Phylogenetic systematists generally use either the principle of parsimony[8] or maximum likelihood to select the optimal tree from among the set of all possible trees and thus select the tree with the fewest evolutionary transformations (character state changes) or with an optimized likelihood score. The use of gene sequence

[8]Parsimony is a method of logic in which economy in reasoning is sought. The principle of parsimony, also known as Ockham's razor, has strong support in science. William of Ockham (Occam), the fourteenth-century English philosopher, stated the principle as "plurality must not be posited without necessity." A modern rendering would read, "An explanation of the facts should be no more complicated than necessary" or "Among competing hypotheses, favor the simplest one." Scientists in all disciplines follow this rule daily, and it can be viewed as a consequence of deeper principles that are supported by statistical inferences. Thus, parsimonious solutions or hypotheses are those that explain the data in the simplest way. Evolutionary biologists rely on the principle of logical parsimony for the same reason other scientific disciplines rely on it: doing so presumes the fewest ad hoc assumptions and produces the most testable (i.e., the most easily falsified) hypotheses. If evidential support favored only one hypothesis, we would have little need for parsimony as a method. The reason we must rely on parsimony in science is that there is virtually always more than one hypothesis that can explain our data. Parsimony considerations come into play most strongly when a choice must be made among equally supported hypotheses.

In phylogenetic reconstruction, any given data set can be explained by a great number of possible trees. A three-taxon data set has 3 possible dichotomous (all lines divide into just two branches) trees that explain it. A four-taxon data set has 15 possible dichotomous trees, a five-taxon data set has 105 possible dichotomous trees, and so on. Thus, the evidence alone does not sufficiently narrow the class of admissible hypotheses, and some extra-evidential criterion (parsimony) is required. Again, the virtue of choosing the shortest (i.e., most parsimonious) tree among a universe of possible trees—the one that requires the fewest character transformations—lies in its testability. William of Ockham, by the way, also denied the existence of universals except in the minds of humans and in language. This notion resulted in a charge of heresy from the Roman Catholic Church, after which he fled and, alas, died of the plague.

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data has spawned a new family of model-based methods that incorporate hypotheses of nucleotide evolution (see Footnote 5). In these methods (i.e., maximum likelihood, distance methods, and Bayesian analyses), DNA nucleotide (or protein) sequences from organisms in the study group are analyzed within a framework of assumptions based on our understanding of how nucleotides (or amino acids) operate and change over time.

By identifying the precise points at which apomorphies occur, phylogenetic trees unambiguously define monophyletic lineages. Hence, these trees are **explicit phylogenetic hypotheses**. Being explicit, they can be tested (and potentially falsified) by anyone. Apomorphies are markers that identify specific places in the tree where new monophyletic taxa arise. For phylogenetic systematists, a phylogeny consists of a genealogical branching pattern expressed as a phylogenetic tree. Each split or dichotomy within the tree produces a pair of newly derived taxa called **sister taxa**, or sister groups (e.g., "sister species"). Sister groups always share an immediate common ancestor. In Figures 2.1 and 2.2, A is the sister group of B + C; D is the sister of E + F; and A + B + C is the sister group of D + E + F.

All of the trees in Figures 2.1 and 2.2 are fully dichotomous. That is, only two branches emerge from each internal node. Sometimes, trees include a **polytomy**, when more than two branches emerge from a node. Polytomies (or multifurcations) can have several different meanings. In this textbook (and most commonly in the literature) polytomies represent uncertainty about the precise evolutionary relationships among the members; it is unclear who is the exact sister group of whom. For example, we are uncertain about whether Porifera or Ctenophora is the sister group to all other animals, and in Figure 28.1 we represent this uncertainty as a polytomy at the base of the tree of Metazoa.

Like all scientific hypotheses, phylogenetic analyses and their resulting trees are tested by the discovery of new data. As new characters or new species are identified and their character states elucidated, new data matrices are developed, and new analyses are undertaken. The first molecular phylogenetic trees were based on a single gene fragment. But as techniques improved, these trees were tested with multiple gene sets and, eventually, with entire genomic data sets. Hypotheses (branches of the tree) that consistently resist refutation are said to be highly corroborated. For example, the clade called Arthropoda has been examined in thousands of analyses using a great variety of data, and it has consistently been shown to constitute a monophyletic group (i.e., it is a highly corroborated phylogenetic hypothesis).

Biological Classification

And you see that every time I made a further division, up came more boxes based on these divisions until I had a huge pyramid of boxes. Finally you see that while I was splitting the cycle up into finer and finer pieces, I was also building a structure. This structure of concepts is formally called a hierarchy and since ancient times has been a basic structure for all Western knowledge.

Robert M. Pirsig
Zen and the Art of Motorcycle Maintenance, 1974

Classifications are necessary for several reasons, not the least of which is to efficiently catalog the enormous number of species of organisms on Earth. Nearly 2 million species of prokaryotes and eukaryotes have been named and described (and a great many more remain undescribed). The insects alone comprise nearly a million named species, and over 380,000 of those are beetles! Classifications provide a detailed system for storage and retrieval of these names. The second, and most important, reason to evolutionary biologists is that classifications serve a descriptive function. This function is served not only by the descriptions that define each taxon, but also, as noted earlier, by the detailed hypotheses of evolutionary relationships among the organisms that inhabit Earth. In other words, classifications are (or should be) constructed from evolutionary relationships and capture the patterns of ancestry and descent depicted in phylogenetic trees.

The construction of a classification may at first appear straightforward. Specimens are grouped into species; related species are grouped into genera (sing., genus); related genera are grouped into families; and so forth. The grouping process creates a system of subordinated, or nested, taxa arranged in a hierarchical fashion following basic set theory (Figure 2.6). If the taxa are properly grouped, following the pattern in a phylogenetic tree (i.e., on the basis of shared derived characteristics), the hierarchy will reflect patterns of evolutionary descent. These hierarchical categories (or ranks) are commonly used for the biological classification of animals:

Kingdom
Phylum
Class
Cohort
Order
Family
Tribe
Genus
Species

Thus, the common eastern Pacific sea star *Pisaster giganteus* is classified as follows:

Category	**Taxon**
Phylum	Echinodermata
Subphylum	Asterozoa
Class	Asteroidea
Order	Forcipulatida
Family	Asteriidae
Genus	*Pisaster*
Species	*Pisaster giganteus*

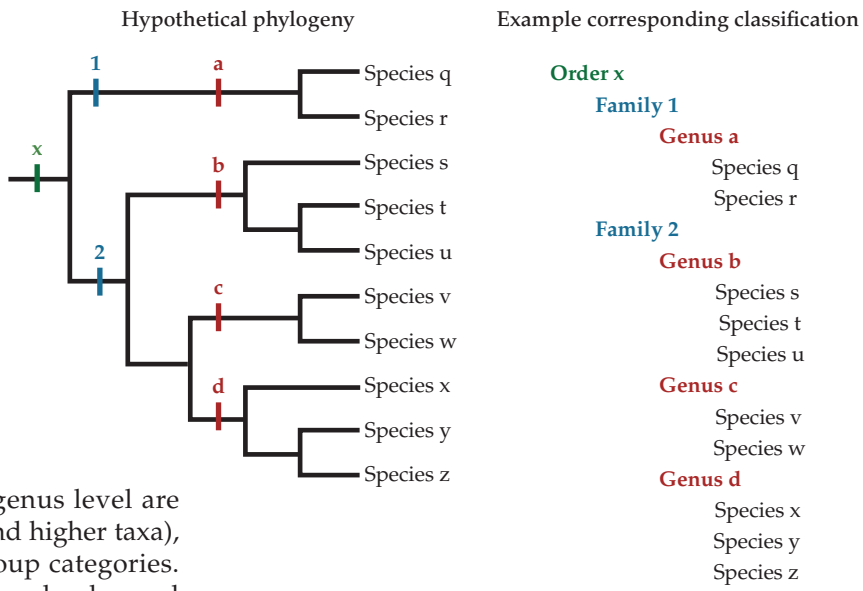

FIGURE 2.6. Phylogenies and classifications. In this phylogeny (left) ten species occur in four possible monophyletic groups (a, b, c, d), but note that b and d could be further subdivided. These four lineages, in turn, derive from two monophyletic groups (1, 2), which in turn derive from a single common ancestor (X). The classification (right) depicts one potential classification that reflects these relationships.

All categories (and taxa) above the genus level are referred to as the higher categories (and higher taxa), as distinguished from the species group categories. Taxonomic ranks may have super-, and sub-, and infracategories as well, for example, superorder, suborder, infraorder.

Converting a phylogeny into a biological classification is not always straightforward. Molecular phylogenetics, in particular, has greatly added to our understanding of animal evolution, and it is also allowing us to generate large and highly detailed phylogenetic trees, with long branching patterns depicting the history of life on Earth (e.g., Figure 2.7). Such detail creates challenges for biologists who like to produce classifications that accurately reflect phylogeny, because the traditional Linnean hierarchical ranks are too few in number to capture the great depth and detail of these trees. Many of the new multigene or genomic trees have scores of branching points, or even hundreds of branches that appear as long comblike topologies. But the standard Linnean ranks number only nine or ten, or about four times that, at best, when the prefixes super-, sub-, and infra- are also used.

There are a few solutions to this dilemma, but none of them is perfect (Figure 2.8). The most straightforward solution is to not use ranks at all in the classification, instead just indenting the subordinated groups in ways that reflect the phylogeny—an **unranked classification** (Figure 2.8, classification scheme B). Another solution is the phylogenetic sequencing convention, described previously. A third solution (and probably still the most frequently seen) is to create classifications that *do not* precisely mirror the phylogeny, referring readers to the tree if they want to understand the precise relationships of the taxa in a classification. Unranked classifications are useful when the phylogeny of a group is still quite poorly known (e.g., Chapters 15, Annelida, and 13, Mollusca). Fully ranked classifications can get cumbersome when "pushed to the limit" of available taxonomic categories (e.g., Chapter 17, Platyhelminthes). The upshot is, things are changing and the "traditional" classification schemes of the twentieth century are beginning to look rather different these days. In this book, we mostly use ranked classifications that mirror, or at least do not conflict with, the phylogeny of the groups in question. In a few instances, we have had to use fully or partly unranked classifications (e.g., annelids and molluscs).

Further confusion is added when names that have been used for many decades are difficult to discard. Some of these **legacy names** have been redefined to represent monophyletic groups, or clades, such as Protostomia and Deuterostomia. Others, however, are now known to represent nonmonophyletic groups, yet the names have not yet disappeared from textbooks and the scientific literature; for example, the gastropod group "heteropods" (which is a polyphyletic group of pelagic gastropods with laterally compressed translucent bodies and reduced or lost shells), and the arthropod group Crustacea (a paraphyletic group). In this book, as a general rule we recognize only monophyletic groups, and we point out the few instances where we make exceptions.

FIGURE 2.7 This phylogenetic tree of hexapod relationships (Misof et al. 2014) illustrates the challenges of converting large molecular-based phylogenies into classifications. The tree includes over 130 hexapod nodes. In order to erect a classification based on this tree, decisions must be made as to which nodes (clades) to name, whether or not to limit the named clades to the 30 or so traditional Linnean ranks or use unranked names, and whether to make the classification perfectly match the phylogeny. To see one way of dealing with these classification issues, see Chapter 22 (Hexapoda). Note that the seven members of Crustacea included in the analysis are shown to be a paraphyletic cluster at the base of the hexapod clade (i.e., "Crustacea" is a paraphyletic grouping; Chapter 21) and that the sister group of Hexapoda is the crustacean clade Remipedia. Note also that this is a dated phylogeny (the time scale, in millions of years, is shown at the top and bottom of the figure). (From B. Misof et al. 2014. *Science* 346: 763–767. Reprinted with permission from AAAS.)

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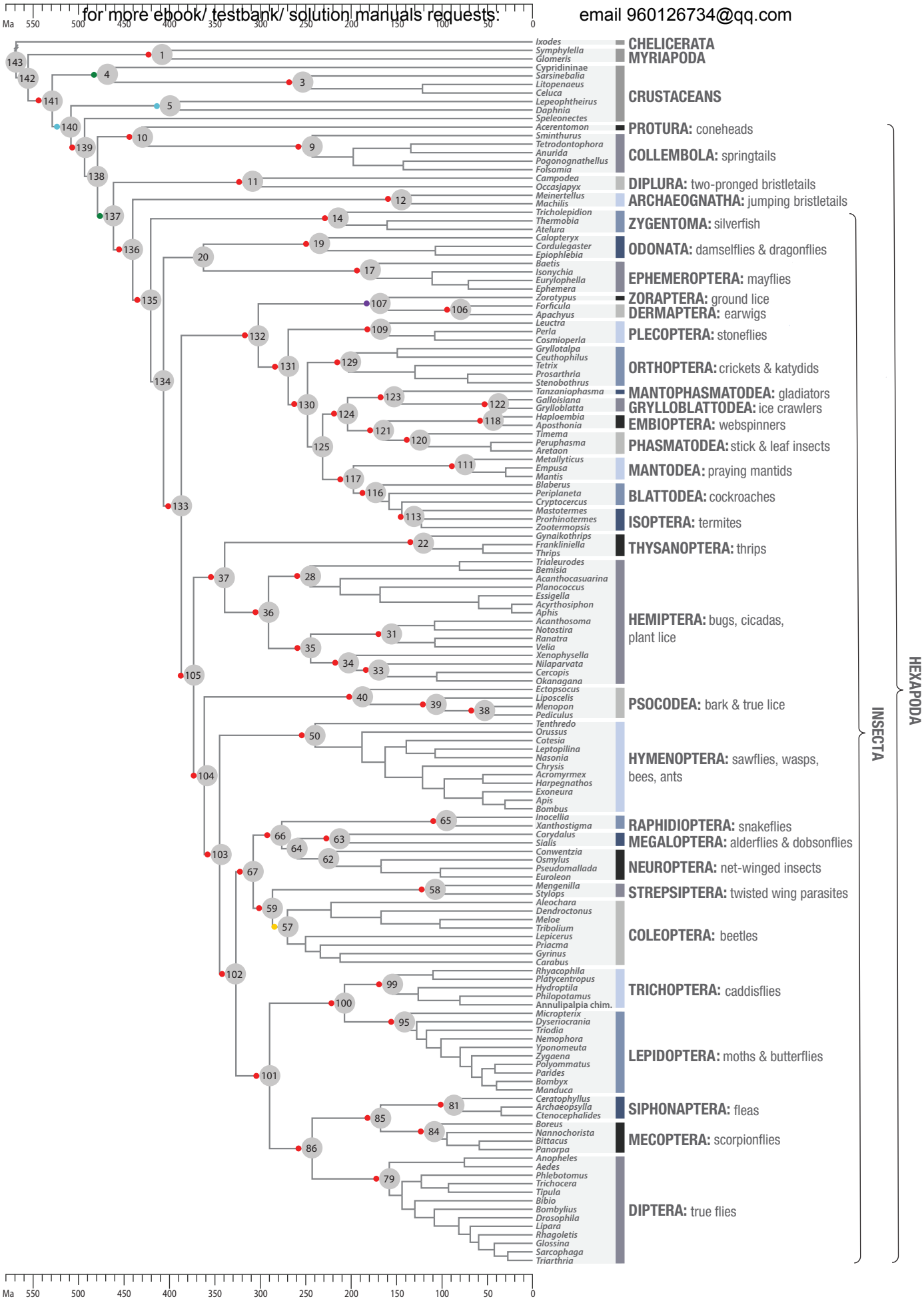

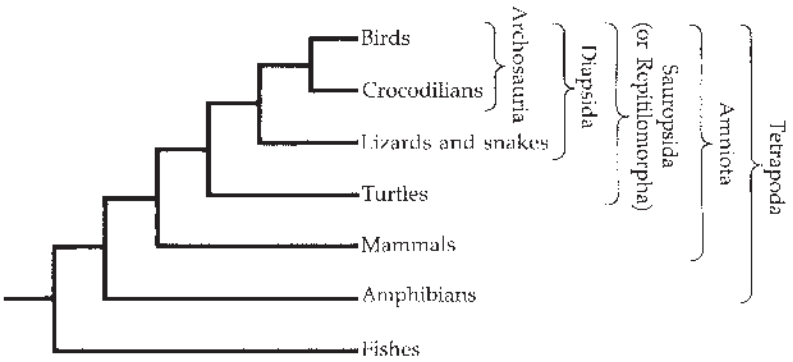

Classification scheme A

Phylum Chordata
- Subphylum Vertebrata
  - Class Pisces (fishes)
  - Class Amphibia (amphibians)
  - Class Reptilia (turtles, crocodilians, snakes, lizards)
  - Class Aves (birds)
  - Class Mammalia (mammals)

Classification scheme B

Phylum Chordata
- Vertebrata
  - Tetrapoda
    - Lissamphibia (amphibians)
    - Amniota
      - Mammalia (mammals)
      - Sauropsida (Reptiliomorpha)
        - Anapsida (turtles)
        - Diapsida
          - Lepidosauria (snakes, lizards)
          - Archosauria
            - Crocodilia (crocodilians)
            - Aves (birds)

FIGURE 2.8. Converting a tree into a classification scheme. Vertebrates offer a well-known example of how different a phylogenetic classification may look from a traditional classification. The tree in this figure depicts a popular view of relationships among the major groups of living vertebrates. Classification scheme A depicts a traditional classification of the vertebrates, still seen in many books, in which crocodilians are classified with lizards, snakes, and turtles in the taxon Reptilia, while birds are retained as a separate taxon, Aves. In this classification, the class Reptilia is paraphyletic (because it excludes the birds). Classification scheme B strictly reflects the phylogenetic tree, mirroring the branching pattern with subordinated taxa (unranked in this case); thus, the reptiles are broken into separate taxa in recognition of their genealogical relationships—the snakes and lizards (Lepidosauria) are classified together as a separate sister group to Archosauria (crocodilians and birds).

Nomenclature

The names employed within classifications are governed by rules and recommendations that are analogous to the rules of grammar that govern European languages. The most fundamental goals of **biological nomenclature** are the creation of classifications in which (1) any single kind of organism has one and only one correct name, and (2) no two kinds of organisms bear the same name. All of the codes of nomenclature for the various groups of life address these two fundamental requirements. Nomenclature is an important tool of biologists that facilitates communication and stability.[9]

Prior to the mid-1700s, animal and plant names consisted of one to several words or often simply a descriptive phrase. In 1735, at the age of just 28, the great Swedish naturalist Carl von Linné (Carolus Linnaeus, in the Latinized form he preferred) established a system of naming organisms now referred to as **binomial nomenclature**. Linnaeus's system required that every organism have a two-part scientific name, that is, be a **binomen**. The two parts of a binomen are the generic, or genus, name and the specific name, or specific epithet. For example, the scientific name for one of the common Pacific coast sea stars is *Pisaster giganteus*. These two names together constitute the binomen; *Pisaster* is the animal's generic (genus) name, and *giganteus* is its **specific epithet**. The specific epithet is never used alone, but must be preceded by the generic name, and the animal's "species name" is thus the complete binomen. Use of the first letter of a genus name preceding the specific epithet is also acceptable once the name has appeared spelled out on the page or in a short article (e.g., *P. giganteus*).

The 1758 version of Linnaeus's system was the tenth edition of his famous *Systema Naturae*, in which he listed all animals known to him at that time and included critical guidelines for classifying organisms. Linnaeus distinguished and named over 4,400 species of animals, including *Homo sapiens*. Linnaeus's *Species Plantarum* (in which he named over 8,000 species) did the same for the plants in 1753. Linnaeus was one of the first naturalists to emphasize the use of similarities among species (or among other taxa) in constructing a classification, rather than the use of differences between them. In doing so, he unknowingly began classifying organisms by virtue of their genetic, and hence evolutionary, relatedness. Linnaeus produced

[9] We generally avoid using common, or vernacular, names in this book, simply because they are frequently misleading. Most invertebrates have no specific common name, and those that do typically have more than one name. For example, several dozen different species of sea slugs are known as "Spanish dancers." All manner of creatures are called "bugs," most of which are not true bugs (Hemiptera) at all, for example, "ladybugs," "sowbugs," "potato bugs," and so on. Recently, there has been a movement to codify common names, in an attempt to establish a single preferred vernacular for any given species. This movement is taking place mainly among vertebrate specialists, and there is, as yet, no widely accepted initiative to do this for invertebrates.

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his *Systema Naturae* 100 years prior to the appearance of Darwin and Wallace's theory of evolution by means of natural selection (1859), and thus his use of similarities in classification foreshadowed the subsequent emphasis by biologists on evolutionary relationships among taxa. Linnaeus was granted nobility in 1761 (and became Carl von Linné); he died in 1778.

Binomens are Latin (or Latinized) because of the custom followed in Europe prior to the eighteenth century of publishing scientific papers in Latin, the universal language of the educated people of the time. For several decades after Linnaeus, names for animals and plants proliferated, and there were often several names for any given species (different names for the same species are called **synonyms**). The name in common use was usually the most descriptive one, or often it was simply the one used by the preeminent authority of the time. In addition, some generic names and specific epithets were composed of more than one word each. This lack of nomenclatural uniformity led, in 1842, to the adoption of a code of rules formulated under the auspices of the British Association for the Advancement of Science, called the Strickland code. In 1901 the newly formed International Commission on Zoological Nomenclature adopted a revised version of the Strickland code, called the **International Code of Zoological Nomenclature** (**ICZN**). Botanists had adopted a similar code for plants in 1813, the *Théorie Élémentaire de la Botanique*, which became in 1930 the International Code of Botanical Nomenclature (there is also a separate but complementary code for cultivated plants). Since then, it has been revised as the International Code of Nomenclature for Algae, Fungi, and Plants. There is also an International Code of Nomenclature of Bacteria.

The ICZN established January 1, 1758 (the year the tenth edition of Linnaeus's *Systema Naturae* appeared), as the starting date for modern zoological nomenclature. Any names published the same year, or in subsequent years, are regarded as having appeared after the *Systema*. The ICZN also slightly changed the description of Linnaeus's naming system, from binomial nomenclature (names of two parts) to **binominal nomenclature** (names of two names). However, one still sees the former designation in common use. This subtle change implies that the system must be truly binary; that is, both genus and species epithet names can be only one word each. Although the system is binary, it also accepts the use of subspecies names, creating a **trinomen** (three names) within which is contained the mandatory binomen. For example, the sea star *Pisaster giganteus* is known to have a distinct form occurring in the southern part of its range, which is designated as a subspecies, *Pisaster giganteus capitatus*. All codes of biological nomenclature share the following five basic principles:

1. Botanical, bacterial, and zoological codes are independent of each other. It is therefore permissible, although not recommended, for a plant genus and an animal genus to bear the same name (e.g., *Aotus* is the generic name of both golden peas and night monkeys).
2. A taxon can bear one and only one correct name.
3. No two genera within a given code can bear the same name (i.e., generic names are unique), and no two species within one genus can bear the same name (i.e., binomens are unique).
4. The correct or valid name of a taxon is based on priority of publication (first usage), with a few exceptions for very old names that have not been in use for a long period of time.
5. For the categories of superfamily in animals and order in plants, and for all categories below these, taxon names must be based on type specimens, type species, or type genera.[10]

When strict application of a code results in confusion or ambiguity, problems are referred to the appropriate commission for a "legal" decision. Rulings of the International Commission on Zoological Nomenclature are published regularly in its journal, the *Bulletin of Zoological Nomenclature*. Note that the international commissions rule only on nomenclature or "legal" matters, not on questions of scientific or biological interpretation; these latter problems are the business of systematists. Obviously, the correct name of a species (and any future changes in that name) has great importance to all fields of biology (e.g., ecology, conservation biology, physiology) and also in the field of law, where many environmental decisions are made today, because scientists (and governments) must know the correct names of their study organisms in order to communicate about them.

Names given to animals and plants are usually descriptive in some way, or perhaps indicative of the geographic area in which the species occurs. Others are named in honor of persons for one reason or another. Occasionally one runs across purely whimsical names, or even names that seem to have been formulated for seemingly diabolical reasons.[11]

The **biological species definition** (or genetic species concept), as codified by Ernst Mayr, defines species as groups of interbreeding (or potentially interbreeding)

[10]When a systematist first names and describes a new species, she or he takes a "typical" or representative individual, declares it a type specimen, and deposits it in a safe repository such as a large natural history museum. If later workers are ever uncertain about whether they are working with the same species described by the original author, they can compare their material to the type specimen. Although of substantially less value, the designation of a "typical" or type species for a genus, or a type genus for a family, serves a somewhat similar purpose in establishing, a "typical" species or genus upon which a genus or family is based.

natural populations that are reproductively isolated from other such groups. Obviously, this definition fails to accommodate nonsexual species. George Gaylord Simpson and Edward O. Wiley developed the **evolutionary species concept**, which states that a species is a single lineage of ancestor-descendant populations that maintains its identity separate from other such lineages and that has its own evolutionary tendencies and historical fate. In reality, of course, biologists rely heavily on morphological aspects of organisms and on gene sequence data as surrogates in gauging these conceptual views of species. That is, we conceive of species as genetic or evolutionary entities, but we recognize them primarily by their phenotypic or gene sequence characters. Hence, an understanding of such characters is of great importance; read on.

Higher taxa (categories and taxa above the species level) are natural groups of species (or lineages) chosen by biologists for naming in order to reflect our state of knowledge regarding their evolutionary relationships. Higher taxa, if correctly constructed, represent ancestor-descendant lineages (clades) that, like species, have an origin, a common ancestry and descent, and eventually a death (extinction of the lineage); thus they too are evolutionary units with definable boundaries. There are no rules for how many species should make up a genus—only that it be a natural group. Nor are there rules about how many genera constitute a family, or whether any group of genera should be recognized as a family, or a subfamily, or an order, or any other categorical rank. What matters is simply that the named group (the taxon) be a natural group. Hence, it is incorrect to assume that families of insects are in some way evolutionarily comparable to families of molluscs, or orders of worms comparable to orders of crustaceans. Nor are there any rules about categorical rank and geological or evolutionary age. These aspects of higher taxa are often misunderstood. Interestingly, this being said, family-level taxa often tend to be the most stable taxonomic groupings, usually recognizable even to laypersons—think, for example, of cats (Felidae), dogs (Canidae), abalone (Haliotidae), ladybird beetles (Coccinellidae), mosquitoes (Culicidae), octopuses (Octopodidae), or weevils (Curculionidae). This stability seems to be an artifact of the history of taxonomy, but it nonetheless makes families convenient higher taxa to study and discuss. However, biologists err when they compare equally ranked higher taxa from different groups in ways that presuppose them to be somehow equivalent.

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[11] Among the many clever names given to animals are *Agra vation* (a tropical beetle that was extremely difficult for Dr. Terry Erwin to collect) and *Lightiella serendipida* (a small crustacean; the generic name honors the famous Pacific naturalist S. F. Light, 1886–1947, while the species epithet is taken from "serendipity," a word coined by Walpole in allusion to the tale of "The Three Princes of Serendip," who in their travels were always discovering, by chance or sagacity, things they did not seek—the term is said to aptly describe the circumstances of the initial discovery of this species). There are actually over 500 described species of *Agra* (those carabid beetles known as "elegant canopy beetles"), including *Agra eponine*, named after the street urchin in *Les Miserables* who, in the Broadway version of the story, personified tragic beauty ("such is the state of the tropical forests where these beetles live," according to Dr. Erwin, who also named this species). Another of Erwin's names is *Agra ichabod*, referring to the fact that the holotype is missing its head, the allusion referring to the frightened schoolteacher Ichabod Crane's phantom nemesis, the Headless Horseman, in "The Legend of Sleepy Hollow." The nineteenth-century British naturalist W. E. Leach erected numerous genera of isopod crustaceans whose spellings were anagrams of the name Caroline. Exactly who Caroline was (and the nature of her relationship with Professor Leach) is still being debated, but the prevailing theory implicates Caroline of Brunswick, who was in the public eye at this time in history. It is said that Caroline was badly treated by her husband (the Prince Regent, later George IV) and that she was herself a lady of questionable fidelity. Leach, from Devon, may have taken the side of support for Caroline by honoring her with a long series of generic names, including *Cirolana*, *Lanocira*, *Rocinela*, *Nerocila*, *Anilocra*, *Conilera*, *Olincera*, and others.

A light-hearted attitude toward naming organisms has not always been without Freudian overtones, as there also exist *Thetys vagina* (a large, hollow, tubular pelagic salp), *Succinea vaginacontorta* (a hermaphroditic snail whose vagina twists in corkscrew fashion), *Phallus impudicus* (a slime-covered mushroom), and *Amanita phalloides* and *Amanita vaginata* (two species of highly toxic mushrooms around which numerous Indigenous ceremonies and legends exist). *Humbert humberti* is a wasp named after Vladimir Nabokov's Humbert Humbert, the narrator in the great novel *Lolita* who was obsessed with his 12-year old, soon-to-be stepdaughter. *Crepidula fornicata* is a hermaphroditic slipper shell (gastropod) that forms stacks of alternating male- and female-functioning individuals (males on top turn into females as they grow). Injecting a lyrical dose of sexual innuendo into taxonomy is not new. Linnaeus himself incorporated a few good zingers into his writings and, in fact, drew parallels between plant sexuality and human love. In 1729 he wrote of flower petals, "[These] serve as bridal beds which the Creator has so gloriously arranged, adorned with such noble bed curtains, and perfumed with so many soft scents, that the bridegroom with his bride might there celebrate their nuptials with so much the greater solemnity." Such sexually explicit writing (in the early eighteenth century) did not go uncriticized, and Linnaeus had his detractors. The German botanist Johann Siegesbeck (a Demonstrator at the Botanical Garden at St. Petersburg) called it "loathsome harlotry" and commented, "Who would have thought that bluebells, lilies, and onions could be up to such immorality?" Linnaeus had his revenge, however, when he named a small, ugly, foul-smelling, mud-inhabiting European weed (St. Paul's wort) *Siegesbeckia*.

Other fun names include *Upupa epops*, euphoniously named for the call of the hoopoe (a bird), and the fish *Zappa confluentus*, which was named by a fan of Frank Zappa. The Grateful Dead have a fly named in their honor (*Dicrotendipes thanatogratus*). And there is the vampire squid *Vampyroteuthis infernalis* (the "vampire squid from hell"), a bivalve named *Abra cadabra*, a blood-sucking spider *Draculoides bramstokeri*, and a wasp *Aha ha*. Even Linnaeus created a curious name for a common ameba, *Chaos chaos*. And, in a stroke of whimsy, the entomologist G. W. Kirkaldy created the bug genera *Polychisme* ("Polly kiss me"), *Peggichisme*, *Marichisme*, *Dolychisme*, and *Florichisme*. There are fish genera named *Zeus*, *Satan*, *Zen*, *Batman*, and *Sayonara*. There are insect genera named *Cinderella*, *Aloha*, *Oops*, and *Euphoria*; the siboglinid genus *Bobmarleya*; and a lucinid clam with a periostracum looking like dreadlocks named *Rasta*. The spider genus *Orsonwelles* contains such species as *O. macbeth* and *O. othello*. Some other clever binomens include *Leonardo davincii* (a moth), *Phthiria relativitae* (a fly), and *Ba humbugi* (a snail). A few biologists have gone overboard in erecting names for new animals, and many binomens exceed 30 letters in length, including *Strongylocentrotus droebachiensis* (32 letters), for the common North Pacific sea urchin, and *Lagenivaginopseudobenedenia*, a 27-letter genus name for a group of monogenean flukes.

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Chapter Summary

In this chapter we have introduced you to the field of systematics, the oldest and most foundational field among the biological sciences. The main goal of systematists is to describe and organize the many forms of life in evolutionarily meaningful ways, whether those genetic linkages are depicted as a branching diagram (or phylogenetic tree) or a nested list (classification). This task would be straightforward if we knew how all species were related to one another. But since we do not know for certain what Darwin's "great Tree of Life" looks like, we must infer the shape of the tree through phylogenetic inference. In recent years, the field of molecular phylogenetics has revealed a great deal about how species are related to one another, but much more remains to be accomplished.

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CHAPTER 3

Introduction to the Animal Kingdom

Animal Architecture and Body Plans

Animal bodies are marvelous things—so complex, yet so consistent and true to form within a species. All the parts seem to work together in perfect harmony, like the architecture of a beautiful building, which is how it should be after millions of years of evolutionary fine-tuning. This chapter is about the architecture of animals. The German language includes a wonderful word that expresses the essence of animal architecture—*bauplan* (pl. *baupläne*). The word means, literally, "a structural plan or design," but a direct translation is not entirely adequate. The concept of a *bauplan* captures in a single word the essence of structural range and architectural limits, as well as the functional aspects of a design. The term "body plan" is a close English equivalent. If an organism is to "work," all of its body components must be both structurally and functionally compatible. The entire organism encompasses a definable body plan, and the specific organ systems themselves also encompass structural plans; in both cases the structural and functional components of the particular plan establish both capabilities and limits.

The diversity of form in the biological world is dazzling, yet there are real limits to what may be successfully molded by evolutionary processes. All animals must accomplish certain basic tasks in order to survive and reproduce. They must acquire, digest, and metabolize food and distribute its usable products throughout their bodies. They must obtain oxygen for cellular respiration, while at the same time ridding themselves of metabolic wastes and undigested materials. The strategies employed by animals to maintain life are extremely varied, but they rest upon relatively few biological, physical, and chemical principles, regardless of what body plan they have. Within the constraints imposed by particular body plans, animals have a limited number of options available to accomplish life's tasks. For this reason, a few recurring fundamental themes are apparent. This chapter is a general review of these themes: the structural/functional aspects of invertebrate body plans and the basic survival strategies employed within each. It is a description of how invertebrates are put together and how they manage to survive and reproduce. Each subject discussed here reflects fundamental principles of animal mechanics, physiology, and adaptation. We realize that much of this chapter presents material that students learn in introductory biology courses, but here we provide specific viewpoints that set the stage for topics covered in more detail in each "animal" chapter of this book.

Keep in mind that even though this chapter is organized on the basis of what might be called the "components" of animal structure, whole animals are integrated functional combinations of these components. Furthermore, there is a strong element of predictability in the concepts discussed in this chapter.

For example, given a particular type of symmetry, one can make reasonable guesses about other aspects of an animal's structure that should be compatible with that symmetry—some combinations work, others do not. Herein are explained many of the concepts and terms used throughout this book, and we encourage you to become familiar with this material now as a basis for understanding the remainder of the text.

Body Symmetry

A fundamental aspect of an animal's body plan is its overall shape or geometry. In order to discuss invertebrate architecture and function, we must first acquaint ourselves with a basic aspect of body form: symmetry. Symmetry refers to the regular arrangement of body structures relative to a particular axis of the body. Animals that can be bisected or split along at least one plane, so that the resulting halves are similar to one another, are said to be symmetrical. For example, a shrimp can be bisected vertically through its midline, head to tail, to produce right and left halves that are mirror images of one another. Some animals have no body axis and no plane of symmetry; these are said to be **asymmetrical**. Many sponges, for example, have an irregular growth form and lack any clear plane of symmetry. Similarly, placozoans, which may depict ameboid forms, are asymmetrical (Figure 3.1).

One form of symmetry is **spherical symmetry**. It is seen in creatures whose bodies lack an axis and have the form more or less of a sphere, with the body parts arranged concentrically around, or radiating from, a central point (Figure 3.2). A sphere has an infinite number of planes of symmetry that pass through its center to divide it into like halves. Spherical symmetry is rare in nature; in the strictest sense, it is found only in certain protists and a few sponges. Organisms with spherical symmetry share an important functional attribute with asymmetrical organisms, in that both groups lack polarity. That is, there exists no clear differentiation along an axis. In all other forms of symmetry, some level of polarity has been achieved; and with polarity comes specialization of body regions and structures.

A body displaying **radial symmetry** has the general form of a cylinder, with one or more main axes around which the various body parts are arranged (Figure 3.3). In a body displaying perfect radial symmetry, the body parts are arranged equally around the axis, and any plane of sectioning that passes along that axis results in similar halves. That is to say, both halves of an animal divided down the middle, along a plane of symmetry, have the same exact structures in the same exact relationship to one another (rather like a cake being divided and subdivided into equal halves and quarters). Nearly perfect radial symmetry is rare in nature but occurs in some sponges and perhaps in some cnidarian polyps

(A)

Courtesy of G. Giribet

(B)

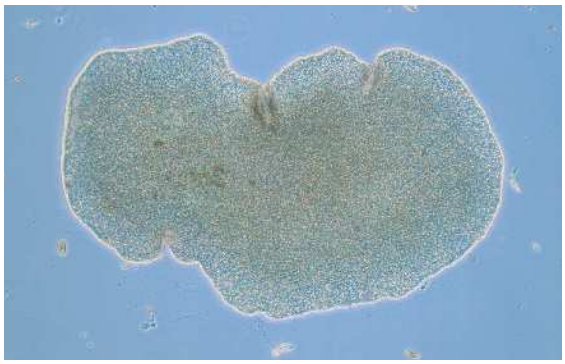

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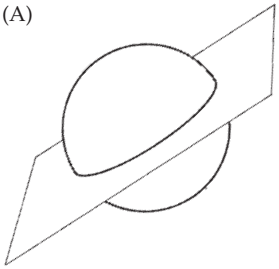
FIGURE 3.1 Examples of asymmetrical animals. (A) A Caribbean shallow water demosponge. (B) A placozoan.

(Figure 3.3A,B). But most radially symmetrical animals have evolved modifications on this theme. **Biradial symmetry**, for example, occurs where portions of the body are specialized and only two planes of sectioning

(A)



(B)

Courtesy of G. Giribet

FIGURE 3.2 Spherical symmetry in animals. (A) An example of spherical symmetry; any plane passing through the center divides the organism into like halves. (B) An undescribed species of a Caribbean sponge in the genus *Tethya*.

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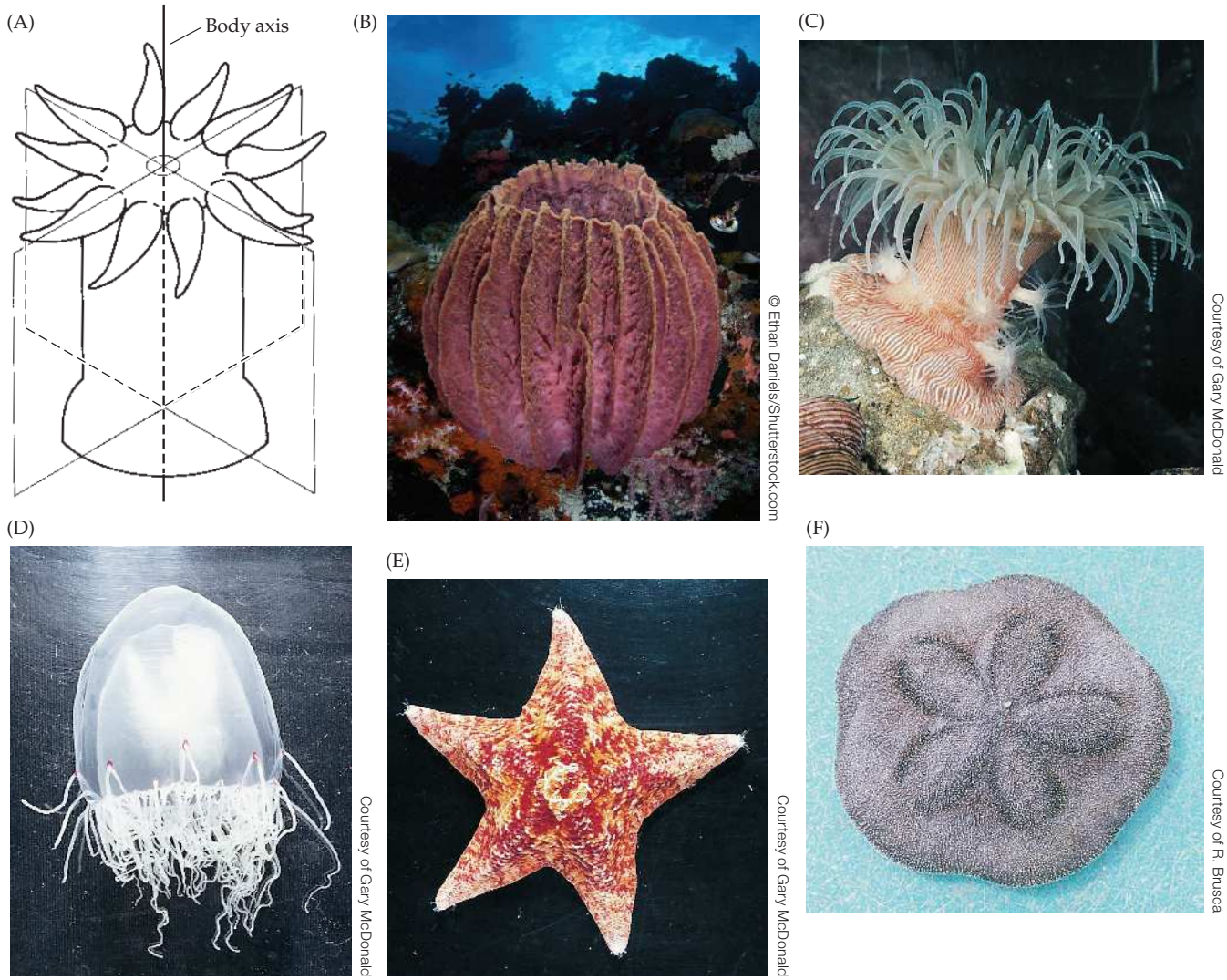

FIGURE 3.3 Radial symmetry in invertebrates. The body parts are arranged radially around a central oral-aboral axis. (A) Graphical representation of perfect radial symmetry. (B) The barrel-like sponge *Xestospongia*. (C) The sea anemone *Epiactis*, whose mouth alignment and internal organization produce biradial symmetry. (D) The hydromedusa *Scrippsia*, with quadriradial symmetry. (E) The starfish *Patiria*, with pentaradial symmetry. (F) The sea biscuit *Clypeaster*, with pentaradial symmetry. (G) In this view of a stylized ctenophore, multiple planes of symmetry can be seen to divide the animal into nearly equal halves, making it multiradial. Some of these are the stomodeal plane, the anal pore plane, and the tentacular plane. Ctenophores also have rotational symmetry, which is defined as a shape that looks precisely the same after some rotation of 180° or less (in this case, a full 180° is required to accomplish this). (G after M. Q. Martindale and J. Q. Henry. 1998. *Amer Zool* 38: 672–684.)

can divide the animal into perfectly similar halves. Common examples of biradial organisms are many sea anemones (Figure 3.3C). Ctenophores have various forms of biradial symmetry, but they can also show a type of rotational symmetry (Figure 3.3G). Rotational symmetry is defined as a shape that looks precisely the same after some rotation of 180° or less. In the case of the generalized ctenophore shown in Figure 3.3G, the animal would be precisely the same after a 180° rotation, giving it rotational symmetry. But other planes of radial symmetry, such as through the gut (stomodeal plane), tentacles (tentacular plane), or anal pores, divide the animal into two halves that have the same exact structures, in the same exact relationship to one another.

Further specializations of a basic radial body plan can produce nearly any combination of multiradiality. For example, many jellyfishes possess **quadriradial symmetry** (Figure 3.3D). Most echinoderms have **pentaradial symmetry** (Figure 3.3E,F), although given the location of the madreporite, this is imperfect, and thus starfish actually possess a form of pentaradial bilaterality. But this is splitting hairs. And many multiarmed starfish are also known.

A radially symmetrical animal has no front or back end; rather it is organized about an axis that passes through the center of its body, like an axle through a wheel. When a gut is present, this axis passes through the mouth-bearing (oral) surface to the opposite (aboral) surface. Radial symmetry is most common in sessile and sedentary animals (e.g., sponges, starfish, and sea anemones) and drifting pelagic species living in three-dimensional environments (e.g., jellyfishes). Given these lifestyles, it is clearly advantageous to be able to confront the environment equally from a variety of directions. In such creatures the feeding structures (tentacles) and sensory receptors are distributed at equal intervals around the periphery of the organism so that they contact the environment more or less equally in all directions. Furthermore, many bilaterally symmetrical animals have become functionally radial in certain ways associated with sessile lifestyles. For example, their feeding structures may be in the form of a whorl of radially arranged tentacles, an arrangement allowing more efficient interactions with the immediate environment.

The body parts of **bilaterally symmetrical** animals are oriented about an axis that passes from the front (anterior) to the rear (posterior) end. A single plane of symmetry—the **midsagittal plane** (or median sagittal plane)—passes along the axis of the body to separate right and left sides. Any longitudinal plane passing perpendicular to the midsagittal plane and separating the upper (dorsal) from the lower (ventral) side is called a **frontal plane** (Figure 3.4). Any plane that cuts across the body perpendicular to the main body

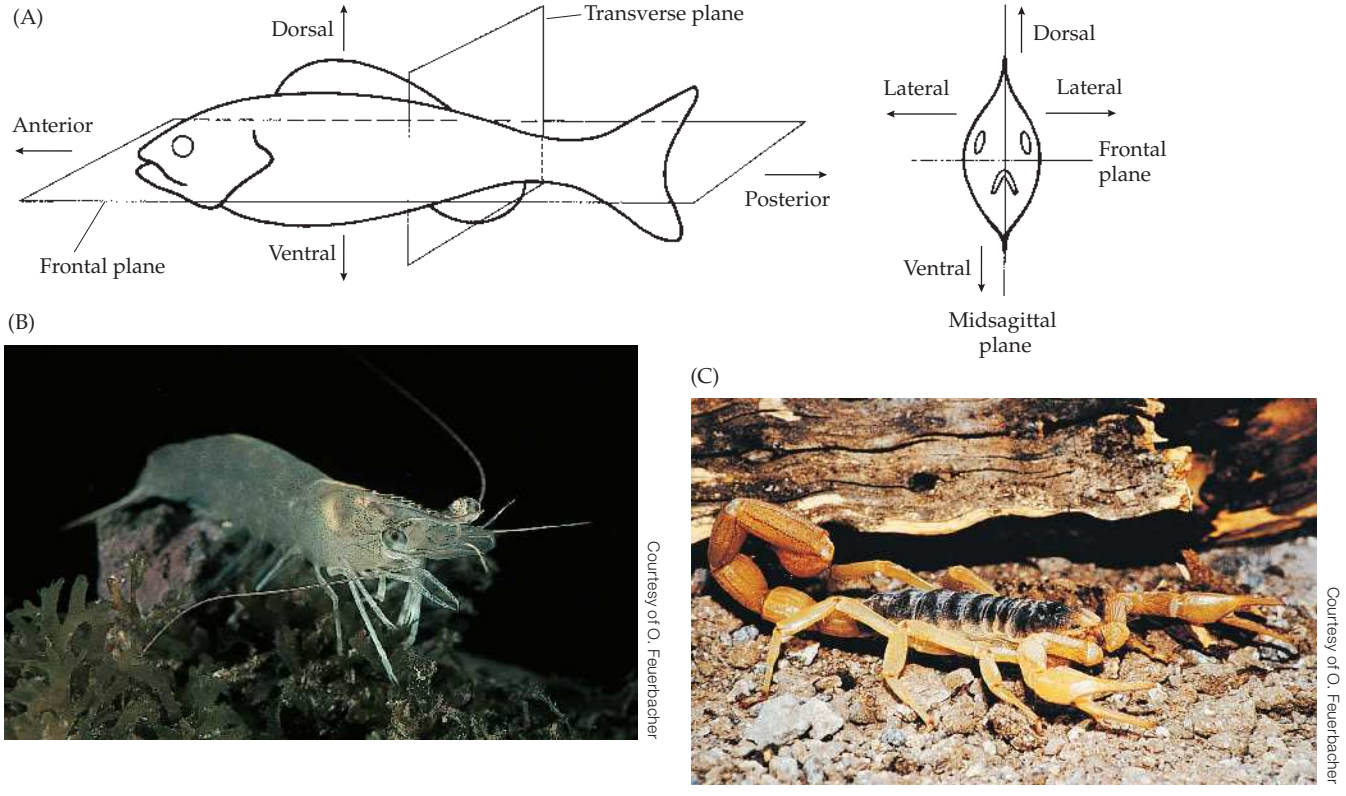

FIGURE 3.4 Bilateral symmetry in animals; a single plane—the midsagittal plane—divides the body into equal halves. (A) Diagrammatic illustration of bilateral symmetry, with terms of orientation and planes of sectioning. A shrimp (B) and a scorpion (C) show obvious bilateral symmetry.

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axis and the midsagittal plane is called a **transverse plane** (or, simply, a cross section). In bilaterally symmetrical animals the term "lateral" refers to the sides of the body, or to structures away from (to the right and left of) the midsagittal plane. The term "medial" refers to the midline of the body, or to structures on, near, or toward the midsagittal plane.

Whereas radial and rotational symmetry are typically associated with sessile or drifting animals, bilaterality is generally found in animals with highly directional mobility. In these animals, the anterior end of the body confronts the environment first. Associated with bilateral symmetry and unidirectional movement is a concentration of feeding and sensory structures at the anterior end of the body. The evolution of a specialized "head," containing those structures and the nervous tissues that innervate them, is called **cephalization** (from the Greek *kephalos*, "head"). Furthermore, the surfaces of the animal differentiate as dorsal and ventral regions, the latter becoming locomotory and the former being specialized for protection. A variety of secondary asymmetrical modifications of bilateral (and radial) symmetry have occurred, for example, the spiral coiling of snails and hermit crabs. Furthermore, many radial animals have become secondarily bilateral, at least for their main body organization, as is the case of sea cucumbers or some irregular sea urchins.

Cellularity, Body Size, Germ Layers, and Body Cavities

One of the main characteristics used to define grades of animal complexity is the presence or absence of true tissues. Tissues are aggregations of morphologically and physiologically similar cells that perform a specific function. Protists do not possess tissues, but occur only as single cells or as simple colonies of cells. In a sense, they are all at a unicellular grade of construction. But beyond protists is the vast array of multicelled animals, the Metazoa. The Metazoa are often divided into two major groups—the non-Bilateria and the Bilateria, as described below. These names may be used to group the Metazoa by their level of overall structural complexity. The nonbilaterians comprise a nonmonophyletic grouping of "primitive" metazoans; bilaterians are almost certainly a monophyletic group, or clade. The non-Bilateria include Porifera, Placozoa, Cnidaria, and Ctenophora. In the last two phyla, embryogenesis produces two distinct germ layers—ectoderm and endoderm—and thus they are referred to as being diploblastic. Among the bilaterians a third embryonic germ layer forms, the mesoderm, and thus the Bilateria are said to be triploblastic. These concepts are elaborated below.

Each of these two grades of body complexity is associated with inherent constraints and capabilities, and within each grade there are obvious limits to size. As the Scottish biologist D'Arcy Thompson wrote, "Everything has its proper size ...men and trees, birds and fishes, stars and star-systems, have... more or less narrow ranges of absolute magnitudes." As a cell (or an organism) increases in size, its volume increases at a rate faster than the rate of increase of its surface area (surface area increases as the square of linear dimensions; volume increases as the cube of linear dimensions). Because a cell ultimately relies on transport of material across its plasma membrane for survival, this disparity quickly reaches a point at which the cytoplasm can no longer be adequately serviced by simple cellular diffusion. Some unicellular protists develop complexly folded surfaces or are flattened or threadlike in shape. Such creatures can be quite large, but eventually a limit is reached; thus we have no meter-long amebas.

To increase in size, ultimately the only way around the **surface-to-volume dilemma** is to increase the number of cells constituting a single organism; hence the Metazoa. But size increase in the Metazoa is also limited. Those Metazoa lacking complex specializations of tissues and organs must rely on diffusion into and out of the body, and this is inadequate to sustain life unless a majority of the body's cells are near or in contact with the external environment. In fact, diffusion is an effective method of oxygenation only when the diffusion path is less than about 1.0 mm. So here, too, there are limits. An animal simply cannot increase indefinitely in volume when most of its cells must lie close to the body surface. Some animals solve this problem to some degree by arranging their cellular material so that diffusion distances from cell to environment are comfortably short. One method of accomplishing this is to pack the internal bulk of the body with nonliving (or largely nonliving) material, such as the jellylike mesoglea of medusae and ctenophores. Another is to assume a body geometry that maximizes the surface area. Increase in one dimension leads to a vermiform body plan, like that of cestid ctenophores (Ctenophora; Figure 6.2E) or ribbon worms (Nemertea). Increase in two dimensions results in a flat, sheetlike body like that of flatworms (Platyhelminthes). In these cases the diffusion distances are kept short. Sponges effectively increase their surface area by a process of complex branching and folding of the body, both internally and externally. This folding keeps most of the body cells close to the environment.

If these were the only solutions to the surface-to-volume dilemma, the natural world would be filled with tiny, thin, flat animals and convoluted, spongelike creatures. However, many organisms increase in size by one to several orders of magnitude during their ontogeny, and life-forms on Earth span about 19 orders of magnitude (in mass). Thus, another solution arose, probably multiple times, during the course of animal evolution that allowed for increases in body size. This solution was to bring the "environment" functionally closer to each cell in the body by the use of internal transport

and exchange systems with large surface areas. A significant three-dimensional increase in body size thus necessitated the development of sophisticated internal transport mechanisms (e.g., circulatory systems) for nutrients, oxygen, waste products, and so on. These evolving transport structures became the organs and organ systems of higher animals. For example, the body volume of humans is so large that we require a highly branched network of gas exchange surfaces (our lungs) to provide an adequate surface area for gas diffusion. This network has about 1,000 square feet of surface—as much area as half a tennis court! The same constraints apply to food absorption surfaces; hence the evolution of very long, highly folded, or branched guts.

The embryonic tissue layers of metazoans are called **germ layers** (from the Latin *germen*, "a sprout, bud, or embryonic primordium"), and it is from these germ layers that all adult structures develop. Chapter 4 provides an overview of germ layer formation and other aspects of metazoan developmental patterns. But here we need to point out that the germ layers initially form as outer and inner sheets or coherent masses of embryonic cells, termed **ectoderm** and **endoderm** (or entoderm), respectively. In the embryogeny of the phyla Cnidaria and Ctenophora, only these two germ layers develop (or if a middle layer does develop, it is produced by the ectoderm, is largely noncellular, and is not considered a true germ layer). These animals are regarded as **diploblastic** (Greek *diplo*, "two"; *blast*, "bud" or "sprout"). In the embryogeny of most animals, however, a third cellular germ layer, the **mesoderm**, arises between the ectoderm and the endoderm; these metazoans are said to be **triploblastic**. All Bilateria are triploblastic. The long-standing term "diploblastic" may at first seem a bit misleading, as many cnidarians and ctenophores do have a "middle body layer"; but, importantly, it is not derived embryologically from a distinct middle germ layer as in the Bilateria. In this book, we use the terms "diploblastic" and "triploblastic" in this embryological germ-layer sense.

The evolution of a mesoderm greatly expanded the evolutionary potential for animal complexity. As we shall see, the triploblastic phyla have achieved many more highly sophisticated body plans than are possible within the confines of a diploblastic body plan. Simply put, a developing triploblastic embryo has more building material to work with than does a diploblastic embryo.

One of the major trends in the evolution of the triploblastic Metazoa has been the development of a fluid-filled cavity between the outer body wall and the digestive tube, that is, between the adult derivatives of the ectoderm and the endoderm. The evolution of this space created a radically new architecture, a tube-within-a-tube design in which the inner tube (the gut and its associated organs) was largely freed from the constraint of being attached to the outer tube (the body wall). The fluid-filled cavity not only served as a mechanical buffer between these two largely independent tubes, but also allowed for the development and expansion of new structures within the body, served as a storage chamber for various body products (e.g., gametes), provided a medium for circulation, and was in itself an incipient hydrostatic skeleton. The nature of this cavity (or the absence of it) is associated with the formation and subsequent development of the mesoderm, as discussed in detail in Chapter 4.

Three grades of construction occur in triploblastic Metazoa: **acoelomate**, **blastocoelomate**, and **coelomate**. The acoelomate grade (Greek *a*, "without"; *coel*, "hollow, cavity") occurs in numerous triploblastic phyla: Xenacoelomorpha, Platyhelminthes, Entoprocta, Cycliophora, Gnathostomulida, Micrognathozoa, Nematomorpha, Gastrotricha, some Loricifera and some Nematoda. In these animals, the mesoderm forms a more or less solid mass of tissue, sometimes with small open spaces (lacunae), between the gut and body wall (Figure 3.5A). In nearly all other triploblastic animals, an actual space develops as a fluid-filled cavity between the body wall and the gut. In many phyla (e.g., annelids and

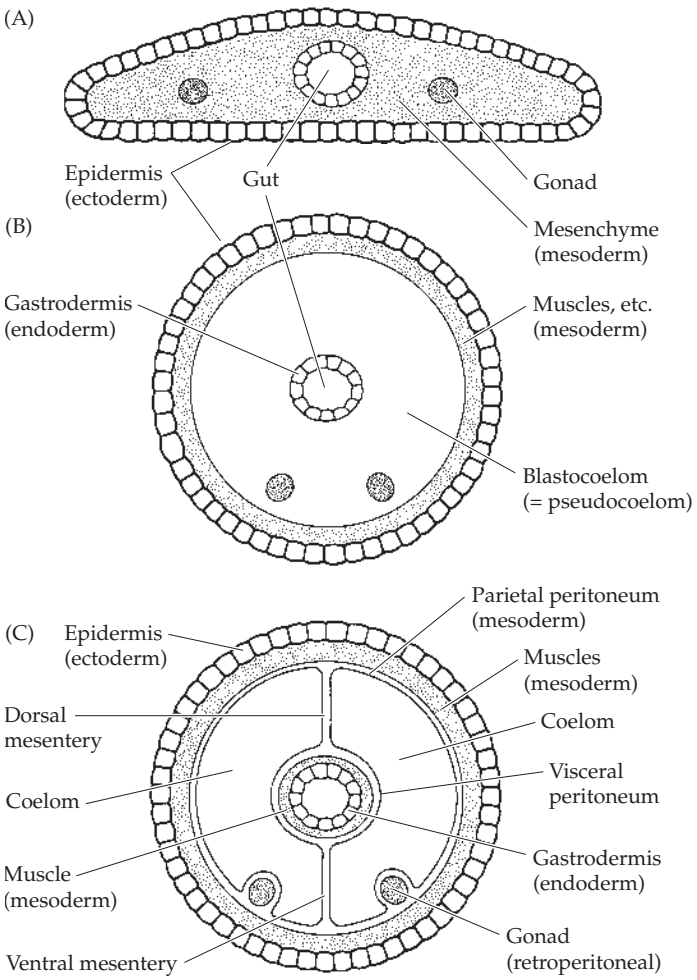

FIGURE 3.5 Principal body plans of triploblastic Metazoa (diagrammatic cross sections). (A) The acoelomate body plan. (B) The blastocoelomate body plan. (C) The coelomate (= eucoelomate) body plan.

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echinoderms), this cavity arises within the mesoderm itself and is completely enclosed within a thin lining called the **peritoneum**, which is derived from the mesoderm. Such a cavity is called a true **coelom (eucoelom)**. Notice that the organs of the body are not actually free within the coelomic space itself, but separated from it by the peritoneum (Figure 3.5C). The peritoneum is usually a squamous epithelial layer, at least that portion of it covering the gut and internal organs.

Several groups of triploblastic Metazoa (e.g., Rotifera, some Nematoda, some Loricifera, most Priapula, Tardigrada, and some Kinorhyncha) possess small or large body cavities that are neither formed from the mesoderm nor fully lined by peritoneum or any other form of mesodermally derived tissue. Such a cavity used to be called a "pseudocoelom" (Greek *pseudo*, "false"; *coel*, "hollow, cavity") (Figure 3.5B). The organs of these animals actually lie free within the body cavity and are bathed directly in its fluid. In most cases the space represents persistent remnants of the embryonic blastocoel, and since there is nothing "false" about it, we use the more descriptive term **blastocoelom** in this text. Although originally used to organize animals by their evolutionary complexity, the organization of the body cavity shows only a loose correlation to phylogeny.

Within the constraints inherent in each of the basic body organizations discussed above, animals have evolved a multitude of variations on these themes. Throughout the remainder of this chapter, we describe the fundamental organizational plans of major body systems as they have evolved within these basic body plans. In subsequent chapters, we describe how members of the various phyla have modified these basic plans through their own particular evolutionary program or direction.

Locomotion and Support

As eukaryotic life progressed from the single-celled stage to multicellularity, body size increased dramatically. And this increase in body size, coupled with directed movement, was accompanied by the evolution of a variety of support structures and locomotor mechanisms. Because these two body systems evolved mutually and usually work in a complementary fashion, they are conveniently discussed together. And of course, there was a rapid evolutionary boost in body size and support in the Cambrian, approximately 540 to 515 million years ago—an event known as the Cambrian Explosion, or Cambrian Radiation. The reasons for this rapid radiation of larger animals are still being debated (Chapter 1).

There are four fundamental locomotor patterns in Metazoa: ameboid movement (of certain body cells, and perhaps of placozoans), ciliary and flagellar movement, hydrostatic propulsion, and locomotor limb movement. There are three basic kinds of support systems: structural endoskeletons, structural exoskeletons, and hydrostatic skeletons. In this section we briefly describe the basic architecture and mechanics of the various combinations of these systems. We begin with a review of an important concept to describe movement in fluids, Reynolds number.

Reynolds Number

Most invertebrate lineages inhabit water, and aquatic environments present obstacles and advantages to support and locomotion that are quite different from those of terrestrial environments. Just staying in one place in the face of swiftly moving water, without being damaged or dislodged, can require both support and flexibility. Animals moving through water (or moving water over their bodies—the effect is much the same) face problems of fluid dynamics created by the interaction between a solid body and a surrounding liquid. What happens during this interaction is tied to the concept of Reynolds number, a unitless value based on the experiments of Osborne Reynolds (1842–1912). Reynolds number represents a ratio of inertial force to viscous force. At higher Reynolds numbers, inertial force predominates and determines the behavior of water flow around an object. At lower Reynolds numbers, viscous force predominates and determines the behavior of the water flow. The importance of this concept is being increasingly applied to biological systems. Some interesting generalizations can be made about aquatic locomotion and suspension feeding in light of Reynolds numbers. Reynolds number is expressed by the following equation:

$$R_e = plU/v$$

where p equals the density of fluid, l is some measurement of the size of the solid body, U equals the relative velocity of the fluid over the body surface, and v is the viscosity of the fluid. The formula was derived by Reynolds to describe the behavior of cylinders in water. Of course, since animal bodies are not perfect cylinders, the size variable (l) is difficult to standardize. Nonetheless, meaningful relative (comparative) values can be derived and applied to living creatures in water.

Without belaboring this issue beyond its importance here, we can see that the challenges of a large animal swimming through water are very different from those of a small animal. Large animals such as fishes, whales, or even humans, by virtue of their size or high velocity or both, move in a world of high Reynolds numbers. With increased body size, fluid viscosity becomes less and less significant as far as the animal's energy output during locomotion is concerned. At the same time, however, inertia becomes more and more important. A large animal must expend more energy than a small animal does to put its body in motion. But, by the same token, inertia works in favor of the moving large animal by

carrying it forward when the animal stops swimming. When large animals move at high Reynolds numbers, the effect of inertia also imparts motion to the water around the animal's body. Thus, as the Reynolds number increases, a point is reached at which the flow of water changes from laminar to turbulent, decreasing swimming efficiency.

Small organisms generally move in a world of low Reynolds numbers. For example, a larva 1 mm in diameter, moving at a speed of 1 mm/sec, has a Reynolds number of about 1.0. Inertia and turbulence are virtually nonexistent, but viscosity becomes important—increasingly so as body size and velocity decrease (i.e., as the Reynolds number decreases). Small organisms swimming through water have been likened to a human swimming through liquid tar or thick molasses, but this isn't quite accurate. In animals swimming in a world of low Reynolds numbers, as water moves over the surface of the animal, some of the fluid sticks to and moves with the surface of the animal's body. The effect of this situation is that tiny creatures, such as many small metazoans, start and stop instantaneously, and the motion of the water set up by their swimming also ceases immediately if the animal stops moving. Thus, small creatures neither pay the price nor reap the benefits of the effects of inertia. The organism only moves forward when it is expending energy to swim; as soon as it stops moving its cilia or flagella or appendages, it stops—and so does the fluid surrounding it. Each seta on a tiny crustacean's appendage, for example, will carry a layer of water with it as it is moved. Closely spaced setae will carry so much water that an appendage acts like a paddle; more widely spaced setae allow water to flow between them and thus can act as a sieve. Tiny organisms swimming at low Reynolds numbers (i.e., < 1.5) must expend an incredible amount of energy to propel themselves through their "viscous" surroundings.

Ameboid Locomotion

Ameboid movement is used principally by certain protists and by numerous kinds of ameboid cells that occur within the bodies of most Metazoa. Ameboid cells possess a gel-like **ectoplasm**, which surrounds a more fluid **endoplasm** (Figure 3.6). Movement is facilitated by changes in the states of these regions of the cell. At one or several points on the cell surface, **pseudopods** (or pseudopodia) develop; and as endoplasm flows into a growing pseudopod (or pseudopodium), the cell creeps in that direction. This seemingly simple process actually involves complex changes in cell fine structure, chemistry, and behavior. The innermost endoplasm moves "forward" while the outermost endoplasm takes on a granular appearance and remains fairly stable. The advancing portion of endoplasm pushes forward and then becomes semirigid ectoplasm at the tip of the advancing pseudopodium. Concurrently, endoplasm is recruited from the trailing end of the cell, from where it streams forward to join in the "growing" pseudopod. Many protists, and certain cells of eukaryotes, have wide, blunt-tipped pseudopods called **lobopods** (or lobopodia)—not to be confused with the walking appendages of some panarthropods.

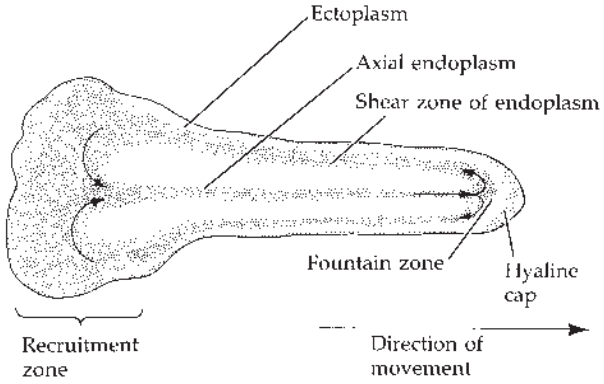

FIGURE 3.6 Ameboid locomotion. Pseudopod formation in a single cell (such as certain cells in the blood or hemolymph of metazoans) enables ameboid movement.

Cilia and Flagella

Cilia or flagella, or both, occur in virtually every animal phylum, with the qualified exception of the Arthropoda, where only flagella occur, and only in the sperm cells of some species. Structurally, cilia and flagella are nearly identical (and clearly homologous), but the former are shorter and tend to occur in relatively larger numbers (in patches or tracts), whereas the latter are long and generally occur singly or in pairs. During cell development, each new flagellum or cilium arises from an organelle called the **kinetosome** (sometimes called a basal body or a blepharoplast), to which it remains anchored.

The movement of cilia and flagella creates a propulsive force that either moves the organism through a liquid medium or, if the animal (or cell) is anchored, creates a movement of fluid over it. Such action always occurs at very low Reynolds numbers. When the animal is large, the viscosity may be increased by secretion of mucus, which lowers the Reynolds number. The general structure of a flagellum or cilium consists of a long, flexible rod, the outer covering of which is an extension of the plasma membrane of the cell (Figure 3.7A). Inside is the **axoneme**—a circle of nine paired microtubules (often called doublets) that runs the length of the flagellum or cilium. One microtubule of each doublet bears two rows of projections, the **dynein arms**, directed toward the adjacent doublet. Flagella and cilia move as the microtubules slide up or down against one another, bending the flagellum or cilium in one direction or another. Microtubule

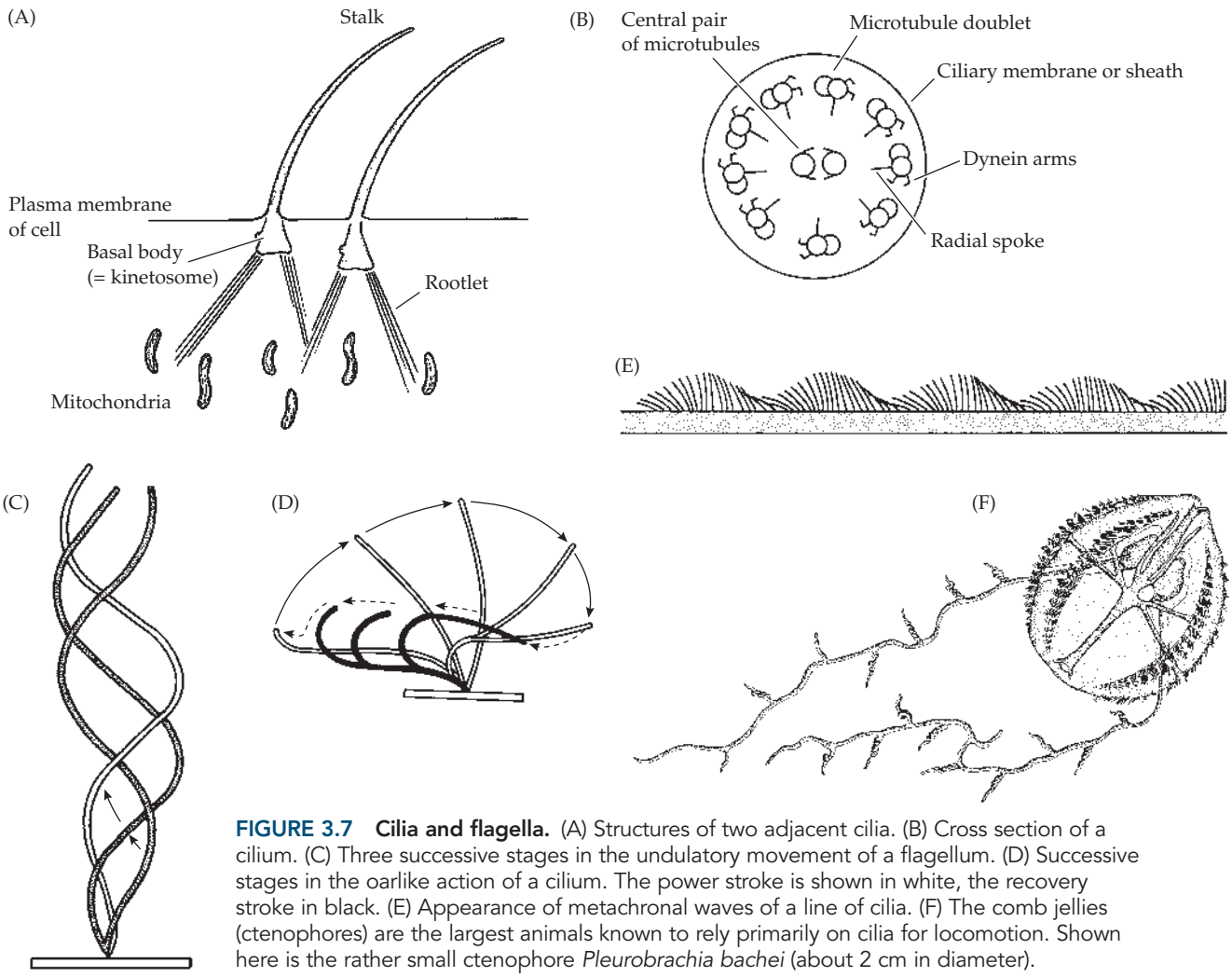

FIGURE 3.7 Cilia and flagella. (A) Structures of two adjacent cilia. (B) Cross section of a cilium. (C) Three successive stages in the undulatory movement of a flagellum. (D) Successive stages in the oarlike action of a cilium. The power stroke is shown in white, the recovery stroke in black. (E) Appearance of metachronal waves of a line of cilia. (F) The comb jellies (ctenophores) are the largest animals known to rely primarily on cilia for locomotion. Shown here is the rather small ctenophore *Pleurobrachia bachei* (about 2 cm in diameter).

sliding is driven by the dynein arms, particularly by protein complexes called **radial spokes** that arise from the arms. The radial spokes attach to each doublet microtubule immediately adjacent to the inner row of dynein arms and project centrally. Down the center of the doublet circle is an additional pair of **microtubules**. This familiar 9+2 pattern is characteristic of nearly all flagella and cilia (Figure 3.7B).[1] Flagellar/ciliary microtubules are modified hollow tubules similar to those present in the matrix of most cells. The principal function of these cellular tubules appears to be support, so the cytoplasmic microtubules act as a sort of simple "endoskeleton" that helps cells retain their shape. Microtubules are also components of the mitotic spindle and help distribute the chromosomes during cell division.

In addition to the locomotor function for which small metazoans use cilia or flagella, they have an enormous variety of functions in many other animals. For example, they create feeding and gas exchange currents, they line digestive tracts and facilitate food movement, and they propel sex cells and larvae. They also form sensory structures of many kinds. Here we focus on their use as locomotor structures.

Analysis by high-speed photography reveals that the movement of these structures is complex and differs among taxa and even among different locations on the same organism. Some flagella beat back and forth, while others beat in a helical rotary pattern that drives some sperm and other flagellated cells something like the propeller of an outboard motor (Figure 3.7C). Depending on whether the undulation moves from base to tip or from tip to base, the effect will be, respectively, to push or pull the cell along.

Some flagella possess tiny, hairlike side branches called **mastigonemes** that increase the effective surface area and thus improve the propulsive capability. The beat of a cilium is generally simpler, consisting of a power stroke and a relaxed recovery stroke (Figure 3.7D). When many cilia are present on a cell, they often occur in distinct tracts, and their action is integrated, with beats usually moving in metachronal waves over the cell surface (Figure 3.7E,F). Since

[1]Dyneins are a family of adenosine triphosphatases that cause microtubule sliding in ciliary and flagellar axonemes.

at any one time some cilia are always performing a power stroke, metachronal coordination ensures a uniform and continuous propulsive force.

It was once suggested that ciliary tracts on individual cells were coordinated by a primitive sort of cellular "nervous system," but this hypothesis was never confirmed. Current thinking suggests that the coordinated beating of cilia is probably due to hydrodynamic constraints imposed on them by the interference effects of the surrounding water layers and by the simple mechanical stimulation of moving, adjacent cilia. Nevertheless, some ciliary responses in animals are clearly under neural control, for example, reversal of power stroke direction. Cilia are used for locomotion by members of several metazoan phyla (including Placozoa, Rhombozoa, Ctenophora, Platyhelminthes, Rotifera, some gastropod molluscs, and others) and by the larval stages of a great many taxa.

Muscles and Skeletons

Almost all animals have some sort of a skeleton, the major functions of which are to maintain body shape, provide support, serve as attachments for muscles, transmit the forces of muscle contraction to perform work, and extend relaxed muscles. These functions may be attained by either hard tissues or secreted skeletons, or even by the turgidity of body fluids or tissues under pressure. Muscles, skeletons, and body form are closely integrated, both developmentally and functionally. When rigid skeletal elements are present, they can serve as fixed points for muscle attachment. For example, the rigid and jointed exoskeleton of arthropods allows for a complex system of levers that results in very precise and restricted limb movements. Many invertebrates lack hard skeletons and can change their body shape by alternate contraction and relaxation of various muscle groups attached to tough connective tissues or to the inside of the body wall. These "soft-bodied" invertebrates usually have a hydrostatic skeleton.

The hydrostatic skeleton The performance of a hydrostatic skeleton is based on two fundamental properties of liquids: their incompressibility and their ability to assume any shape. Because of these features, body fluids transmit pressure changes rapidly and equally in all directions. It is important to realize a basic physical limitation concerning the action of muscles—they can only perform work by getting shorter (contracting).[2] In hydrostatic skeletons, a body region is extended (or protruded) by the contractile force of a muscle being imparted to a fluid-filled body compartment, creating a hydrostatic pressure that displaces the wall of the compartment. Such indirect muscle actions can be compared to squeezing a rubber glove filled with water, thereby extending and stiffening the fingers. The enclosure of a fluid-filled chamber (e.g., a coelom) within sets of opposing muscle layers establishes a system in which muscles in one part of the body can contract, forcing body fluids into another region of the body, where the muscles relax; the body is thus extended or otherwise changed in shape (Figure 3.8).

In the most common plan, two muscle layers surround a fluid-filled body cavity, and the fibers of the layers run in different directions (e.g., a circular muscle layer and a longitudinal muscle layer). A soft-bodied invertebrate can move forward by using its hydrostatic skeleton in the following way: The circular muscles at the posterior end of the animal contract, and thus the

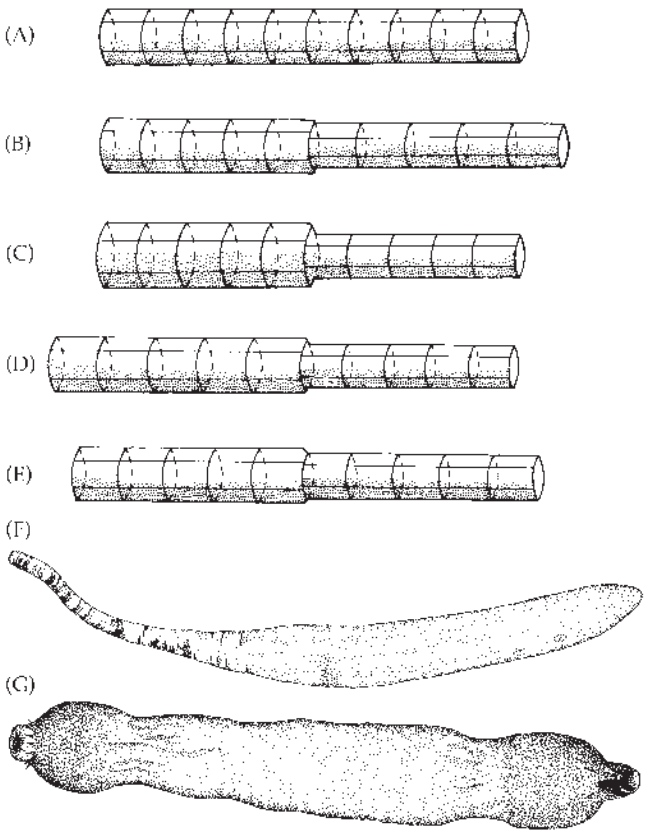

FIGURE 3.8 The hydrostatic skeleton. (A–E) The initial state and the four possible results of contraction of the circular muscles at one end of a cylindrical animal with a hydrostatic skeleton. (A) The muscles are all relaxed. (B) The circular muscles of the right-hand end have contracted and this end has elongated; the left-hand end has remained unaltered. (C) The length of the right-hand end has remained the same but the diameter of the left-hand end has increased. (D) The length of the right-hand end and the diameter of the left-hand end have remained the same, but the length of the left-hand end has increased. (E) The lengths of both ends have increased, but their respective diameters have remained the same. (F,G) Two animals that rely on hydrostatic skeletons for support and locomotion. (F) The sipunculan worm *Phascolosoma*. (G) The thalassematid worm *Urechis caupo*.

[2]Bear in mind that muscles can contract isometrically and do no work.

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hydrostatic pressure generated pushes anteriorly to extend the relaxed longitudinal muscles of the front of the body. Then contraction of the posterior longitudinal muscles pulls the rear end of the body forward. This sequence of muscle contractions results in a directed and controlled movement forward. Such movement requires that the posterior end be anchored when the anterior end is extended, and that the anterior end be anchored when the posterior end is pulled forward. This system is commonly used for locomotion by many worms that generate posterior-to-anterior metachronal waves of muscle action, resulting in what is called peristalsis. A similar hydrostatic system can be used to temporarily or intermittently extend selected parts of the body, such as the feeding proboscis of worms, tube feet of echinoderms, and siphons of clams.

Reliance on only circular and longitudinal muscles could result in twists and kinks when a hydrostatic system engaged itself against the resistance of the substratum. Hence, most animals that rely on hydrostatic movement also have helically wound, diagonal muscle fibers—a left- and right-handed set, intersecting at an angle between 0 and 180 degrees. The diagonal muscles allow extension and contraction, even at a constant volume, without stretching and while preventing kinking and twisting. A good analogy is the children's finger toy—the helically woven straw cylinder into which one youngster convinces another to insert his two index fingers; pushing your fingers together increases the diameter of the cylinder (and decreases the length), and pulling your fingers apart decreases the diameter (and increases the length). All of this is accomplished without an appreciable stretching or compression of the straw fibers (or the diagonal muscles of an invertebrate). When a cylinder is extended, the fiber angle decreases; when it is compressed, the angle increases.

The volume of the working fluid in a hydrostatic skeleton should remain constant, thus any leakage should not be greater than the rate at which the fluid can be replaced. Body fluids must be retained despite "holes" in the body wall, such as the excretory pores of many coelomate animals, the mouth openings of cnidarians, etc. Such openings are often encircled by sphincter muscles that can close and control the loss of body fluids.

One way in which movement by a hydrostatic skeleton can be made more precise is to divide an animal up into a series of separate compartments. For example, in many annelid worms, partitioning of the coelom and body muscles into segments with separate neural control enables body expansions and contractions to be confined to a few segments at a time. By manipulating particular sets of segmental muscles, most annelids not only can move forward and backward but can turn and twist in complex maneuvers.

The rigid skeleton In "hard-bodied" invertebrates, a fixed or rigid skeleton prevents the gross changes in body form seen in soft-bodied invertebrates. This reduction in flexibility is a trade-off that gives hard-bodied animals several advantages: the capacity to grow larger (an advantage that is especially useful in terrestrial habitats, which lack the buoyancy provided by aquatic environments), more precise or controlled body movements, better defense against predators, and often greater speed of movement.

Hard skeletons can be broadly classed as either endoskeletons or exoskeletons. Among Bilateria, endoskeletons are generally derived from mesoderm, whereas exoskeletons are derived from ectoderm; both usually have organic and inorganic components. It has been hypothesized that rigid skeletons may have originated by chance, as byproducts of certain metabolic pathways. By sheer accident (preadaptation or exaptation), for example, the accumulation of nitrogenous wastes and their incorporation into complex organic molecules might have resulted in the evolution of the chitinous exoskeleton so common among invertebrates. Similar speculation suggests that a metabolic system that originally functioned to eliminate excess calcium from the body might have produced the first calcareous shell of molluscs. In any event, marine invertebrates are capable of forming, through their various biological activities, a vast array of minerals, some of which cannot be formed inorganically in the biosphere. Indeed, the ever-increasing amounts of these biominerals have radically altered the character of the biosphere since the origin of hard skeletons in the earliest Cambrian. Most common among these biominerals are various carbonates, phosphates, halides, sulfates, and iron oxides.

Invertebrate skeletons may be of the articulating type (e.g., the exoskeletons of arthropods, clams, and brachiopods and the endoskeleton of some echinoderms), or they may be of the nonarticulating type, as seen in the simple one-piece exoskeletons of snails and in the rigid endoskeletons composed of interlocking fused plates of sea urchins and sand dollars. Animal endoskeletons may be as simple as the microscopic calcareous or siliceous spicules embedded in the body of a sponge, cnidarian, or sea cucumber, or they may be as complex as the bony skeleton of vertebrates (Figure 3.9) or the jaws of micrognathozoans (Figure 11.16). Hard skeletons of calcium carbonate have evolved in many animal (and some algal) phyla, but the use of silica in a mineralized skeleton occurs only in sponges (Porifera). Vertebrate skeletal tissues include a calcium phosphate–collagen matrix. In invertebrates, collagen often forms a substratum upon which calcareous spicules or other skeletal structures form, but with a single exception (certain gorgonians) collagen is never incorporated directly into the calcareous skeletal material.[3]

[3]Collagen, of course, also is the primary component of basement membrane that underlies epithelia in all Metazoa, providing structural integrity to tissues.

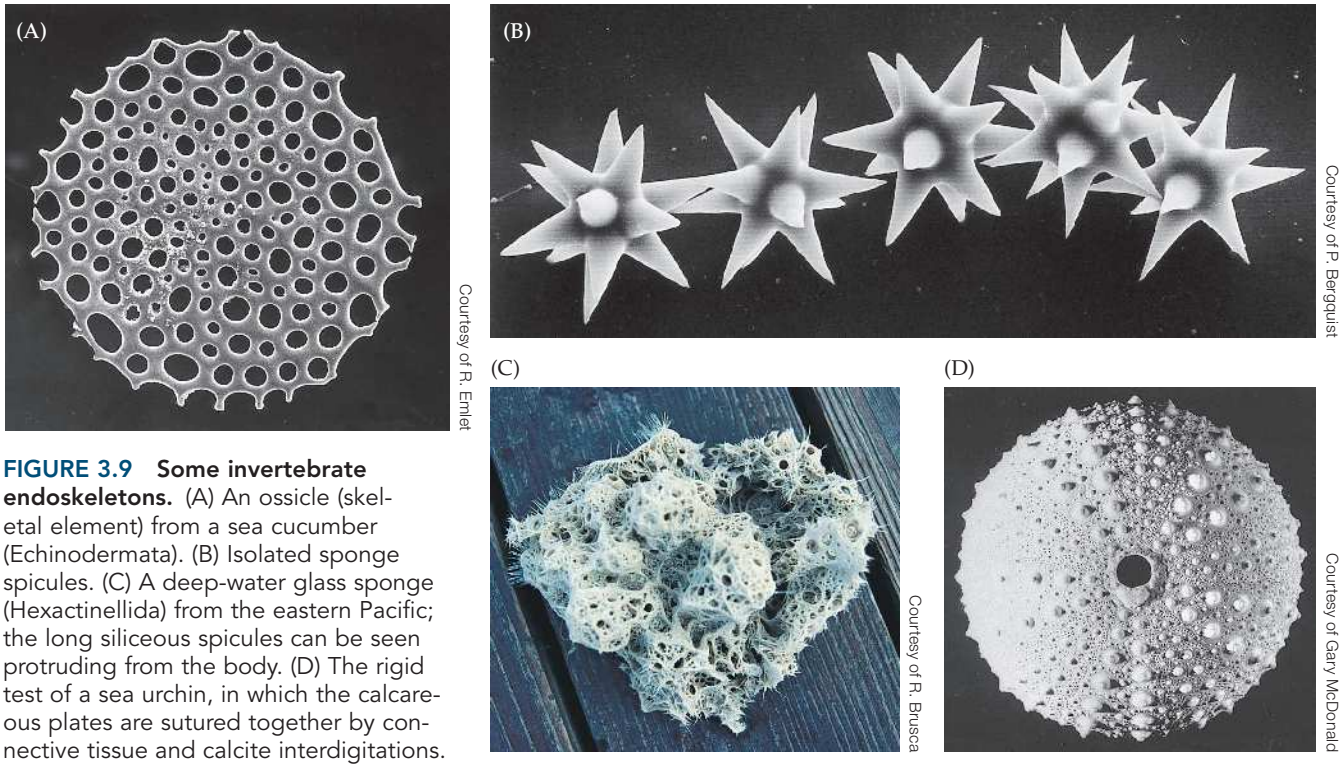

FIGURE 3.9 Some invertebrate endoskeletons. (A) An ossicle (skeletal element) from a sea cucumber (Echinodermata). (B) Isolated sponge spicules. (C) A deep-water glass sponge (Hexactinellida) from the eastern Pacific; the long siliceous spicules can be seen protruding from the body. (D) The rigid test of a sea urchin, in which the calcareous plates are sutured together by connective tissue and calcite interdigitations.

From their epidermis, many Metazoa secrete a nonliving external layer called the cuticle, which serves as an exoskeleton. A cuticle is an extracellular matrix secreted by and covering the epidermis. It may be composed of various different organic materials, such as a glycocalyx matrix, collagen, keratin, chitin, and cellulose. It may also be mineralized to form spicules or shells. The cuticle varies in thickness and complexity, but it often has several layers of differing structure and composition. In the arthropods, for example, the cuticle is a complex combination of the polysaccharide chitin and various proteins.[4] This skeleton may be strengthened by the formation of internal cross-linkages (a process called **tanning**) and by the addition of calcium and pigments. The chitinous layer of most invertebrates is the first line of defense against infective microbes and desiccation. In most insects, the outermost layer is impregnated with wax, which decreases its permeability to water. The cuticle is often ornamented with spines, tubercles, scales, or striations; frequently it is divided into rings or segments, a feature lending flexibility to the body (Figure 3.10).

Most skeletons act as body elements against which muscles operate and by which muscle action is converted to body movement. Because muscles cannot elongate by themselves, they must be stretched by antagonistic forces—usually other muscles, hydrostatic forces, or elastic structures. In animals possessing rigid but articulated skeletons, antagonistic muscles often appear in pairs, for example, flexors and extensors. These muscles extend across a joint and are used to move a limb or other body part (Figure 3.11). Most muscles have a discrete origin, where the muscle is anchored, and an insertion, which is the point of major body or limb movement. A classic vertebrate example of this system is the biceps muscle of the human arm, in which the origin is on the scapula and the insertion is on the radius bone of the forearm; contraction of the biceps causes flexion of the arm by decreasing the angle between the upper arm and the forearm. Movement of a limb toward the body is brought about by **flexor muscles**, of which the biceps is an example (Figure 3.11A,B). The muscle antagonistic to the biceps is the triceps, an **extensor muscle** whose contraction extends the forearm away from the body. Other common sets of antagonistic muscles and actions are **protractors** and **retractors**, which respectively cause anterior and posterior movement of entire limbs at their place of juncture with the body; and **adductors** and **abductors**, which move a body part toward or away from a particular point of reference. Although vertebrates have

[4]The term "chitin" refers to a family of closely related chemical compounds, which, in various forms, are produced by and incorporated into the cuticles of many invertebrates. Certain types of chitin are also produced by some fungi and diatoms. Chitins are high-molecular-weight, nitrogenous polysaccharide polymers that are tough yet flexible (Figure 3.10C). In addition to its supportive and protective functions in the formation of exoskeletons, chitin is also a major component of the teeth, jaws, and grasping and grinding structures of a wide variety of invertebrates. That chitin is one of the most abundant macromolecules on Earth is evidenced by the estimated 1,011 tons produced annually in the biosphere—most of it in the ocean.

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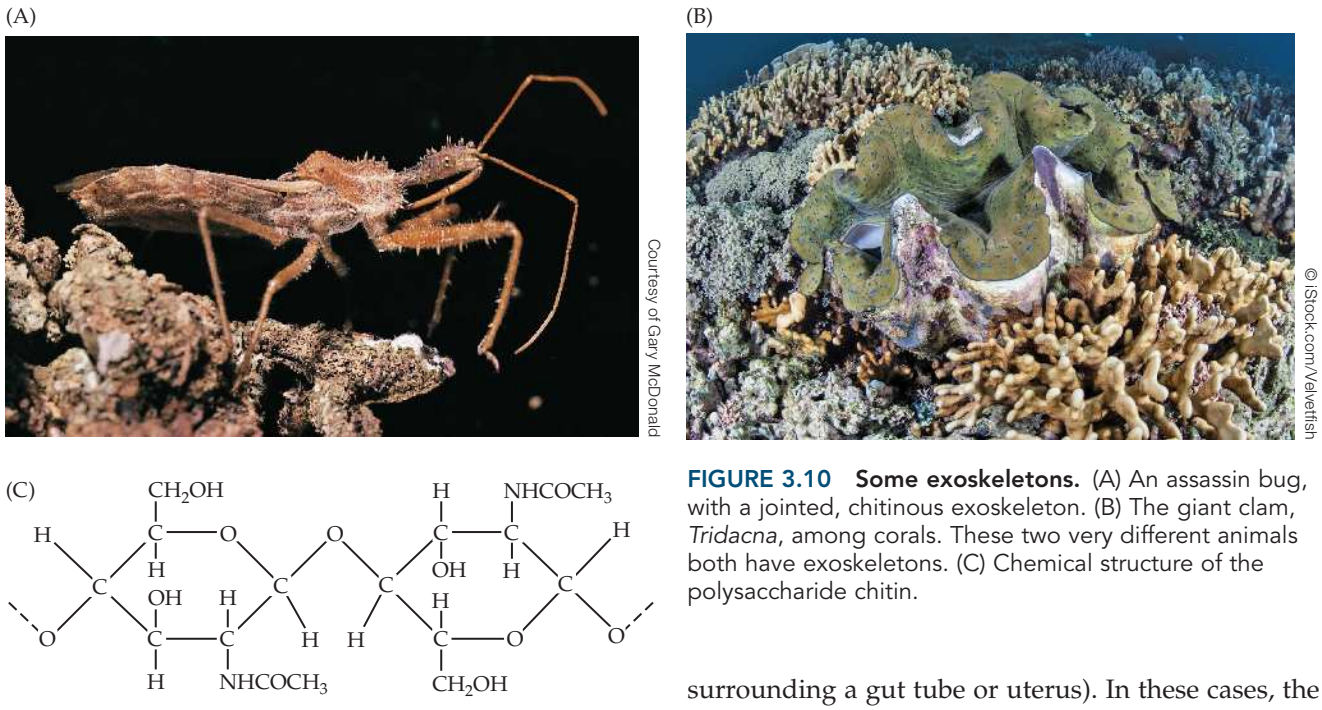

FIGURE 3.10 Some exoskeletons. (A) An assassin bug, with a jointed, chitinous exoskeleton. (B) The giant clam, *Tridacna*, among corals. These two very different animals both have exoskeletons. (C) Chemical structure of the polysaccharide chitin.

endoskeletons and arthropods have exoskeletons, most muscles of arthropods are arranged in antagonistic sets similar to those seen in vertebrates (Figure 3.11C). The muscles of arthropods attach to the inside of the skeletal parts, whereas those of vertebrates attach to the outside, but they both operate systems of levers.

Not all muscles attach to rigid endo- or exoskeletons. Some form masses of interlacing muscle fibers, like those in the body wall of a worm, the foot of a snail, or the muscle layers in the walls of "hollow" organs (like those surrounding a gut tube or uterus). In these cases, the muscles have no definite origin and insertion but act on each other and the surrounding tissues and body fluids to affect changes in the shape of the body or body parts.

The basic physiology and biochemistry of muscle contraction is the same in vertebrates and invertebrates, although a variety of specialized variations on the basic model have evolved. For example, the adductor muscle of most clams (the muscle that holds the shell closed) is divided into two parts. One part is heavily striated and used for rapid shell closure (the phasic, or "quick," muscle); the other is smooth, or tonic, and is used to hold the shell closed for hours or

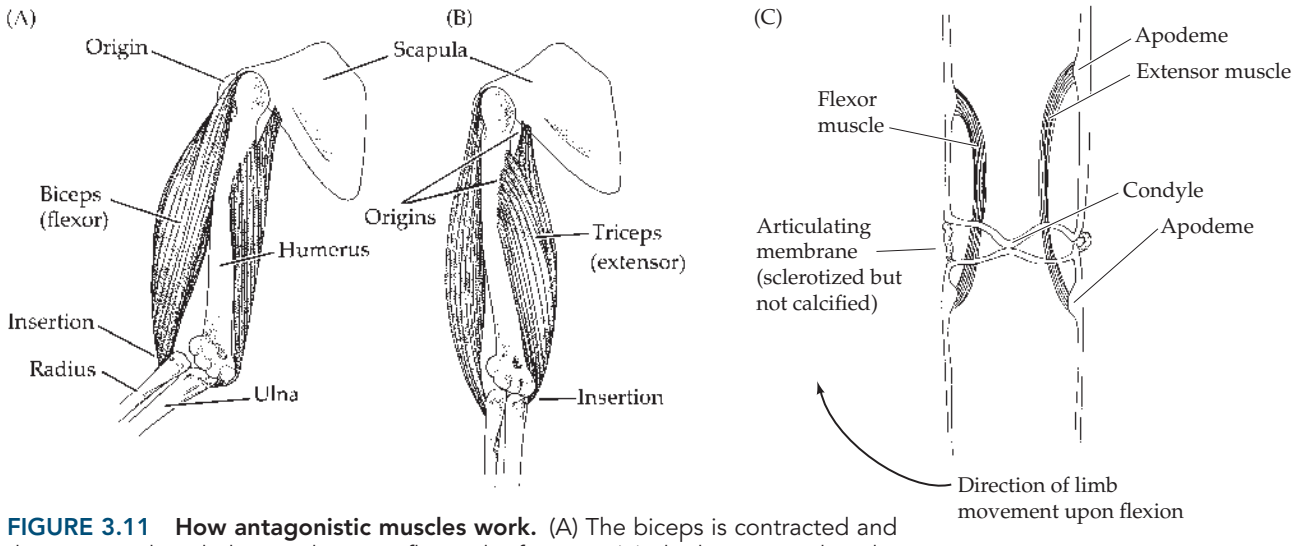

FIGURE 3.11 How antagonistic muscles work. (A) The biceps is contracted and the triceps relaxed; this combination flexes the forearm. (B) The biceps is relaxed and the triceps is contracted; this combination extends the forearm. (C) A diagrammatic representation of an arthropod joint, illustrating a similar relationship between flexor and extensor. In arthropods, however, the muscles attach to the inside of the skeleton.

even days at a time (the "catch" muscle). Brachiopods have a similar adductor muscle specialization—a good example of convergent evolution. Other specializations are found in crustacean muscle innervation, which differs from that typically seen in other invertebrates, and in certain insect flight muscles that are capable of contracting at frequencies far higher than can be induced by nerve impulses alone.

Feeding and Digestion

Intracellular and Extracellular Digestion

Virtually all Metazoa must locate, select, capture, ingest, and finally digest and assimilate food. Although the physiology of digestion is similar at the biochemical level, considerable variation exists in the mechanisms of capture and digestion as a result of constraints placed on organisms by their overall body plans.

Digestion is the process of breaking down food by hydrolysis into units suitable to the nutrition of cells. When this breakdown occurs outside the body, it is called **extracorporeal digestion**; when it occurs in a gut chamber of some sort, it is referred to as **extracellular digestion**; and when the process occurs within a cell, it is called **intracellular digestion**. Regardless of the site of digestion, all organisms are ultimately faced with the fundamental challenge of cellular capture of nutritional products (food, digested or not). This cellular challenge is met by the process of **phagocytosis** (literally, "eating by cells") and **pinocytosis** ("drinking by cells"). These processes, collectively called **endocytosis**, are mechanically simple and involve the engulfment of food "particles" at the cell surface.

In 1892 the great comparative anatomist Elie Metchnikoff made a discovery that led to his receiving a Nobel Prize 16 years later. Metchnikoff discovered the process by which certain ameboid cells in the coelomic fluid of starfish engulf and destroy foreign matter such as bacteria. He named this process phagocytosis. In phagocytosis, extensions of a cell's plasma membrane encircle the particle to be captured (whether it be food or a foreign microbe), form an inpocketing on the cell surface, and then pinch off the pocket inside the cell (Figure 3.12A). The resultant intracellular membrane-bounded structure is called a food vacuole. The plasma membrane surrounding the food vacuole is, of course, no longer part of the cell's outer membrane, and in this sense it and whatever is in the vacuole are now "inside" the cell, and the subsequent digestive processes that take place are considered intracellular, not extracellular. However, food inside the food vacuole is not actually incorporated into the cell's cytoplasm until it is digested and the resultant molecules are released.

Sponges largely rely on phagocytosis as a feeding mechanism, and the digestive cells of metazoan guts take up food particles in the same fashion. Once a cell has phagocytosed a food particle and intracellular digestion has been completed, any remaining waste particles may be carried back to the cell surface by what remains of the old food vacuole, which fuses with the plasma membrane to discharge its wastes in a sort of reverse phagocytosis, called **exocytosis**.

Pinocytosis can be thought of as a highly specialized form of phagocytosis, in which molecule-sized particles are taken up by the cell. Such molecules are always dissolved in some fluid (e.g., a body fluid or sea water). During pinocytosis, minute invaginations (pinocytotic channels) form on the cell surface, fill with liquid from the surrounding medium (which includes the dissolved nutritional molecules), and then pinch off to enter the cytoplasm as pinocytotic vesicles (Figure 3.12B). Pinocytosis generally occurs in cells lining some body cavity

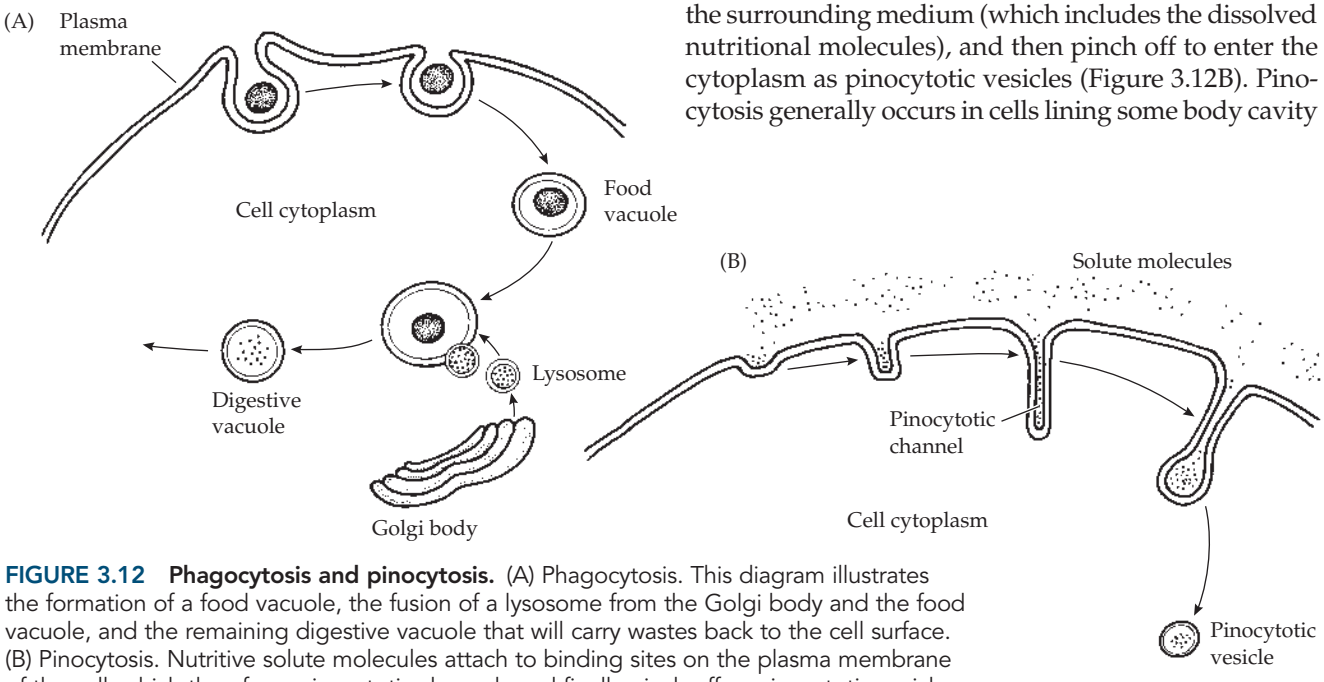

FIGURE 3.12 Phagocytosis and pinocytosis. (A) Phagocytosis. This diagram illustrates the formation of a food vacuole, the fusion of a lysosome from the Golgi body and the food vacuole, and the remaining digestive vacuole that will carry wastes back to the cell surface. (B) Pinocytosis. Nutritive solute molecules attach to binding sites on the plasma membrane of the cell, which then form pinocytotic channels and finally pinch off as pinocytotic vesicles.

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(e.g., the gut) in which considerable extracellular digestion has already taken place and nutritive molecules have been released from the original food source. In some cases, however, nutritional molecules may be taken up directly from seawater, and there is growing evidence that many invertebrates rely substantially on the direct uptake of dissolved organic matter (DOM) from their environment, including many sponge cells, and this is the main way of feeding of placozoans.

Some animals have no true digestive tract (e.g., Porifera, Placozoa, tapeworms, acanthocephalans), but most metazoans possess some sort of dedicated, internal chamber into which food is moved for processing. In some (e.g., Cnidaria, Xenacoelomorpha, Platyhelminthes) there is only one opening through which food is ingested and undigested materials are eliminated. These animals are said to have an **incomplete gut** (or blind gut). Most other Metazoa have both mouth and anus (a **complete gut**, or **through gut**), an arrangement that allows the one-way flow of food and the specialization of different gut regions for functions such as grinding, secretion, storage, digestion, and absorption. As the noted biologist Libbie Hyman so aptly put it, "The advantages of an anus are obvious," and ctenophores have two, although it seems that only one might be functional, though which one is functional is not necessarily the same in different individuals even of the same species!

The overall anatomy and physiology of an animal's gut are closely tied to the type and quality of food consumed. In general, the guts of herbivores are long and often have specialized chambers for storage, grinding, and so on because vegetable matter is difficult to digest and requires long residence times in the digestive system. Carnivores tend to have shorter, simpler guts, and the animal foods they consume are easier to digest.

Feeding Strategies

Just as body architecture influences and limits the digestive modes of invertebrates, it is also intimately associated with the processes of food location, selection, and ingestion. Animals are generally defined as **heterotrophic** organisms (as opposed to autotrophs and saprophytes); they ingest organic material in the form of other organisms or parts thereof. In addition, many invertebrate groups have developed intimate symbiotic relationships with single-celled algae, especially with certain species of dinoflagellates. These invertebrates use photosynthetic byproducts as an accessory (or occasionally as the primary) food source. Notable in this regard are reef-building corals, giant clams (*Tridacna*) (Figure 3.10B), and certain flatworms, acoels, sea slugs, hydroids, ascidians, sea anemones, and even some freshwater sponges. However, the overwhelming majority of invertebrates lead strictly heterotrophic lives.

Biologists classify heterotrophic feeding strategies in a number of ways. For example, organisms can be considered herbivores, carnivores, or omnivores; or they can be classed as grazers, predators, or scavengers. Organisms can also be classified as microphagous or macrophagous by the comparative size of their food or prey, or they can be classified by the environmental source of their food as suspension feeders, deposit feeders, or detritivores. In the remainder of this section, we define some important feeding-strategy terms and explain some common themes of feeding.

Few invertebrates are strictly herbivores or carnivores, even though most show a clear preference for either a vegetable or a meat diet. For example, the Atlantic purple sea urchin *Arbacia punctulata* usually feeds on micro- and macroalgae. However, in certain portions of its range, where algae may become seasonally scarce, epifaunal animals constitute the bulk of this urchin's diet. Omnivores, of course, must have the anatomical and physiological capability to capture, handle, and digest both plant and animal material. Among invertebrates, there are two large categories of feeding strategies in which omnivory prevails: suspension feeding and deposit feeding.

Suspension feeding **Suspension feeding** is the removal of suspended food particles from the surrounding medium by some sort of capture, trapping, or filtration mechanism. Lest you think suspension feeding is a sideline strategy in the animal kingdom, let us remind you that the largest living animals utilize it—baleen whales and several lineages of sharks and rays. This mode of feeding has three basic steps: transport of water past the feeding structures, removal of particles from the water, and transport of the captured particles to the mouth. It is a major mode of feeding in sponges, ascidians, appendicularians, brachiopods, bryozoans, entoprocts, phoronids, most bivalves, and many crustaceans, polychaetes, echinoderms, hemichordates, and gastropods. The main food selection criterion is particle size, and the size limits of food are determined by the nature of the particle-capturing device. In some cases potential food particles may also be sorted on the basis of their specific gravity, or even their perceived nutritional quality.

Suspension-feeding invertebrates generally consume bacteria, phytoplankton, zooplankton, and some detritus. All suspension feeders probably have optimal ranges of particle size; but some are capable, experimentally, of preferentially selecting "enriched" artificial food capsules over nonenriched (nonfood) capsules, an observation suggesting that chemosensory selectivity may occur in situ as well. To capture food particles from their environment, suspension feeders must move part or all of their body through the water, or else water must be moved over their feeding structures. As with locomotion in water, the relative motion between a solid and liquid during suspension feeding creates a system that behaves according to the concept of Reynolds numbers. Virtually all suspension-feeding invertebrates capture

particles from the water at low Reynolds numbers. The flow rates in such systems are very low and the feeding structures are small (e.g., cilia, flagella, setae).

Recall that at low Reynolds numbers viscous forces dominate, and water flow over small feeding structures is laminar and nonturbulent and ceases instantaneously when energy input stops. Thus, in the absence of inertial influence, suspension feeders that generate their own feeding currents expend a great deal of energy. Some suspension feeders conserve energy by depending to various degrees on prevailing ambient water movements to continually replenish their food supplies (e.g., barnacles on wave-swept shores and mole crabs in the wash zone on sandy beaches). Others take advantage of water currents created by other animals, as is typical in many brittle stars and other invertebrates that sit on top of sponges to get their food. For most organisms, however, the effort expended for feeding is a major part of their energy budget.

Only a relatively few suspension feeders are true filterers. Because of the principles outlined above, it is energetically extremely costly to drive water through a fine-meshed filtering device. For small animals, this is somewhat analogous to moving a fine-mesh filter through thick syrup. Such actual sieving does occur, most notably in many bivalve molluscs, many tunicates, some larger crustaceans, and some worms that produce mucous nets. However, most suspension feeders employ a less expensive method of capturing particles from the water, one that does not involve continuous filtration. Many invertebrates simply expose a sticky surface, such as a coating of mucus, to flowing water. Suspended particles contact and adhere to the surface and then are moved to the mouth by ciliary tracts (as in crinoids), setal brushes (as in certain crustaceans), or some other means of transport. Other "contact suspension feeders" living in still water may simply expose a sticky surface to the rain of particulate material settling downward from the water above, thus letting gravity do much of the work of acquiring food. Some oysters are suspected of this feeding strategy, at least on a part-time basis. Several other contact methods of suspension feeding may occur, but all eliminate the costly activity of actual sieving in the highly viscous world of low Reynolds numbers.

Another nonfiltering suspension-feeding method is called "scan and trap." The general strategy here is to move water over part or all of the body, detect suspended food particles, isolate the particles in a small parcel of water, and process only that parcel by some method of particle extraction. The animal thus avoids the energetic expense of continuously driving water over the feeding surface at low Reynolds numbers. The precise methods of particle detection, isolation, and capture vary among invertebrates that use the scan-and-trap technique, and this basic strategy is probably employed by certain crustaceans (e.g., planktonic copepods), many bryozoans, and a variety of larval forms.

Among some crustaceans, certain limbs are equipped with rows of featherlike setae adapted for removing particles from the water (Figure 3.13). The size of the particles captured is often directly proportional to the "mesh" size of the interlaced setae on the food-capture structure. In sessile crustaceans such as barnacles, the feeding appendages are swept through the water or held taut against moving water. In either case, sessile animals are dependent upon local currents to continually replenish their food supply. Motile setal-net feeders, like many larger planktonic crustaceans and certain benthic crustaceans (e.g., porcelain crabs), may have modified appendages that generate a current across the feeding appendages that bear the capture setae. Sometimes these same appendages serve simultaneously for locomotion. In cephalocarid and many branchiopod crustaceans, for example, complex coordinated movements of the highly setose thoracic legs propel the animal forward and also produce a constant current of water (Figure 3.13D). These appendages simultaneously capture food particles from the water and collect them in a median ventral food groove at the leg bases, from which they are passed forward to the mouth region.

Another suspension-feeding device is the mucous net, or mucous trap, wherein a sheet or patches of mucus are used to capture suspended food particles. Most mucous-net feeders consume their net along with the food and then recycle the chemicals used to produce it. Again, sessile and sedentary species often rely largely on local currents to keep a fresh supply of food coming their way. Some, however, especially benthic burrowers, actively pump water through their burrow or tube, where it passes across or through the mucous sheet. A classic example of mucous-net feeding is seen in the annelid worm *Chaetopterus* (Figure 3.14A). This animal lives in a U-shaped tube in the sediment and pumps water through the tube and through a mucous net. As the net fills with trapped food particles, it is periodically manipulated and rolled into a ball, which is then passed to the mouth and swallowed. An example of mucous-trap feeding is seen in the tube-building gastropods (family Vermetidae). These wormlike snails construct colonies of meandering calcareous tubes in the intertidal zone. Each animal secretes a mucous trap that is deployed just outside the opening of the tube, until nearly the entire colony surface is covered with mucus. Suspended particulate matter settles and becomes trapped in the mucus. At periodic intervals, each animal withdraws its mucous sheet and swallows it, whereupon a new sheet is immediately constructed.

Still another type of suspension feeding is the ciliary-mucous mechanism, in which rows of cilia carry a mucous sheet across some structure while water is passed through or across it. Ascidians (sea squirts; Figure 3.14B) move a more or less continuous

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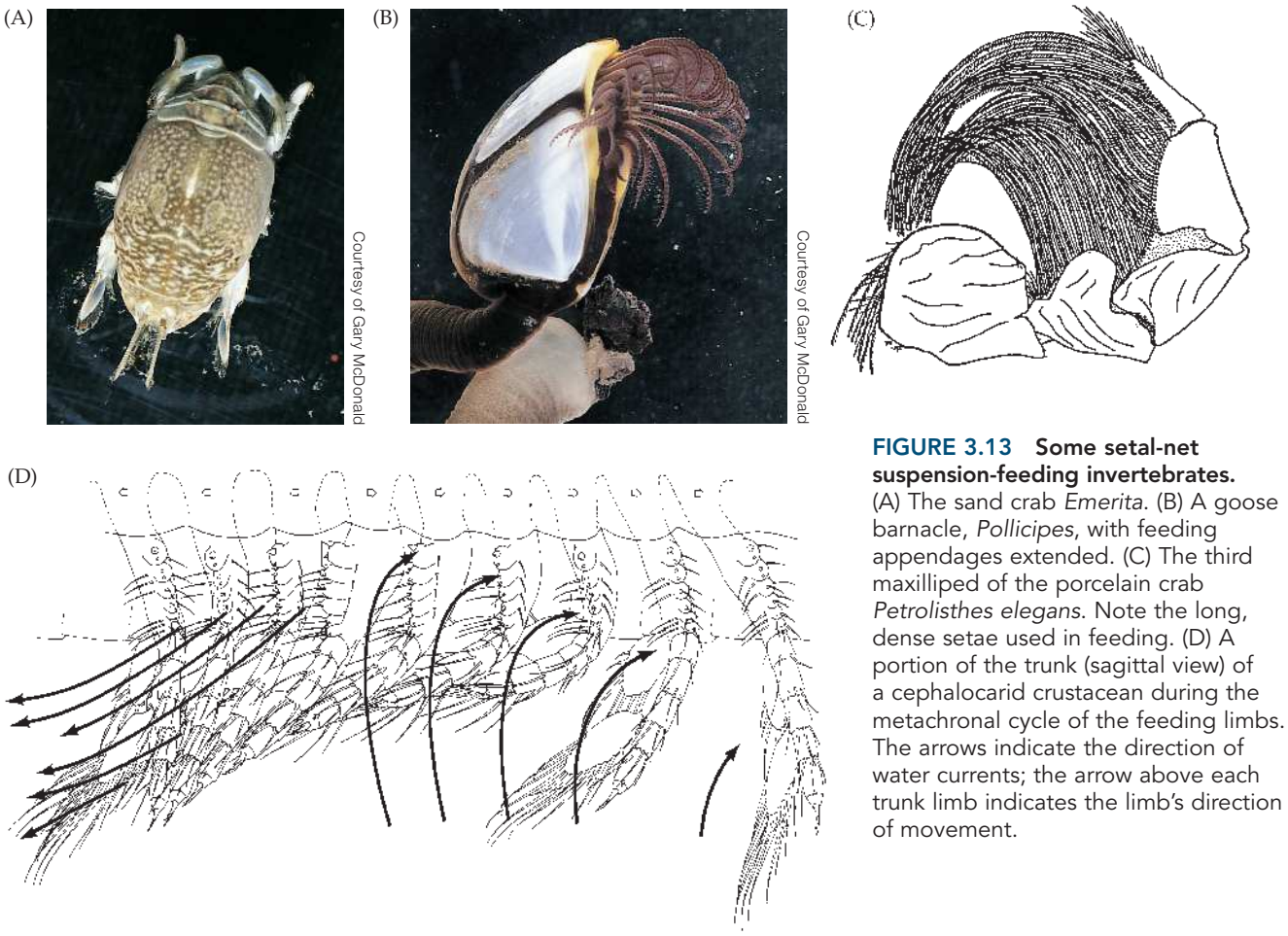


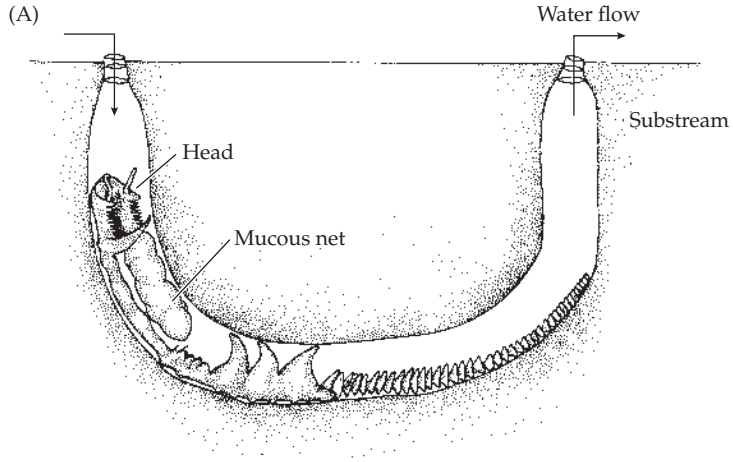
FIGURE 3.13 Some setal-net suspension-feeding invertebrates. (A) The sand crab *Emerita*. (B) A goose barnacle, *Pollicipes*, with feeding appendages extended. (C) The third maxilliped of the porcelain crab *Petrolisthes elegans*. Note the long, dense setae used in feeding. (D) A portion of the trunk (sagittal view) of a cephalocarid crustacean during the metachronal cycle of the feeding limbs. The arrows indicate the direction of water currents; the arrow above each trunk limb indicates the limb's direction of movement.

mucous sheet across their sievelike pharynx, while at the same time pumping water through it. Fresh mucus is secreted at one side of the pharynx while the food-laden mucus at the other side is moved into the gut for digestion. Several hemichordate and polychaete groups also make use of the ciliary-mucous feeding technique (Figure 3.14C). For example, some species of tube-dwelling fan worms feed with a crown of tentacles that are covered with cilia and mucus and bear ciliated grooves that slowly move captured food particles to the mouth. Many sand dollars capture suspended particles, especially diatoms, on their mucus-covered spines; food and mucus are transported by the tube feet and ciliary currents to food tracts, and then to the mouth.

And another kind of suspension feeding is tentacle or tube feet suspension feeding. In this strategy, some sort of tentacle-like structure captures larger food particles, with or without the aid of mucus. Food particles captured by this mechanism are generally larger than those captured by setal or mucous traps or sieves. Examples of tentacle or tube feet suspension feeding are most commonly encountered in the echinoderms (e.g., many brittle stars and crinoids as well as dendrochirotid sea cucumbers) and cnidarians (e.g., certain sea anemones, gorgonians, and corals) (Figure 3.15).

Much research has been done on suspension feeding, and we now know what size range of particles many animals feed on and what kinds of capture rates they have. In general, feeding rates increase with food particle concentration to a plateau, above which the rate levels off. At still higher particle concentrations, entrapment mechanisms may become overtaxed or clogged and feeding may be inhibited or simply cease. In sessile and sedentary suspension feeders, for example, pumping rates decrease quickly as the amount of suspended inorganic sediment (mud, silt, and sand) increases beyond a given concentration. For this reason, the amount of sediment in coastal waters limits the distribution and abundance of certain invertebrates such as clams, corals, sponges, and ascidians. Many tropical coral reefs are dying as a result of increased coastal sediment loads generated by runoff from land areas subjected to deforestation or urban development.

Deposit feeding The **deposit feeders** make up another major group of omnivores. These animals obtain nutrients from the sediments of soft-bottom habitats (muds and sands) or terrestrial soils, but their techniques for feeding are diverse. Direct deposit feeders simply swallow large quantities of

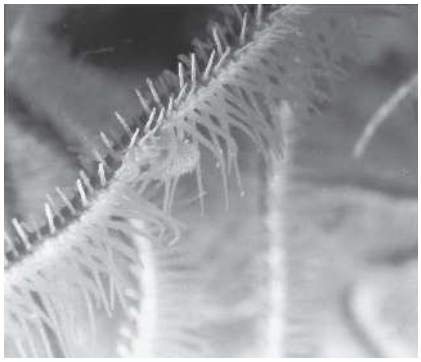


Courtesy of Gary McDonald

Courtesy of Karl Banse

FIGURE 3.14 Some mucous-net and ciliary-mucous suspension feeders. (A) The annelid worm *Chaetopterus* in its burrow. Note the direction of water flow through its mucous net. (B) The solitary ascidian *Styela* has incurrent and excurrent siphons through which water enters and leaves the body. Inside, the water passes through a sheet of mucus covering holes in the wall of the pharynx. (C) A maldanid polychaete, *Praxillura maculata*. This animal constructs a membranous tube that bears 6–12 stiff radial spokes. A mucous web hangs from these spokes and passively traps passing food particles. The worm's head is seen sweeping around the radial spokes to retrieve the mucous web and its trapped food particles.

sediment—mud, sand, soil, organic matter, everything. In some cases, they may consume hundreds of times their body weight daily. The usable organics are digested and the unusable materials passed out the anus. The resultant fecal material is essentially "cleaned dirt." This kind of deposit feeding is seen in many polychaete annelids (Figure 3.16A), some snails, some sea urchins, and most earthworms and sea cucumbers. Some deposit feeders utilize tentacle-like structures to consume sediment; these include some sea cucumbers, most sipunculans, certain bivalves, and several types of polychaetes (Figure 3.16B,C). Tentacle-utilizing deposit feeders preferentially remove only the uppermost deposits from the sediment surface and thus consume a far greater percentage of living organisms (especially bacteria, diatoms, and protists) and detrital organic material that accumulates there than do the burrowing deposit feeders. These tentacle-utilizing animals are generally called **selective deposit feeders**. Aquatic deposit feeders may also rely to a significant extent on fecal material that accumulates on the bottom, and many will actively consume their own fecal pellets (**coprophagy**), which may contain some undigested or incompletely digested organic material as well as microorganisms. Studies have shown that only about half



Courtesy of George F. Warner

FIGURE 3.15 Tube feet suspension feeding. Food-particle capture in the brittle star *Ophiothrix fragilis*. The photographs show two views of a captured food particle being transported by the arm tentacles to the mouth.

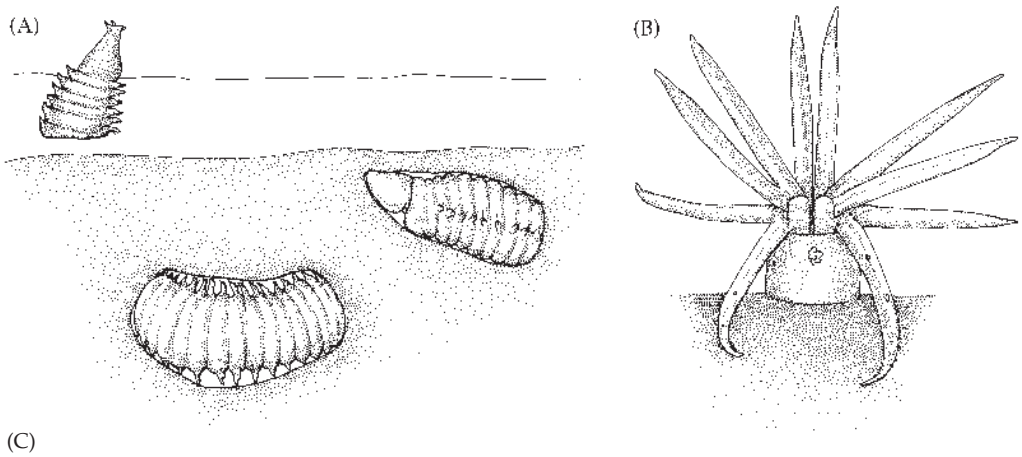


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FIGURE 3.16 Some deposit-feeding invertebrates. (A) A lumbrinerid polychaete burrowing in the sediment. This worm is a subsurface deposit feeder. (B) The sabellid polychaete *Manayunkia aestuarina* in its feeding posture. A pair of branchial filaments are being used to feed. The large particle falling in front of the tube has just been expelled from the branchial crown by a rejection current. (C) A surface deposit-feeding holothurian (*Synapta*).

of the bacteria ingested by marine deposit feeders is digested during passage through the gut. In all cases, deposit feeders are microphagous.

The ecological role of deposit feeding in sediment turnover is a critical one. When burrowing deposit feeders are removed from an area, organic debris accumulates, subsurface oxygen is depleted by bacterial decomposition, and anaerobic sulfur bacteria eventually bloom. On land, earthworms and other burrowers are important in maintaining the health of agricultural and garden soils.

Herbivory The following discussion deals with macroherbivory, or the consumption of macroscopic plants and algae. **Herbivory** is common throughout the animal kingdom.[5] It is most dramatically illustrated when certain invertebrate herbivores undergo a temporary population explosion. Famous examples are outbreaks of locusts, which can destroy virtually all plant material in their path of movement. In a similar fashion, herbivory by extremely high numbers of the Pacific sea urchin *Strongylocentrotus purpuratus* results in the wholesale destruction of kelp beds. Unlike suspension- and deposit-feeding herbivory, in which mostly single-celled and microscopic plant matter is consumed, macroherbivory requires the ability to "bite and chew" large pieces of vegetable matter. Although the evolution of biting and chewing mechanisms has taken place within the architectural framework of a number of different invertebrate lineages, it is always characterized by the development of hard (usually calcified or chitinous) "teeth," which are manipulated by powerful muscles. Members of a number of major invertebrate taxa have evolved macroherbivorous lifestyles, including molluscs, polychaetes, arthropods, and sea urchins.

Most molluscs have a unique structure called a **radula**, which is a muscularized, beltlike rasp armed with chitinous teeth that can be hardened with iron oxides. Herbivorous molluscs use the radula to scrape algae off rocks or to tear pieces of algal fronds or the leaves of terrestrial plants. The radula acts like a curved file that is drawn across the feeding surface (Figure 3.17C,D). Some polychaetes, such as nereids (family Nereidae), have sets of large chitinous teeth on an eversible pharynx or proboscis. The proboscis is protracted by hydrostatic pressure, exposing the teeth, which by muscular action tear or scrape off pieces of algae that are swallowed when the proboscis is retracted. As might be expected, the toothed pharynx of polychaetes is also suited for carnivory, and many primarily herbivorous polychaetes can switch to meat eating when algae are scarce. Sap-sucking sea slugs (Gastropoda: Sacoglossa) feed by piercing algal cells and sucking out the cellular contents. In some species of sacoglossans, the slugs sequester and use the living chloroplasts from the algae they feed on as a "solar energy source"—a unique behavior among metazoans.

Macroherbivory in arthropods is best illustrated by certain insects and crustaceans. Both of these large groups have powerful mandibles capable of biting off pieces of plant material and subsequently grinding or chewing them before ingestion. Some macroherbivorous

[5] Although in the broad sense, herbivory is a form of predation (on plants), for clarity of discussion we restrict the use of "herbivory" to vegetable eating and the use of "predation" to animal eating.

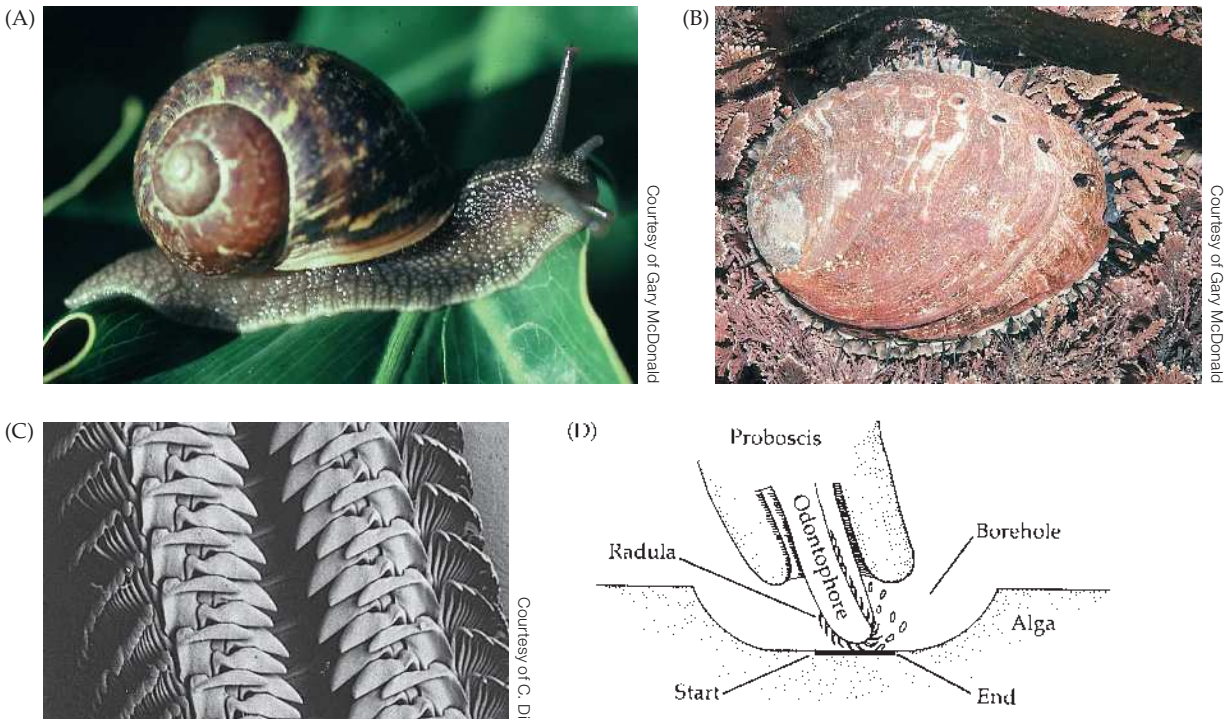

FIGURE 3.17 Some herbivorous invertebrates. (A) The common land snail *Cornu aspersum* (formerly *Helix aspersa*), munching on some foliage. (B) The red abalone *Haliotis rufescens*. (C) The radula, or rasping organ, of *H. rufescens*. (D) Diagram of a radula removing food particles from an alga (sagittal section). (E) The tropical Pacific sea urchin *Toxopneustes roseus*.

arthropods are able to temporarily switch to carnivory when necessary. This switching is rarely seen in the terrestrial herbivores because it is almost never necessary; terrestrial plant matter can almost always be found. In marine environments, however, algal supplies may at times be very limited. Some invertebrates have become specialized to feed on dead cellulose through their relationship with endosymbiotic bacteria, such as the sea daisies (Echinodermata: Asteroidea) and shipworms. Shipworms (highly specialized bivalve molluscs in the family Teredinidae) feed on floating logs, pier pilings, and ship bottoms in the sea (Figure 3.18).

Carnivory and scavenging The most sophisticated methods of feeding are those that require the active capture of live animals, or predation. Most carnivorous predators will, however, consume dead or dying animal matter when live food is scarce. Only a few generalizations about the many kinds of predation are presented here; detailed discussions of various taxa are presented in their appropriate chapters.

Active predation often involves five recognizable steps: prey location (predator orientation), pursuit (usually), capture, handling, and finally ingestion. Prey location usually requires a certain level of nervous system sophistication in which specialized sense organs are present (discussed later in this chapter). Many carnivorous invertebrates rely primarily on chemosensory location of prey, although many also use visual orientation, touch, and vibration detection. Chemoreceptors tend to be equally distributed around the bodies of radially symmetrical carnivores (e.g., jellyfish) but, coincidentally with cephalization, most invertebrates have their gustatory and olfactory receptors ("tasters" and "smellers") concentrated in the anterior region of their body or even in the head, if this anterior region is differentiated. A number of insects, including fruit flies, mosquitoes, and moths, rely on CO_2 sensing to locate their food source, but the sensing mechanisms are not yet fully characterized.

Predators may be classified by how they capture their prey—as motile stalkers, lurking predators (ambushers), sessile opportunists, or grazers (Figure 3.19). Stalkers actively pursue their prey; they include

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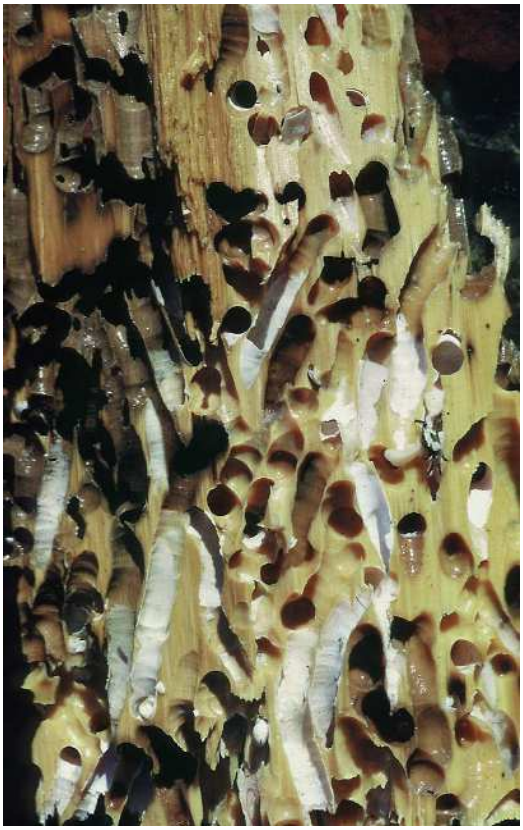

Courtesy of P. Fankboner

FIGURE 3.18 Shipworms. Wood from the submerged part of an old dock piling, split open to show the work of the wood-boring bivalve shipworm *Teredo navalis* (Mollusca). The shell valves are so reduced that they can no longer enclose the animal; instead they are used as "auger blades" in boring. The walls of the burrow are lined with a smooth, calcareous, shell-like material.

members of such disparate groups as polyclads, nemerteans, polychaete worms, gastropods, octopuses and squids, crabs, starfish, and many terrestrial arthropods. In all these groups, chemosensation is highly important in locating potential prey, although some cephalopods are known to be the most highly visual of all the invertebrate predators.

Lurking predators are those that sit and wait for their prey to come within capture distance, whereupon they quickly seize the victim. Many lurking predators, such as certain species of mantis shrimps (stomatopods), crabs, snapping shrimp (Alpheidae), spiders, and polychaetes, live in burrows or crevices from which they emerge to capture passing prey. There are even ambushing planarian flatworms, which produce mucous patches that form sticky traps for their prey. The cost of building traps is significant. Ant lions, for example, may increase their energy consumption as much as eightfold when building their sand capture pits, and energy lost in mucus secretion by planarians may account for 20% of the worm's energy. Predatory invertebrates, especially lurking predators, are frequently more or less territorial.

Sessile opportunists operate in much the same fashion as lurking predators do, but they lack the mobility of the latter. The same may be said for drifting opportunists, such as most jellyfishes. Many sessile predators, such as barnacles and cnidarians, are actually suspension feeders with a strong preference for live prey. A unique kind of carnivorous scavenging is seen in bone-eating annelid worms (*Osedax* spp.) that employ bacterial endosymbionts to facilitate their consumption of marine vertebrate bones that fall to the seafloor.

Grazing carnivores move about the substratum picking at the epifauna. Grazers may be indiscriminate, consuming whatever happens to be present, or they may be fairly choosy about what they eat. In either case, their diet consists largely of sessile and slow-moving animals, such as sponges, bryozoans, tunicates, snails, small crustaceans, and worms. Most grazers are omnivorous to some degree, consuming plant material along with their animal prey. Many crabs and shrimps are excellent grazers, continuously moving across the bottom and picking through the epifauna for tasty morsels. Sea spiders (pycnogonids) and some carnivorous sea slugs can also be classed as grazers on hydroids, bryozoans, sponges, tunicates, and other sessile epifauna. Ovulid snails (family Ovulidae) inhabit, and usually mimic, the gorgonians and corals upon which they slowly crawl about, nipping off polyps as they go.

One special category of carnivory is cannibalism, or intraspecific predation. Gary Polis (1981) examined over 900 published reports describing cannibalism in about 1,300 different species of animals. In general, he found that species of large animals (and also larger individuals in any given species) are the most likely to be cannibals. By far, the majority of the victims are juveniles. However, in a number of invertebrate groups, the tables turn and cannibalism occurs when smaller individuals band together to attack and consume a larger individual. Furthermore, females tend generally to be more cannibalistic than males, and males tend to be eaten far more often than females. In many species, filial cannibalism is common, in which a parent eats its dying, deformed, weak, or sick offspring. Polis concluded that cannibalism is a major factor in the biology of many species and may influence population structure, life history, behavior, and competition for mates and resources. He went so far as to point out that *Homo sapiens* may be "the only species capable of worrying whether its food is intra- or extraspecific."

Dissolved organic matter The total living biomass of the world's oceans is estimated to be about 2×10^9 tons of organic carbon (roughly 500 times the amount of organic carbon in the terrestrial environment). Furthermore, an additional 20×10^9 tons of particulate organic matter is estimated to occur in the seas, and another 200×10^9 tons of organic carbon (C) may occur in the seas as **dissolved organic matter (DOM)**.

(A)

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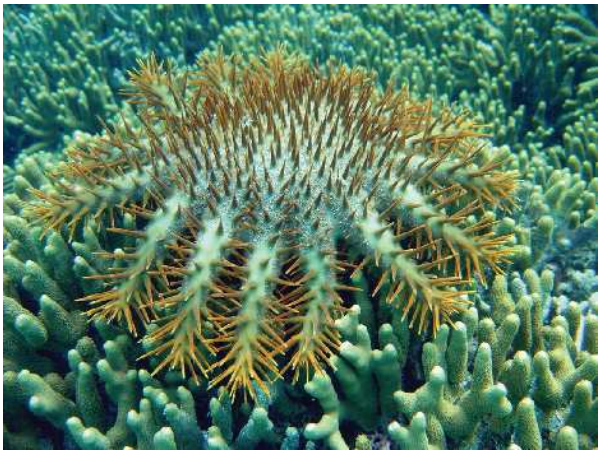
(B)



Courtesy of David Burdick/NOAA

(C)

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(D)

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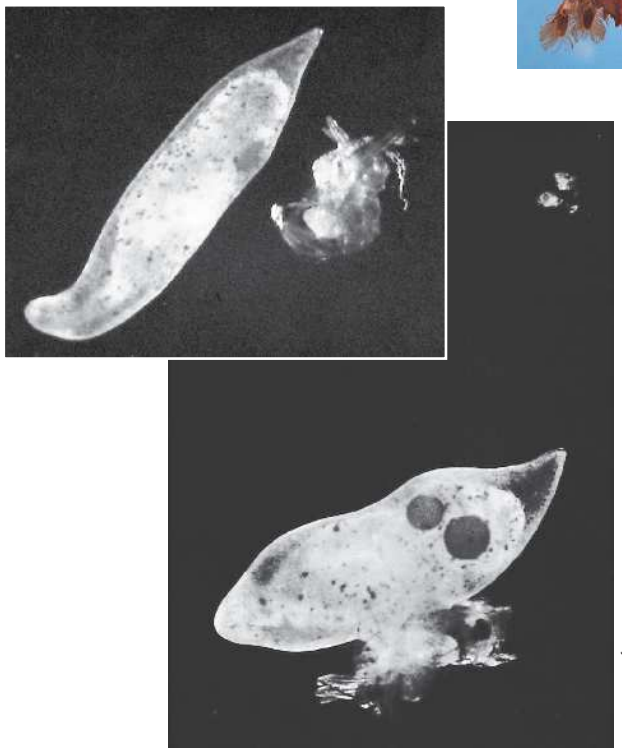

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(G)

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(H)

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◀ **FIGURE 3.19 Some predatory invertebrates.** (A) Most octopuses are active hunting predators; this one is a member of the genus *Eledone*. (B) The crown-of-thorns starfish, *Acanthaster*, feeds on corals. (C) The moon snail, *Polinices*, drills holes in the shells of bivalve molluscs to feed on the soft parts. (D) A mantis shrimp (stomatopod) and (E) its raptorial strike to capture a passing fish. (F) The predatory flatworm *Mesostoma* attacking a mosquito larva. (G) A cone snail (*Conus*) eating a fish. (H) The Atlantic dog whelk (*Nucella lapillus*), a predatory gastropod feeding on small barnacles.

Thus, at any moment in time, only a small fraction of the organic carbon in the world's seas actually exists in living organisms. Amino acids and carbohydrates may be the most common dissolved organics. Typical oceanic values of DOM range from 0.4 to 1.0 mg C/liter, but they may reach 8.0 mg C/liter near shore. Pelagic and benthic algae release copious amounts of DOM into the environment, as do certain invertebrates. Coral mucus, for example, is an important fraction of suspended and dissolved organic material over reefs, and it contains significant amounts of energy-rich compounds, including mono- and polysaccharides and amino acids. Other sources of DOM include decomposing tissue, detritus, fecal material, and metabolic byproducts discharged into the environment.

The idea that DOM may contribute significantly to the nutrition of marine invertebrates has been around for over 100 years. Marine microorganisms are known to use DOM, but its relative role in the nutrition of aquatic Metazoa is uncertain. Available data strongly suggest that members of all marine taxa (except perhaps arthropods and vertebrates) are capable of absorbing DOM to some extent, and in the case of ciliary-mucous suspension feeders, marine larvae, and many echinoderms and mussels, the ability to rapidly take up dissolved free amino acids from a dilute external medium is well established. But because of the complex chemical nature of dissolved organics, and the difficulty of measuring their rates of influx and loss, we still lack strong evidence of the actual use, or relative nutritional importance, of DOM to invertebrates.

Evidence from numerous studies indicates that absorption of DOM occurs directly across the body wall of invertebrates, as well as via the gills. Also, inorganic particles of colloidal dimensions provide a surface on which small organic molecules are concentrated by adsorption, to be captured and utilized by suspension-feeding invertebrates. Interestingly, most freshwater organisms seem incapable of removing small organic molecules from solution at anything like the rates characteristic of marine invertebrates. In fresh water, the uptake of DOM is probably retarded by the processes of osmoregulation.

Chemoautotrophy A special form of autotrophy that occurs in certain bacteria relies not on sunlight and photosynthesis as a source of energy to make organic molecules from inorganic raw materials (**photoautotrophy**), but rather on the oxidation of certain inorganic substances. This is called **chemoautotrophy**. Chemoautotrophs use CO_2 as their carbon source, obtaining energy by oxidizing hydrogen sulfide (H_2S), ammonia (NH_3), methane (CH_4), ferrous ions (Fe^{2+}), or some other chemical, depending on the species. These prokaryotes are not uncommon in aerated soils, and certain species live as symbionts in the tissues of a few marine invertebrates.

Some of the most interesting of these chemoautotrophic organisms derive their energy from the oxidation of hydrogen sulfide released at hydrothermal vents on the deep-sea floor—where, in fact, they are the sole primary producers in the ecosystem. In this environment, chemoautotrophic bacteria inhabit the tissues of certain mussels, clams, and vestimentiferan tube worms, where they produce organic compounds that are utilized by their hosts. Similar invertebrate-bacteria relationships have been discovered in shallow cold-water petroleum and salt (brine) seeps, where the chemoautotrophic microorganisms live off the methane- and hydrogen sulfide–rich waters associated with such seafloor environments. In all these cases, the bacteria actually live within the cells of their hosts. In bivalves, the bacteria inhabit the gill cells and extract methane or other chemicals from the water that flows over those structures. In the case of the tube worms, the hosts must transport the H_2S to their bacterial partners, which live in tissues deep within the animals' bodies. The worms have a unique type of hemoglobin that transports not only oxygen (for the worm's metabolism) but sulfide as well.

Excretion and Osmoregulation

Excretion is the elimination from the body of metabolic waste products, including carbon dioxide and water (produced primarily by cellular respiration) and excess nitrogen (produced as ammonia from deamination of amino acids). The excretion of respiratory CO_2 is generally accomplished by structures that are separate from those associated with other waste products and is discussed in the Circulation and Gas Exchange section.

The excretion of nitrogenous wastes is usually intimately associated with osmoregulation—the regulation of water and ion balance within the body fluids—so these processes are considered together here. Excretion, osmoregulation, and ion regulation serve not only to rid the body of potentially toxic wastes, but also to maintain concentrations of the various components of body fluids at levels appropriate for metabolic activities. As we shall see, these processes are structurally and functionally tied to the overall level of body complexity and construction, the nature of other physiological systems, and the environment in which an animal lives. We again emphasize the necessity of

looking at whole animals, the integration of all aspects of their biology and ecology, and the possible evolutionary histories that could have produced compatible and successful combinations of functional systems.

Nitrogenous Wastes and Water Conservation

The source of most of the nitrogen in an animal's system is amino acids produced from the digestion of proteins. Once absorbed, these amino acids may be used to build new proteins, or they may be deaminated and the residues used to form other compounds (Figure 3.20). The excess nitrogen released during deamination is typically liberated from the amino acid in the form of ammonia (NH_3), a highly soluble but quite toxic substance that must be either diluted and eliminated quickly or converted to a less toxic form. Typically, one nitrogenous waste form tends to predominate in a given species, and the nature of that chemical is generally related to the availability of environmental water.

The major excretory product in most marine and freshwater invertebrates is ammonia, since their environment provides an abundance of water as a medium for rapid dilution of this toxic substance. Such animals are said to be **ammonotelic**. Being highly soluble, ammonia diffuses easily through fluids and tissues, and much of it is lost straight across the body walls of some ammonotelic animals. Animals that do not possess discrete excretory organs (e.g., sponges, cnidarians, xenacoelomorphs, and echinoderms) are more or less limited to the production of ammonia and thus are restricted to aquatic habitats.

Terrestrial invertebrates (indeed, all land animals) have water conservation challenges. They simply cannot afford to lose much body water in the process of diluting their wastes. These animals convert their nitrogenous wastes to more complex but far less toxic substances. These compounds are energetically expensive to produce, but they often require relatively little or no dilution by water, and they can be stored within the body prior to excretion.

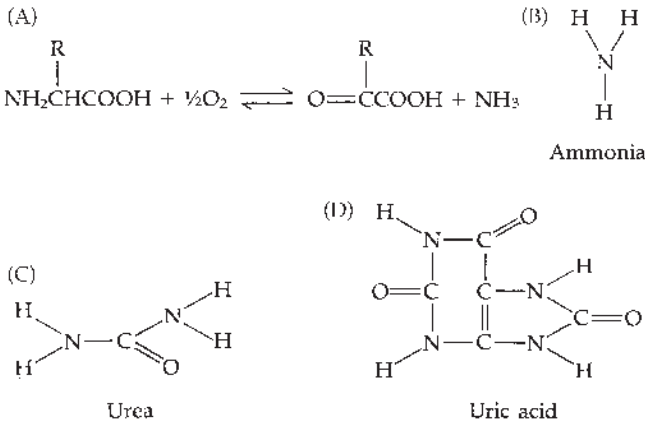

FIGURE 3.20 Nitrogenous waste products. (A) The general reaction for deamination of an amino acid producing a keto acid and ammonia. (B–D) The structures of three common excretory compounds. (B) Ammonia. (C) Urea. (D) Uric acid.

There are two major metabolic pathways for the detoxification of ammonia: the urea pathway and the uric acid pathway. The products of these pathways, **urea** and **uric acid**, are illustrated in Figure 3.20, along with ammonia for comparison. **Ureotelic animals** include amphibians, mammals, and cartilaginous fishes (sharks and rays); urea is a relatively rare and insignificant excretory compound among invertebrates. On the other hand, the ability to produce uric acid is critically associated with the success of certain invertebrates on land. **Uricotelic animals** have capitalized on the relative insolubility (and very low toxicity) of uric acid, which is generally precipitated and excreted in a solid or semisolid form with little water loss. Most land-dwelling arthropods and snails have evolved structural and physiological mechanisms for the incorporation of excess nitrogen into molecules of uric acid. We emphasize that various combinations of these and other forms of nitrogen excretion are found in most animals. In some cases, individual animals can actually vary the proportion of these compounds they produce, depending on short-term environmental changes affecting water loss.

Osmoregulation and Habitat

In addition to its relationship to excretion, osmoregulation is directly associated with environmental conditions. The composition of seawater is very similar to that of the body fluids of most invertebrates, in terms of *total* concentration *and* the concentrations of many particular ions. Thus, the body fluids of many marine invertebrates and their habitats are close to being isotonic. We hasten to add, however, that probably no animal has body fluids that are exactly isotonic with seawater, and therefore all are faced with the need for some degree of ionic and osmoregulation. Nonetheless, marine invertebrates certainly do not face the extreme osmoregulatory problems encountered by land and freshwater forms.

As shown in Figure 3.21, the body fluids of freshwater animals are strongly hypertonic with respect to their environment, and thus they face serious problems of water influx as well as the potential loss of precious body salts. Terrestrial animals are exposed to air and thus to problems of water loss. The evolutionary invasion of land and fresh water was accompanied by the development of mechanisms that solved these problems, and only a relatively small number of invertebrate groups have managed to do this. Animals inhabiting freshwater and terrestrial habitats generally have excretory structures that are responsible for eliminating or retaining water as needed, and they often possess modifications of the body wall to reduce overall

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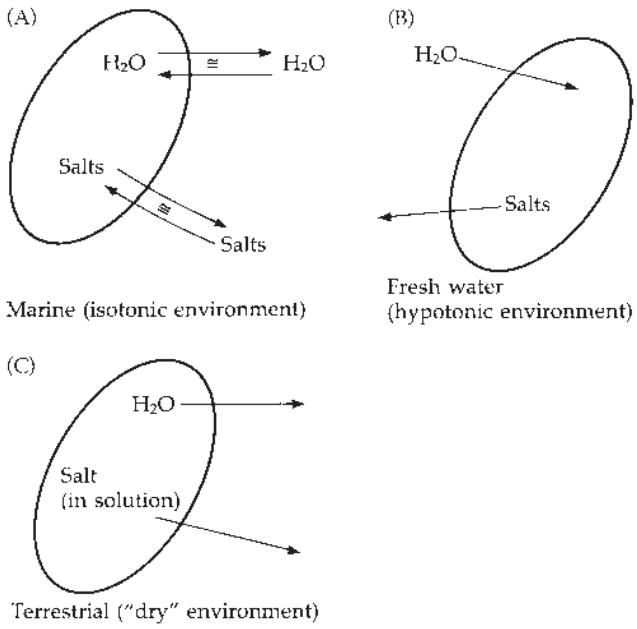

FIGURE 3.21 Relative osmotic and ionic conditions existing in marine, freshwater, and terrestrial invertebrates and their environments. The arrows indicate the directions in which water and salts move passively in response to concentration gradients. Remember that in each of these cases, movement occurs in both directions, but it is the potential net movement along the gradient that is important and is what the freshwater and terrestrial animals must constantly battle against. For marine invertebrates, the body fluids and the environment are nearly isotonic, so there is little net movement in either direction. (A) The organism and its environment are isotonic. (B) The organism is hypertonic. (C) The organism is hypotonic.

permeability. The most successful invertebrate body plans on land, and in some ways of all environments, are those of the arthropods and gastropods. Their effective excretory structures and/or thickened exoskeletons provide them with physiological osmoregulatory capabilities plus a barrier against desiccation.

Osmoregulatory problems of aquatic animals are, of course, determined by the salinity of the environmental water relative to the body fluids (Figure 3.21). Organisms respond physiologically to changes in environmental salinities in one of two basic ways. Some, such as most freshwater forms (certain crustaceans and clitellate annelids), maintain their internal body fluid concentrations regardless of external conditions and are thus called **osmoregulators**. Others, including a number of intertidal and estuarine forms (mussels and some other bivalves, and a variety of soft-bodied animals), allow their body fluids to vary with changes in environmental salinities; they are appropriately called **osmoconformers**. Again, even the body fluids of marine, so-called osmoconformers are not exactly isotonic with respect to their surroundings; thus, these animals must osmoregulate slightly. Neither of these strategies is without limits, and tolerance to various environmental salinities varies among different species. Those that are restricted to a very narrow range of salinities are said to be **stenohaline**, while those that tolerate relatively extensive variations, such as many estuarine animals, are **euryhaline**.

Although the preceding discussion may seem clear-cut, it is an oversimplification. Experimental data from whole animals tell only part of the story of osmoregulation. When a whole marine animal is placed in a hypotonic medium, it tends to swell (if it is an osmoconformer) or to maintain its normal body volume (if it is an osmoregulator). Even at this gross level, most invertebrates usually show evidence of both conforming and regulating. For instance, an osmoconformer generally swells for a period of time in a lowered-salinity environment and then begins to regulate. Its swollen volume will decrease, although probably not to its original size. The same is true of most osmoregulators when faced with a decrease in environmental salinity, but the degree of original swelling is much reduced. In both cases, the swelling of the body is a result of an influx of environmental water into the extracellular body fluids (blood, coelomic fluids, and intercellular fluids). Within limits, this excess water is handled by excretory organs and various surface epithelia of the gut and body wall. However, a second part of the osmoregulatory phenomenon takes place at the cellular level.

As the tonicity (relative concentrations) of the body fluids drops with the entrance of water, the cells in contact with those fluids are placed in conditions of stress—they are now in hypotonic environments. These stressed cells swell to some degree because of the diffusion of water into their cytoplasm, but not to the degree one might expect, given the magnitude of the osmotic gradient to which they are subjected. Cellular-level osmoregulation is accomplished by a loss of dissolved materials from the cell into the surrounding intercellular fluids. The solutes released from these cells include both inorganic ions and free amino acids. Thus, osmoconformers are not passive animals that inactively tolerate extremes of salinities. Nor are marine invertebrates free from osmotic problems, even though we read statements that they are "98% water" or other such comments.

Excretory and Osmoregulatory Structures

Water expulsion vesicles The form and function of organs or systems associated with excretion and osmoregulation are related not only to environmental conditions, but also to body size (especially the surface-to-volume ratio) and other basic features of an organism's body plan. In very small creatures, most metabolic wastes diffuse easily across the body covering because these organisms have sufficient body surface (environmental contact) relative to their volume. However, this high surface-area-to-volume ratio presents a distinct

osmoregulatory problem, particularly for freshwater forms. Freshwater protists and freshwater sponges typically possess specialized organelles called **contractile vacuoles** or **water expulsion vesicles** (WEVs), which actively excrete excess water. These structures accumulate cytoplasmic water and expel it from the cell. Both of these activities apparently require energy, as suggested in part by the large numbers of mitochondria typically associated with WEVs. The idea that WEVs are primarily osmoregulatory in function is supported by a good deal of evidence. Most convincing is the fact that their rates of filling and emptying change dramatically when the cell is exposed to different salinities.

Nephridia Although certain invertebrates possess no known excretory structures, most nephrozoans have some sort of ectodermally derived nephridia that serve for excretion or osmoregulation, or both. The simplest type of nephridium to appear in the evolution of animals was the **protonephridium** (Figure 3.22A). Protonephridial systems are characterized by a tubular arrangement opening to the outside of the body via one or more nephridiopores and terminating internally in closed unicellular units. These units are the cap cells (or terminal cells) and may occur singly or in clusters. Each cell is folded into a cup shape, creating a concavity leading to an excretory duct (nephridioduct) and eventually to the nephridiopore. Two generally recognized types of protonephridia are **flame bulbs**, bearing a tuft of numerous cilia within the cavity, and **solenocytes**, usually with only one or two flagella. There is some evidence that several different types of flame bulb protonephridia have been independently derived from solenocyte precursors, but the details of nephridial evolution are still controversial.

The cilia or flagella drive fluids down the nephridioduct, thereby creating a lowered pressure within the tubule lumen. This lowered pressure draws body fluids, carrying wastes, across the thin cell membranes and into the duct. Selectivity is based primarily on molecular size. Protonephridia are common in acoelomates, many blastocoelomates, and some annelids but are rare among most adult coelomates (although they occur frequently in various larval types). Protonephridia are

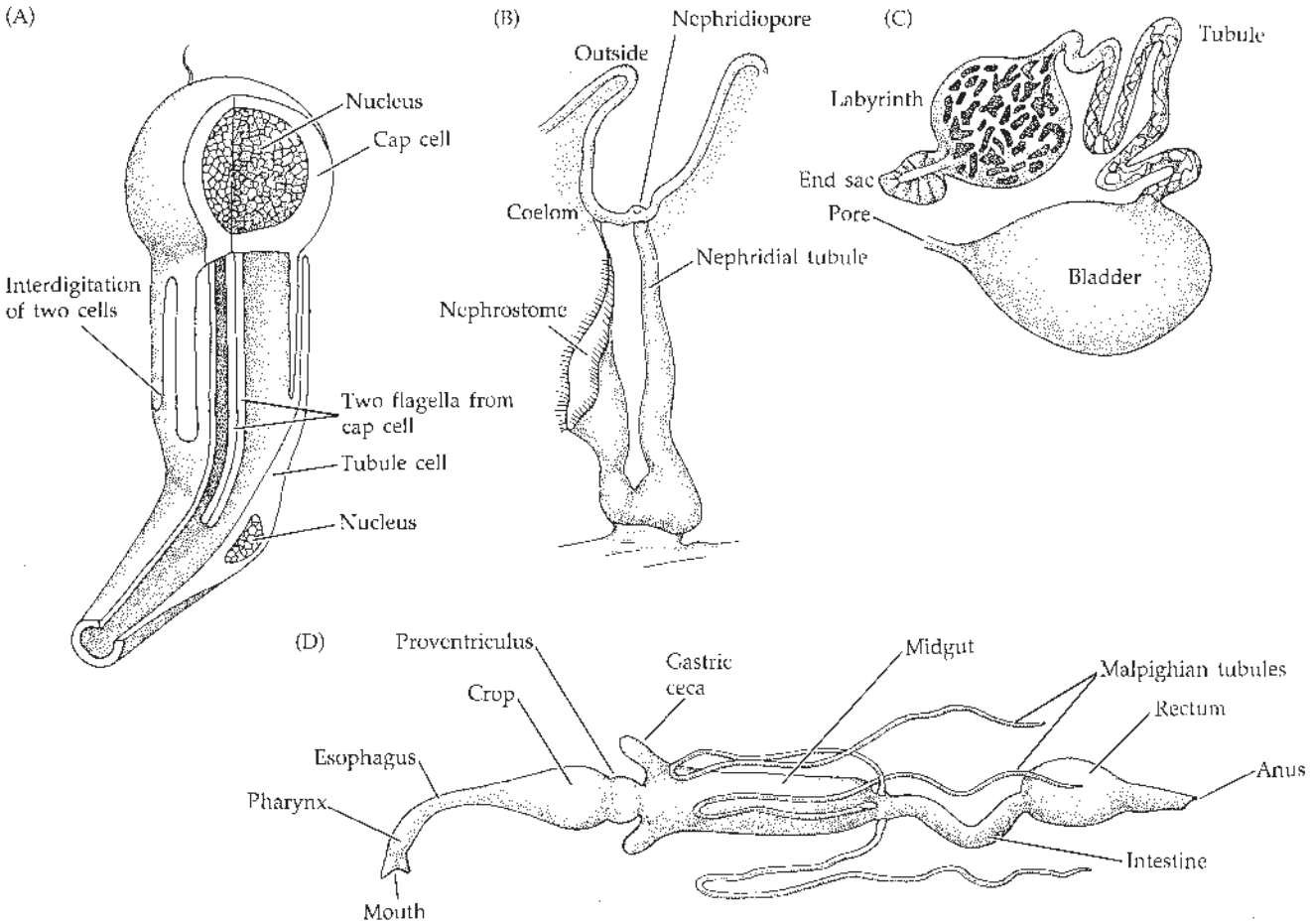

FIGURE 3.22 Some invertebrate excretory structures. (A) A single protonephridium, with the cap cell and tubule cell (cutaway view). (B) A simple metanephridium from a marine annelid. The nephrostome opens to the coelom, and the nephridiopore opens to the exterior. (C) The internally closed nephridium (antennal gland) of a crustacean. (D) An insect's digestive tract; excretory Malpighian tubules extract wastes from the hemocoel and empty them into the gut.

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probably more important in osmoregulation than in excretion, and in taxa with both marine and freshwater species (e.g., Entoprocta) they are typically more abundant in the latter group. In most of these animals, nitrogenous wastes are expelled primarily by diffusion across the general body surface.

A second and more complex type of excretory structure among invertebrates is the **metanephridium** (Figure 3.22B). There is a critical structural difference between protonephridia and metanephridia: both are open to the outside, but metanephridia are open internally to the body fluids as well, although arthropods have closed metanephridia. Metanephridia are also multicellular. The inner end typically bears a ciliated funnel (nephrostome), and the duct is often elongated and convoluted and may include a bladderlike storage region. Metanephridia function by taking in large amounts of body fluid through the open nephrostome and then selectively absorbing most of the reclaimable components back into the body fluids through the walls of the bladder or the excretory duct.

In very general terms, we can relate the structural and functional differences between proto- and metanephridia to the body plans with which they are commonly associated. Whereas protonephridia can adequately serve animals that have solid bodies (acoelomates), body cavities of small volume (blastocoelomates), or very small bodies (e.g., larvae), metanephridia cannot. Open funnels would be ineffective in acoelomates and would quickly drain small blastocoelomates of their limited body fluids. Conversely, protonephridia are generally not capable of handling the relatively large body and fluid volumes typical of coelomate invertebrates. Thus, in many large coelomate animals (e.g., annelids, molluscs, onychophorans) one or more pairs of metanephridia are typically found.

We have very broadly interpreted the terms "protonephridia" and "metanephridia" in the above discussion, and we use them as explained above throughout this text unless specified otherwise. However, there are more complications than our simple usage suggests. For example, there is a frequent association of nephridia, especially metanephridia, with structures called coelomoducts. **Coelomoducts** are tubular connections arising from the coelomic lining and extending to the outside via special pores in the body wall. Their inner ends are frequently funnellike and ciliated, resembling the nephrostomes of metanephridia. Coelomoducts may have arisen evolutionarily as a means of allowing the escape of gametes to the outside; they are, in fact, considered homologous with the reproductive ducts of many invertebrates. Primitively, the coelomoducts and nephridia were separate units; however, through evolution they have in many cases fused in various fashions to become what are called **nephromixia**.

Generally speaking, there are three types of nephromixia. When a coelomoduct is joined with a protonephridium and they share a common duct, the structure is called a **protonephromixium**. When a coelomoduct is united with a metanephridium, the result is either a **metanephromixium** or **mixonephridium**, depending on the structural nature of the union. Whereas coelomoducts originate from the coelomic lining, the nephridial components arise from the outer body wall, so nephromixia are a combination of mesodermally and ectodermally derived parts. Obviously there is some confusion at times about which term applies to a particular "nephridial" type if the precise developmental origin is not clear. We do not wish to belabor this point, so we leave it here to be resurrected periodically in later chapters.

Other organs of excretion Not all Nephrozoa possess excretory organs that are clearly proto- or metanephridia. In some taxa (e.g., echinoderms, chaetognaths), no definite excretory structures are known. In such cases wastes are eliminated across the surface of the skin or gut lining, perhaps with the aid of ameboid phagocytic cells that collect and transport these products. Other groups possess excretory organs that may represent highly modified nephridia or secondarily derived ("new") structures. For example, the antennal and maxillary glands of crustaceans appear to be derived from metanephridia, whereas the Malpighian tubules of tardigrades, insects, and spiders arose independently (Figure 3.22C,D). Nematodes have a series of different excretory organs not found in other animal phyla. The details of these structures are discussed in appropriate later chapters.

Circulation and Gas Exchange

Internal Transport

The transport of materials from one place to another within an organism's body depends on the movement and diffusion of substances in body fluids. Nutrients, gases, and metabolic waste products are generally carried in solution or bound to other soluble compounds within the body fluid itself or sometimes in loose cells (such as blood cells) suspended in fluid. Any system of moving fluids that reduces the functional diffusion distance that these products must traverse may be referred to as a circulatory system, regardless of its embryological origin or its ultimate design. The nature of the circulatory system is directly related to the size, complexity, and lifestyle of the organism in question. Usually the circulatory fluid is an internal, extracellular, aqueous medium produced by the animal. There are, however, a few instances in which circulatory functions are accomplished at least partly by other means. For instance, sponges and most cnidarians utilize water from the environment as a circulatory fluid, sponges by passing the water through a series of channels in their bodies, and cnidarians by circulating water through the gut (Figure 3.23A,B).

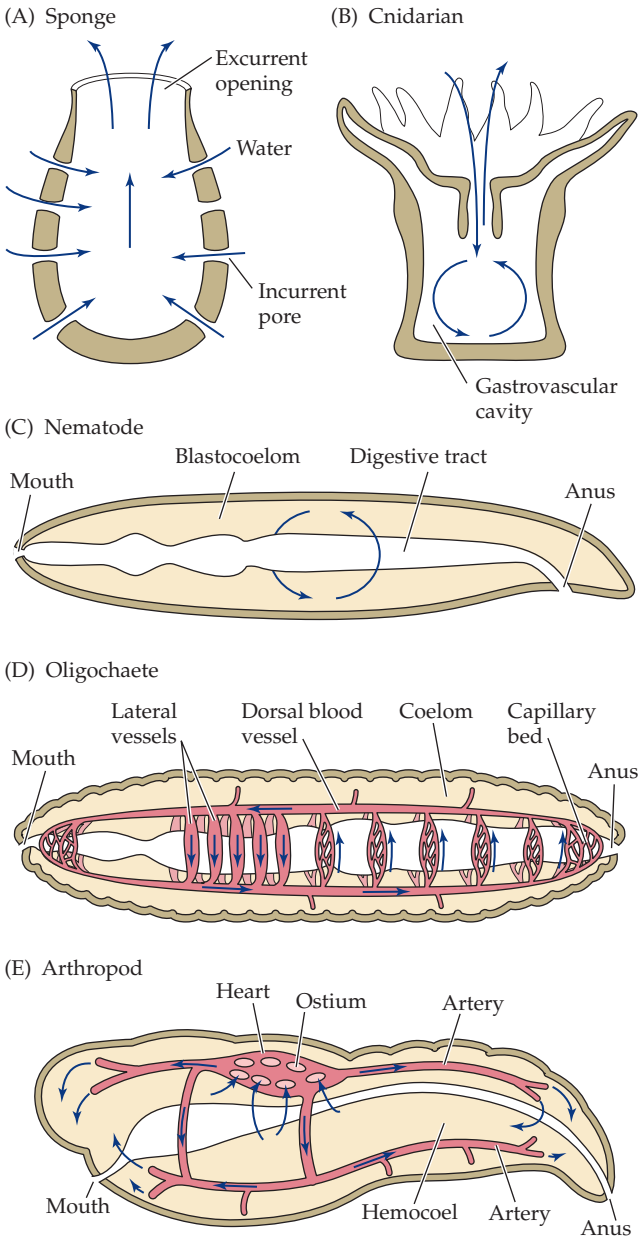

FIGURE 3.23 Invertebrate circulatory systems. Sponges (A) and cnidarians (B) utilize environmental water as their circulatory fluid. (C) Blastocoelomates (e.g., rotifers and nematodes) use their body cavity fluid for internal transport. (D) The closed circulatory system of an earthworm contains blood that is kept separate from the coelomic fluid. (E) Arthropods are characterized by an open circulatory system, in which the blood and body cavity (hemocoelic) fluid are one and the same.

In all Metazoa, the intercellular fluids play a critical role as a transport medium. Even where complicated circulatory plumbing exists, tissue fluids are still necessary to bring dissolved materials in contact with cells, a vital process for life support. In some animals (e.g., flatworms), there are no special chambers or vessels for body fluids other than the gut and intercellular spaces through which materials diffuse on a cell-to-cell level. This condition limits these animals to relatively small sizes or to shapes that maintain low diffusion distances. Most animals, however, have some specialized structure to facilitate the transport of various body fluids and their contents. This structure may include the body cavities themselves or actual circulatory systems of vessels, chambers, sinuses, and pumping organs. Actually, many animals employ both their body cavity and a circulatory system for internal transport.

Blastocoelomate invertebrates use the fluids of the body cavity for circulation (Figure 3.23C). Most of these animals (e.g., rotifers and many nematodes) are quite small, or are long and thin, and adequate circulation is accomplished by the movements of the body against the body fluids, which are in direct contact with internal tissues and organs. Several types of cells are generally present in the body fluids of blastocoelomates. These cells may serve in activities such as transport and waste accumulation, but their functions have not been well studied. A few coelomate invertebrates (e.g., some annelid groups like sipunculans, and most echinoderms) also depend largely on the body cavity as a circulatory chamber.

Circulatory Systems

Beyond the relatively rudimentary circulatory mechanisms discussed above, there are two principal designs or structural plans for accomplishing internal transport (exceptions and variations are discussed under specific taxa). These two organizational plans are closed and open circulatory systems, both of which contain a circulatory fluid, or blood. In **closed circulatory systems** the blood stays in distinct vessels and perhaps in lined chambers; exchange of circulated material with parts of the body occurs in special areas of the system such as capillary beds (Figure 3.23D). Since the blood itself is physically separated from the intercellular fluids, the exchange sites must offer minimal resistance to diffusion; thus one finds capillaries typically have membranous walls that are only a single cell layer thick. Closed circulatory systems are common in animals with well-developed or spacious coelomic compartments (e.g., annelids, nemerteans, phoronids, vertebrates). Such arrangements facilitate the transport of materials that might otherwise be isolated by the mesenteries or peritoneum of the body cavity. In such situations the blood and coelomic fluid may be quite different from one another, both in composition and in function from one body area to another. For example, blood may transport nutrients and gases, while coelomic fluid may accumulate metabolic wastes for removal by nephridia and also serve as a hydrostatic skeleton.

It takes power to keep a fluid moving through a plumbing system. Many invertebrates with closed systems rely on body movements and the exertion of coelomic pressure on vessels (often containing one-way valves) to move their blood. These activities are

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frequently supplemented by muscles of the blood vessel walls that contract in peristaltic waves. In addition, there may be special heavily muscled pumping areas along certain vessels. These regions are sometimes referred to as hearts, but most are perhaps more appropriately called contractile vessels or pulsatile organs.

Open circulatory systems are associated with a reduction of the adult coelom, including a secondary loss of most of the peritoneal lining around the organs and inner surface of the body wall. The circulatory system itself usually includes a distinct heart, as the primary pumping organ, and various vessels, chambers, or ill-defined sinuses (Figure 3.23E). The degree of elaboration of such systems depends primarily on the size, complexity, and to some extent the activity level of the animal. This kind of system, however, is "open" in that the blood, often called the **hemolymph**, empties from vessels into the body cavity and directly bathes the organs. The body cavity is called a **hemocoel**. Open circulatory systems are typical of arthropods and noncephalopod molluscs, and such animals are sometimes referred to as being hemocoelomate.

Just because the open circulatory system seems a bit sloppy in its organization, it should not be viewed as poorly "designed" or inefficient. In fact, in many groups this type of system has assumed a variety of functions beyond circulation. For example, in bivalves and gastropods, the hemocoel functions as a hydrostatic skeleton for locomotion and certain types of burrowing activities. In most spiders, the limbs are extended by forcing hemolymph into the appendages. In aquatic arthropods, it also serves a hydrostatic function when the animal molts and temporarily loses its exoskeletal support. In large terrestrial insects, the transport of respiratory gases has been largely assumed by the tracheal system, and one of the primary responsibilities taken on by the open circulatory system appears to be thermal regulation.

Hearts and Other Pumping Mechanisms

Circulatory systems—open or closed—generally have structural mechanisms for pumping the blood and maintaining adequate blood pressure. Beyond the influence of general body movements, most of these structures fall into the following categories: contractile vessels (as in annelids), ostiate hearts (as in arthropods), and chambered hearts (as in molluscs and vertebrates). The method of initiating contraction of these different pumps (the pacemaker mechanism) may be intrinsic (originating within the musculature of the structure itself) or extrinsic (originating from motor nerves arising outside the structure). The first case describes the myogenic hearts of molluscs and vertebrates; the second describes the neurogenic hearts of most arthropods and, at least in part, the contractile vessels of annelids.

Blood pressure and flow velocities are intimately associated not only with the activity of the pumping mechanism, but also with vessel diameters. Energetically, it costs a good deal more to maintain flow through a narrow pipe than through a wide pipe. This cost is minimized in animals with closed circulatory systems by keeping the narrow vessels short and using them only at sites of exchange (i.e., capillary beds) and by using the larger vessels for long-distance transport from one exchange site to another. In the human circulatory system, for example, arteries have an average radius of 2.0 mm, veins 2.5 mm, and capillaries 0.006 mm. But reducing the diameter of a single vessel increases flow velocity, which poses problems at an exchange site. This problem is solved by the presence of large numbers of small vessels, the total cross-sectional area of which exceeds that of the larger vessel from which they arise. The result is that blood pressure and total flow velocity actually decrease at capillary exchange sites. A drop in blood pressure and a relative rise in blood osmotic pressure along the capillary bed facilitate exchanges between the blood and surrounding tissue fluids. In open systems, both pressure and velocity drop once the blood leaves the heart and vessels and enters the spacious hemocoel.

Gas Exchange and Transport

One of the principal functions of most circulatory fluids is to carry oxygen and carbon dioxide through the body and exchange these gases with the environment. With few exceptions, oxygen is necessary for catabolic cellular respiration. Although a number of invertebrates can survive periods of environmental oxygen depletion—either by dramatically reducing their metabolic rate or by switching to anaerobic respiration—most cannot; they depend upon a relatively constant oxygen supply.

All animals can take in oxygen from their surroundings while at the same time releasing carbon dioxide, a metabolic waste product of respiration. We define the uptake of oxygen and the loss of carbon dioxide at the surface of the organism as gas exchange, reserving the term "respiration" for the energy-producing metabolic activities within cells. Some authors distinguish these two processes with the terms "external respiration" and "cellular (internal) respiration."

Gas exchange in nearly all animals operates according to certain common principles regardless of any structural modifications that serve to enhance the process under different conditions. The basic strategy is to bring the environmental medium (water or air) close to the appropriate body fluid (blood or body cavity fluid) so that the two are separated only by a wet membrane across which the gases can diffuse. The system must be moist because the gases must be in solution in order to diffuse across the membrane. The diffusion process

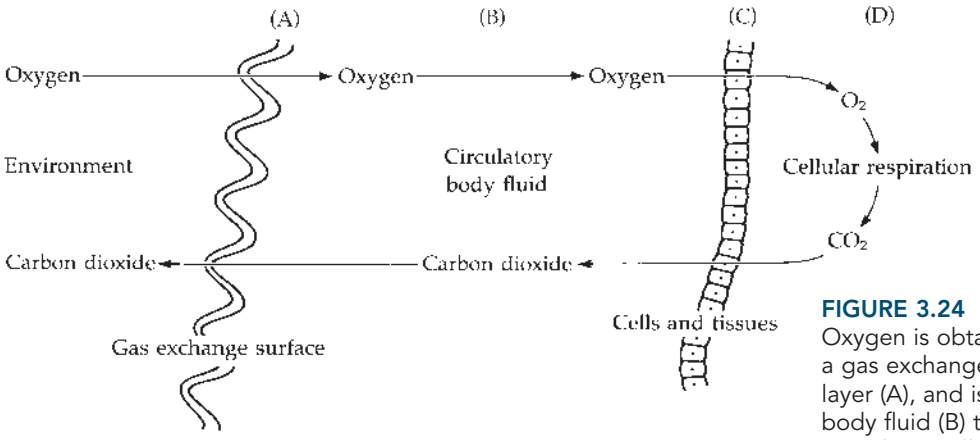

FIGURE 3.24 Gas exchange in animals. Oxygen is obtained from the environment at a gas exchange surface, such as an epithelial layer (A), and is transported by a circulatory body fluid (B) to the body's cells and tissues (C), where cellular respiration occurs (D). Carbon dioxide follows the reverse path. See text for details.

depends on the concentration gradients of the gases at the exchange site; these gradients are maintained by the circulation of internal fluids to and away from these areas (Figure 3.24).

Gas exchange structures Many invertebrates lack special gas exchange structures. In such animals gas exchange is typically integumentary or cutaneous, and it occurs over much of the body surface. Such is the case in many tiny animals with very high surface-to-volume ratios and in some larger soft-bodied forms (e.g., cnidarians and flatworms). Most animals with integumentary gas exchange are restricted to aquatic or damp terrestrial environments where the body surface is kept moist. Integumentary gas exchange also supplements other methods in many animals, even certain vertebrates (e.g., amphibians).

Many marine and many freshwater invertebrates possess gills (Figure 3.25A–C,G), which are external organs or restricted areas of the body surface specialized for gas exchange. Basically, gills are thin-walled processes, well supplied with blood or other body fluids, which promote diffusion between this fluid and the environment. Gills are frequently highly folded or digitate, increasing the diffusive surface area. A great number of nonhomologous structures have evolved as gills in different taxa, and they often serve other functions in addition to gas exchange (e.g., sensory input and feeding). By their very nature, gills are permeable surfaces that must be protected during times of osmotic stress, such as occur in estuaries and intertidal environments. In these instances, the gills may be housed within chambers or be retractable.

A few marine invertebrates employ the lining of the gut as the gas exchange surface. Water is pumped in and out of the hindgut, or a special evagination thereof, in a process called **hindgut irrigation**. Many sea cucumbers and thalassimatid worms use this method of gas exchange (Figure 3.25F).

As you can imagine, protruding gills would not work on dry land. Here, the gas exchange surfaces must be internalized to keep them moist and protected and to prevent body water loss through the wet surfaces. The lungs of terrestrial vertebrates are the most familiar example of such an arrangement. Among the invertebrates, the arthropods have managed to solve the problems of "air breathing" in two basic ways. Scorpions, spiders and their kin possess book lungs, and many other arachnids, most insects, and all centipedes and millipedes possess tracheae (Figure 3.25D,E). **Book lungs** are blind inpocketings with highly folded inner linings across which gases diffuse between the hemolymph and the air. **Tracheae**, however, are branched, usually anastomosed invaginations of the outer body wall and are open both internally and externally.

The tracheae of most insects allow diffusion of oxygen from air directly to the tissues of the body; the blood plays little or no role in gas transport. Rather, intercellular fluid extends partway into the tracheal tubes as a solvent for gases. Atmospheric pressure tends to prevent these fluids from being drawn too close to the external body surface, where evaporation is a potential problem. In addition, the outside openings (**spiracles**) of the tracheae are often equipped with some mechanism of closure. In many insects,

FIGURE 3.25 Some gas exchange structures in invertebrates. (A) The tube-dwelling polychaete worm *Eudistylia*, with its feeding–gas exchange tentacles extended. (B) A sea slug (*Chromodoris*) displaying its branchial plume. (C) The gills of the giant gumboot chiton (*Cryptochiton stelleri*) are visible along the left side of its foot. (D) A general plan of the tracheal system of an insect. (E) A single insect trachea and its branches (tracheoles), which lead directly to a muscle cell. (F) Diagram of a sea cucumber dissected to expose the paired respiratory trees, which are flushed with water by hindgut irrigation. (G) The placement of gills beneath the flaps (carapace) of the thorax in a crustacean (lateral view). (H) A terrestrial banana slug (*Ariolimax*) has a pneumostome that opens to the air sac, or "lung."

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(A)

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(B)

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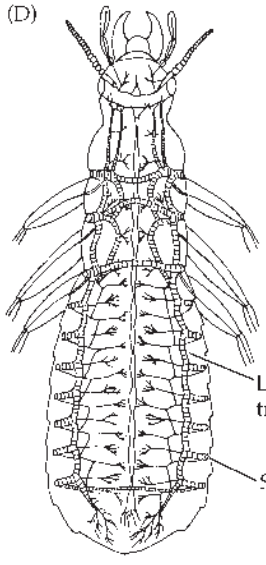

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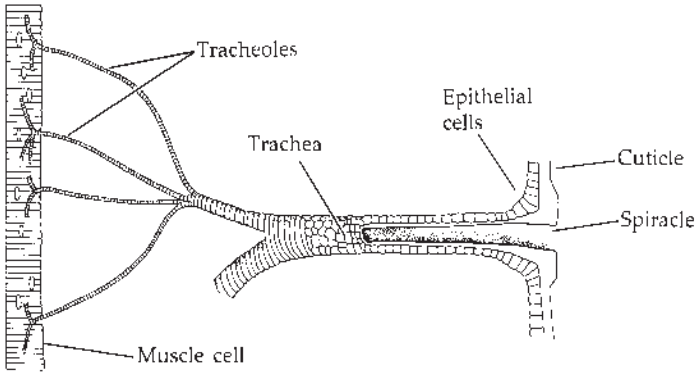

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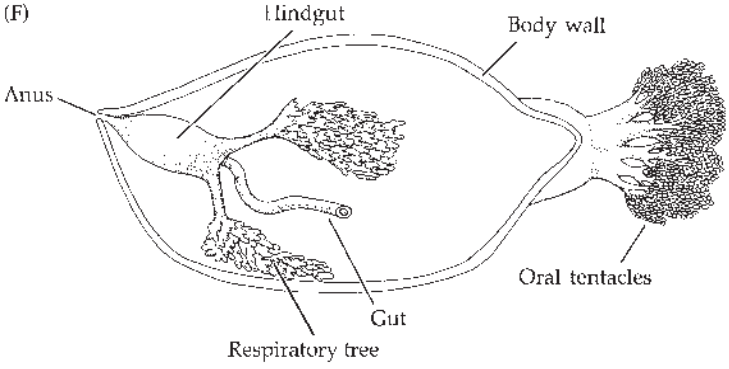

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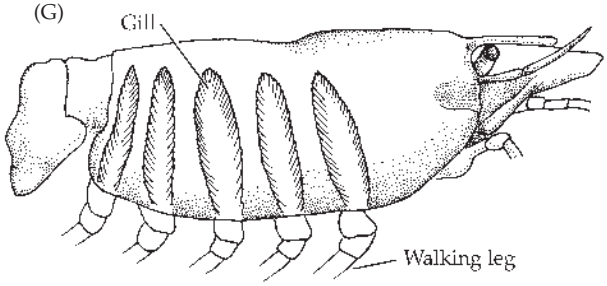

(H)

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especially large ones, special muscles ventilate the tracheae by actively pumping air in and out. Terrestrial isopod crustaceans (e.g., sowbugs and pillbugs) have invaginated gas exchange structures on some of their abdominal appendages. These inpocketings are called **pseudotracheae** but are probably not homologous with the tracheae or the book lungs of insects and spiders.

The only other major group of terrestrial invertebrates whose members have evolved distinct air-breathing structures are the land snails and slugs (Figure 3.25H). The gas exchange structure here is a lung that opens to the outside via a pore called the **pneumostome**. This lung is derived from a feature common to molluscs in general, the mantle cavity, which in other molluscs houses the gills and other organs.

Gas transport Metabolism in animals requires oxidation of organic molecules and catabolic respiration requires available oxygen. Thus, natural selection has favored special molecules, or **respiratory pigments**, that can reversibly bind and transport oxygen, notably hemoglobins, hemocyanins, chlorocruorins, and hemerythrins (see below). As illustrated in Figure 3.24, oxygen must be transported from the sites of environmental gas exchange to the cells of the body, and carbon dioxide must get from the cells where it is produced to the gas exchange surface for release. Generally, groups displaying marked cephalization circulate freshly oxygenated blood through the "head" region first, and secondarily to the rest of the body.

Invertebrates vary considerably in their oxygen requirements. In general, active animals consume more oxygen than sedentary ones. In slow-moving and sedentary invertebrates, oxygen consumption and utilization are quite low. For example, no more than 20% oxygen withdrawal from the gas exchange water current has ever been demonstrated in sessile sponges, bivalves, or tunicates. The amount of oxygen available to an organism varies greatly in different environments. The concentration of oxygen in dry air at sea level is about 210 ml/liter, whereas in water it ranges from near zero to about 10 ml/liter. The variation in aquatic environments is due to such factors as depth, surface turbulence, photosynthetic activity, temperature, and salinity (oxygen concentrations drop as temperature and salinity increase). With the exception of certain areas prone to oxygen depletion (e.g., muds rich in organic detritus), most habitats provide adequate sources of oxygen to sustain animal life. Also, the relatively low capacity of body fluids to carry oxygen in solution is greatly increased by binding oxygen with complex organic compounds called respiratory pigments.

Respiratory pigments differ in molecular architecture and in their affinity for oxygen but all have a metal ion with which the oxygen combines (iron in hemoglobins, hemerythrins, and chlorocruorins; copper in hemocyanins). In most invertebrates, these pigments occur in solution within the blood or other body fluids, but in some invertebrates (and virtually all vertebrates), they may be in specific blood cells. In general, the pigments respond to high oxygen concentrations by "loading" (combining with oxygen) and respond to low oxygen concentrations by "unloading," or dissociating from oxygen (releasing oxygen). The loading and unloading qualities are different for various pigments, in terms of their relative saturations at different levels of oxygen in their immediate surroundings, and are generally expressed in the form of dissociation curves. Respiratory pigments load at the site of gas exchange, where environmental oxygen levels are high relative to the body fluid, and unload at the cells and tissues, where surrounding oxygen levels are low relative to the body fluid. In addition to simply carrying oxygen from the loading to the unloading sites, some pigments may carry reserves of oxygen that are released only when tissue levels are unusually low. Other factors, such as temperature and carbon dioxide concentration, also influence the oxygen-carrying capacities of respiratory pigments.

Hemoglobins are among the most common respiratory pigments in animals. There are a number of different hemoglobins. Some function primarily for transport, whereas others store oxygen and then release it during times of low environmental oxygen availability. Hemoglobins are reddish pigments containing iron as the oxygen-binding metal. They are found in a variety of invertebrates and, with the exception of a few fishes, in all vertebrates. Among the major groups of invertebrates, hemoglobin occurs in many annelids, some crustaceans, some insects, and a few molluscs and echinoderms. Interestingly, hemoglobin is not restricted to the Metazoa; it is also produced by some protists, certain fungi, and in the root nodules of leguminous plants. Among animals, hemoglobin may be carried within red blood cells (erythrocytes) or in coelomic cells (called hemocytes) in a few echinoderms, or it may simply be dissolved in the blood or coelomic fluid.

Two other types of iron-based respiratory pigments occur in certain invertebrates—**hemerythrins** and **chlorocruorins**. The former are violet to pink when oxygenated; the latter are green in dilute concentrations but red in high concentrations. Chlorocruorins generally function as efficient oxygen carriers when environmental levels are relatively high; hemerythrins function more in oxygen storage. Chlorocruorin is found in many annelids, freely floating in body fluids. Hemerythrin is known from some annelids (including sipunculans) and some priapulans and brachiopods.

Hemocyanins are the most commonly occurring respiratory pigments found in the hemolymph of molluscs and arthropods, although they have been identified from at least 11 nephrozoan phyla, in both

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protostomes and deuterostomes. Among arthropods, hemocyanin occurs in chelicerates, a few myriapods, and many crustaceans. There is indirect evidence that it also occurred in trilobites. Hemocyanin has been found in most classes of molluscs. Although hemocyanins, like hemoglobins, are proteins, they display significant structural differences, contain copper rather than iron, and tend to have a bluish color when oxygenated. Unlike most hemoglobins, hemocyanins tend to release oxygen easily and provide a ready source of oxygen to the tissues as long as there is a relatively high concentration of available environmental oxygen. Hemocyanins are always found in solution, never in cells, a characteristic probably related to the necessity for rapid oxygen unloading. Hemocyanins often give a bluish tint to the hemolymph of arthropods, although the presence of carotenoid pigments (beta-carotene and related molecules) commonly imparts a brown or orange coloration.

The widespread detection of hemerythrins, across three domains of life (Archaea, Bacteria, Eukaryota), suggests there are other activities of these proteins, aside from oxygen binding, but we know little about this possibility. In any case, it is apparent that hemerythrins have a long and complex evolutionary history that likely included gene loss and duplication, and possibly even lateral gene transfer.

Table 3.1 gives some of the basic properties of oxygen-carrying pigments. There seems to be no obvious phylogenetic rhyme or reason to the occurrence of these pigments among the various taxa. Respiratory pigments are rare among insects, although hemoglobin has been found in chironomid midges, some notonectids, and certain parasitic flies of the genus *Gastrophilus*. The absence of respiratory pigments among the insects reflects the fact that most of them do not use the blood as a medium for gas transport, but employ extensive tracheal systems to carry gases directly to the tissues. In those insects without well-developed tracheae, oxygen is simply carried in solution in the hemolymph.

Respiratory pigments raise the oxygen-carrying capacity of body fluids far above what would be achieved by transport in simple solution. Similarly, carbon dioxide levels in body fluids (and in sea water) are much higher than would be expected strictly on the basis of its solubility. The enzyme carbonic anhydrase greatly accelerates the reaction between carbon dioxide and water, forming carbonic acid:

$$CO_2 + H_2O \leftrightharpoons H_2CO_3$$

Furthermore, carbonic acid ionizes to hydrogen and bicarbonate ions, so a series of reversible reactions takes place:

$$CO_2 + H_2O \leftrightharpoons H_2CO_3 \leftrightharpoons H^+ + HCO_3^-$$

Because carbon is "tied up" in other forms, the concentration of CO_2 in solution is lowered, thus raising the overall CO_2-carrying capacity of the blood. This set of reactions responds to changes in pH, and in the presence of appropriate cations (e.g., Ca^{2+} and Na^+) it shifts back and forth, serving as a buffering mechanism by regulating hydrogen ion concentration.

Nervous Systems and Sense Organs

All living cells respond to some stimuli and conduct some sort of "information," at least for short distances. Thus, even when no real nervous system is present—the condition found in sponges and placozoans—coordination and reaction to external stimulation do occur. The integration and coordination of bodily activities in Metazoa are in large part due to the processing of information by a true nervous system. The functional units of nervous systems are **neurons**: cells that are specialized for high-velocity impulse conduction. Dense networks of interwoven nerve fibers and their branches and synapses, usually with glial filaments (e.g., brains), are called **neuropils**. A network of cells forming a nerve center in the nervous system is called a **ganglion**.

The generation of an impulse within a true nervous system usually results from a stimulus imposed on the nervous elements. The source of stimulation may be external or internal. A typical pathway of events occurring in a nervous system is shown in Figure 3.26. A stimulus received by some receptor (e.g., a sense organ) generates an impulse that is conducted along a **sensory nerve** (**afferent nerve**) via a series of adjacent neurons to some coordinating center or region of the system. The information is processed and an appropriate response is "selected." A **motor nerve** (**efferent nerve**) then conducts an impulse from the central processing center to an effector (e.g., a muscle), where the response occurs. Once an impulse is initiated within the system,

TABLE 3.1 Properties of oxygen-carrying respiratory pigments

Pigment	Molecular Weight	Metal	Ratio of Metal to O_2	Metal Associate
Hemoglobin	65,000	Fe	1:1	Porphyrin
Hemerythrin	40,000–108,000	Fe	2:1	Protein chains
Hemocyanin	40,000–9,000,000	Cu	2:1	Protein chains
Chlorocruorin	3,000,000	Fe	1:1	Porphyrin

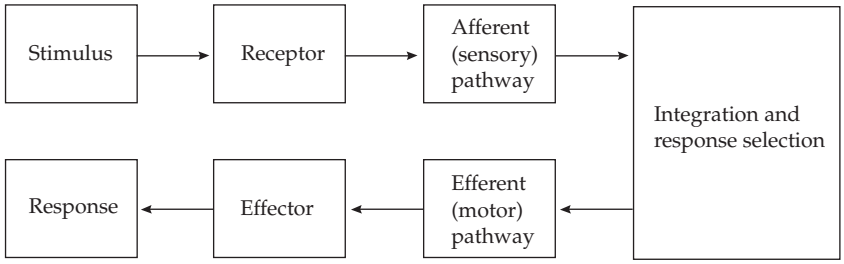

FIGURE 3.26 A generalized pathway within the nervous system. A stimulus initiates an impulse within some sensory structure (the receptor); the impulse is then transferred to some integrative portion of the nervous system via sensory nerves. Following response selection, an impulse is generated and transferred along motor nerves to an effector (e.g., muscle), where the appropriate response is elicited.

the mechanism of conduction is essentially the same in all neurons, regardless of the stimulus. The wave of depolarization along the length of each neuron and the chemical neurotransmitters crossing the synaptic gaps between neurons are common to virtually all nervous conduction. How then is the information interpreted within the system for response selection? The answer to this question involves three basic considerations.

First is the occurrence of a point called a threshold, which corresponds to the minimum intensity of stimulation necessary to generate an impulse. Receptor sites consist of specialized neurons whose thresholds for various kinds of stimuli are drastically different from one another because of structural or physiological qualities. For example, a sense organ whose threshold for light stimulation is very low (compared with other potential stimuli) functions as a light sensor, or photoreceptor. In any such specialized sensory receptor, the condition of differential thresholds essentially screens incoming stimuli so that an impulse normally is generated by only one kind of information (e.g., light, sound, heat, or pressure). Second is the nature of the receptor itself. Receptor units (e.g., sense organs) are generally constructed in ways that permit only certain stimuli to reach the impulse-generating cells. For example, the light-sensitive cells of the human eye are located beneath the eye surface, where stimuli other than light would not normally reach them.

And third, the overall "wiring" or circuitry of the entire nervous system is such that impulses received by the integrative (response-selecting) areas of the system from any particular nerve will be interpreted according to the kind of stimulus for which that sensory pathway is specialized. For example, all impulses coming from a photoreceptor are understood as being light induced. Threshold and circuitry can be demonstrated by introducing false information into the system by stimulating a specialized sense organ in an inappropriate manner: if photoreceptors in the eye are stimulated by electricity or pressure, the nervous system will interpret this input as light. Remember that an impulse can be generated in any receptor by nearly any form of stimulation if the stimulus is intense enough to exceed the relevant threshold. A blow to the eye often results in "seeing stars," or flashes of light, even when the eye is closed. In such a situation, the photoreceptor's threshold to mechanical stimulation has been reached. By the same token, the application of extreme cold to a heat receptor may feel hot.

Nervous systems in general operate on the principles outlined above. However, this description applies largely to nervous systems that have structural centralized regions. Following a discussion below of the basic types of sense organs (receptor units), we discuss centralized and noncentralized nervous systems and their relationships to general body architecture.

Sense Organs

Invertebrates possess an impressive array of receptor structures through which they receive information about their internal and external environments. An animal's behavior is in large part a function of its responses to that information. These responses often take the form of some sort of movement relative to the source of a particular stimulus. A response of this nature is called a **taxis** and may be positive or negative depending on the reaction of the animal to the stimulus. With respect to light or phototaxis, many animals tend to move away from bright light and are thus said to be negatively phototactic.

The activities of receptor units represent the initial step in the usual functioning of the nervous system; they are a critical link between the organism and its surroundings. Consequently, the kinds of sense organs present and their placement on the body are intimately related to the overall complexity, mode of life, and general body plan of any animal. The following general review provides some concepts and terminology that serve as a basis for more detailed coverage in later chapters. The first five categories of sense organs may all be viewed as mechanoreceptors, in that they respond to mechanical stimuli (e.g., touch, vibrations, and pressure). The last three are sensitive to nonmechanical input (e.g., chemicals, light, and temperature). In addition, a few invertebrates have been shown to possess a magnetic compass. For example, during their migrations between North America and central Mexico, monarch butterflies probably navigate using a combination of the sun and the inclination angle component of the Earth's magnetic field to guide their flights, as has been shown for most vertebrate migrators.

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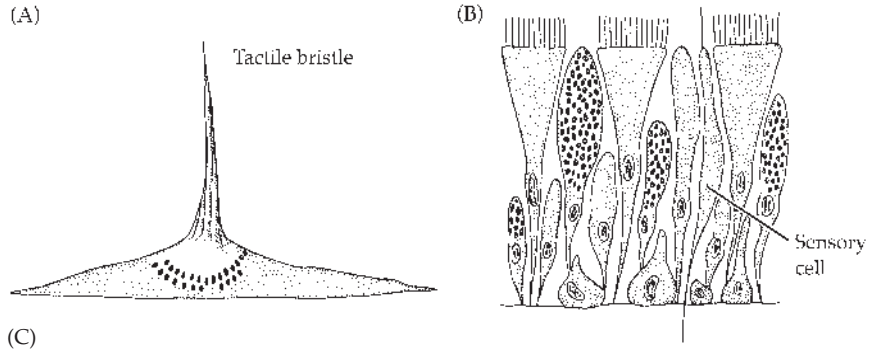

Courtesy of S. Riseman

FIGURE 3.27 Some invertebrate tactile receptors. (A) Tactile organ of *Sagitta bipunctata* (an arrow worm, phylum Chaetognatha). (B) A sensory epithelial cell of a nemertean worm. (C) Long, touch-sensitive setae (and stout grasping setae) on the leg of an isopod, *Politolana* (SEM).

Tactile receptors Touch or tactile receptors are generally derived from modified epithelial cells associated with sensory neurons. The nature of the epithelial modifications depends a great deal on the structure of the body wall. For instance, the form of a touch receptor in an arthropod with a rigid exoskeleton must be different from that in a soft-bodied cnidarian. Most such receptors, however, involve projections from the body surface, such as bristles, spines, setae, and tubercles (Figure 3.27). Objects in the environment with which the animal makes contact move these receptors, thereby creating mechanical deformations that are imposed upon the underlying sensory neurons to initiate an impulse.

Virtually all animals are touch sensitive, but their responses are varied and often integrated with other sorts of sensory input. For example, the gregarious nature of many animals may involve a positive response to touch (positive thigmotaxis) combined with the chemical recognition of members of the same species. Some touch receptors are highly sensitive to mechanically induced vibrations propagated in water, in loose sediments, through solid substrata, or in other materials. Such vibration sensors are common in certain tube-dwelling polychaetes that retract quickly into their tubes in response to movements in their surroundings. Some crustacean ambush-predators are able to detect the vibrations induced by nearby potential prey animals, and web-building spiders quickly and accurately sense prey in their webs through vibrations of the threads. Some spiders have highly sensitive tactile setae on their appendages, called **trichobothria**, that sense airborne vibrations of prey, such as wing beats and perhaps even some sound frequencies.

Georeceptors Georeceptors respond to the pull of gravity, giving animals information about their orientation relative to "up and down." Most georeceptors are structures called **statocysts** (Figure 3.28). Statocysts usually consist of a fluid-filled chamber containing a solid granule or pellet called a **statolith**. The inner lining of the chamber includes a touch-sensitive epithelium from which project bristles or "hairs" associated with underlying sensory neurons. In aquatic invertebrates, some statocysts are open to the environment and thus are filled with water. In some of these the statolith is a sand grain obtained from the animal's surroundings. Most statoliths, however, are secreted within closed cellular capsules by the organisms themselves.

Because of the resting inertia of the statolith within the fluid, any movement of the animal results in a change in the pattern or intensity of stimulation of the sensory epithelium by the statolith. Additionally, when the animal is stationary, the position of the statolith

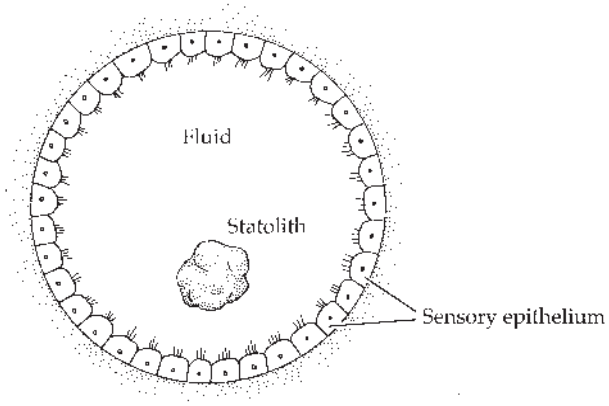

FIGURE 3.28 A generalized statocyst, or georeceptor (section).

within the chamber provides information about the organism's orientation to gravity. The fluid within statocysts of at least some invertebrates (especially certain crustaceans) also acts something like the fluid of the semicircular canals in vertebrates. When the animal moves, the fluid tends to remain stationary—the relative "flow" of the fluid over the sensory epithelium provides the animal with information about its linear and rotational acceleration relative to its environment.

Whether stationary or in motion, animals utilize the input from georeceptors in different ways, depending on their habitat and lifestyle. The information from these statocysts is especially important under conditions where other sensory reception is inadequate. For example, burrowing invertebrates cannot rely on photoreceptors for orientation when moving through the substratum, and some employ statocysts for that purpose. Similarly, planktonic animals face orientation problems in their three-dimensional aqueous environment, especially in deep water and at night; many such creatures possess statocysts.

There are a few exceptions to the standard statocyst arrangements described above. For example, a number of aquatic insects detect gravity by using air bubbles trapped in certain passageways (e.g., tracheal tubes). The bubbles move according to their orientation to the vertical, much like the air bubble in a carpenter's level, and stimulate sensory bristles lining the tube in which they are located.

Proprioceptors Internal sensory organs that respond to mechanically induced changes caused by stretching, compression, bending, and tension are called **proprioceptors**, or simply stretch receptors. These receptors give the animal information about the movement of its body parts and their positions relative to one another. Proprioceptors have been most thoroughly studied in vertebrates and arthropods, where they are associated with appendage joints and certain body extensor muscles. The sensory neurons involved in proprioception are associated with and attached to parts of the body that are stretched or otherwise mechanically affected by movement or muscle tension. These parts may be specialized muscle cells, elastic connective tissue fibers, or membranes that span joints. As these structures are stretched, relaxed, and compressed, the sensory endings of the attached neurons are distorted accordingly and thus stimulated. Some of these receptor arrangements can detect changes not only in position but also in static tension.

Phonoreceptors General sensitivity to sound—phonoreception—has been demonstrated in a number of invertebrates (certain annelid worms and a variety of arthropods), but true auditory receptors are known only in a few groups of insects and perhaps some arachnids and centipedes. Crickets, grasshoppers, and cicadas possess phonoreceptors called **tympanic organs** (Figure 3.29). A rather tough but flexible tympanum covers an internal air sac that allows the tympanum to vibrate when struck by sound waves. Sensory neurons attached to the tympanum are stimulated directly by the vibrations. Most arachnids possess structures called **slit sense organs**, which, although poorly studied, are suspected to perform auditory functions; at least they appear to be capable of sensing sound-induced vibrations. Certain myriapods bear so-called **organs of Tömösváry**, which some workers believe may be sensitive to sound.

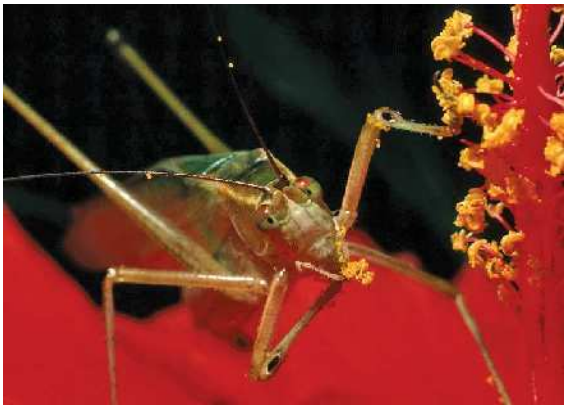
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FIGURE 3.29 An arthropod phonoreceptor, or auditory organ, of the fork-tailed katydid, *Scudderia furcata*. Note the position of the right-side tympanum on the tibia of the first walking leg (arrow).

Baroreceptors The sensitivity of invertebrates to pressure changes—baroception—is not well understood, and no structures for this purpose have been positively identified. However, behavioral responses to pressure changes have been demonstrated in several pelagic invertebrates, including medusae, ctenophores, cephalopods, and copepod crustaceans, as well as in some planktonic larvae. Aquatic insects also sense changes in pressure and may use a variety of methods to do so. Some intertidal crustaceans coordinate daily migratory activities with tidal movements, perhaps partly in response to pressure as water depth changes.

Chemoreceptors Many animals have a general chemical sensitivity, which is not a function of any definable sensory structure but is due to the general irritability of protoplasm itself. When they occur in sufficiently high concentrations, noxious or irritating chemicals can induce responses via this general chemical sensitivity. In addition, most animals have specific chemoreceptors.

Chemoreception is a rather direct sense in that the molecules stimulate sensory neurons by contact, usually after diffusing in solution across a thin epithelial covering. The chemoreceptors of many aquatic invertebrates are located in pits or depressions, through which

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water may be circulated by ciliary action. In arthropods, the chemoreceptors are usually in the form of hollow setae or other projections, within which are chemosensory neurons. While chemosensitivity is a universal phenomenon among invertebrates, a wide range of specificities and capabilities exists.

The types of chemicals to which particular animals respond are closely associated with their lifestyles. Chemoreceptors may be specialized for tasks such as general water analysis, humidity detection, sensitivity to pH, prey tracking, mate location, substratum analysis, and food recognition. Probably all aquatic organisms leak small amounts of amino acids into their environment through the skin and gills as well as in their urine and feces. These released amino acids form an organism's "body odor," which can create a chemical picture of the animal that others detect to identify such characteristics as species, sex, stress level, distance and direction, and perhaps size and individuality. Amino acids are widely distributed in the aquatic environment, where they provide general indicators of biological activity. Many aquatic animals can detect amino acids with much greater sensitivity than our most sophisticated laboratory equipment.

Photoreceptors Nearly all animals are sensitive to light, and most have some kind of identifiable photoreceptors. Although members of only a few of the metazoan phyla appear to have evolved eyes capable of image formation (Cnidaria, Mollusca, Annelida, Arthropoda, and Chordata), virtually all animal photoreceptors share structurally similar light receptor molecules that probably predate the origin of discrete structural eyes. Thus, the structural photoreceptors of animals share the common quality of possessing light-sensitive pigments. These pigment molecules are capable of absorbing light energy in the form of photons, a process necessary for the initiation of any light-induced, or photic, reaction. The energy thus absorbed is ultimately responsible for stimulating the sensory neurons of the photoreceptor unit.

Some animal eyes see only black and white; others perceive the full rainbow and beyond. Some can't gauge the direction of incoming light, while others can spot running prey miles away. The smallest animal eyes may be those on the heads of fairy wasps, the size of a large ameba, while the biggest are the dinner-plate-sized eyes of giant squids. Many animals have two eyes, or four, or eight. Some chitons have hundreds of eyes situated on their shell plates, each with its own lens, retina, and pigment layer. Box jellies typically have 24 eyes, grouped into four clusters on their rhopalia. Four of the six eyes in each rhopalium are simple light-sensing slits and pores. But the other two have light-focusing lenses and can see images. Mantis shrimps can have 12 color receptors (compared with the human 3) and can see infrared and ultraviolet light. Yet with all this diversity, only 2 or 3 types of photoreceptor protein groups have been discovered in metazoans: opsins, cryptochromes, and possibly the taste receptor homolog LITE-1 (a UV light receptor recently identified from nematode worms).

Beyond this basic commonality, however, there is an incredible range of variation in complexity and capability of light-sensitive structures. Arthropods, molluscs, and some polychaete annelids possess eyes with extreme sensitivity, good spatial resolution, and, in some cases, multiple spectral channels. Most classifications of photoreceptors are based upon grades of complexity, and the same categorical term may be applied to a variety of nonhomologous structures, from simple pigmented spots to extremely complicated lensed eyes. Functionally, the capabilities of these receptors range from simply perceiving light intensity and direction to forming images with a high degree of visual discrimination and resolution.

The simplest metazoan photoreceptors are unicellular structures scattered over the epidermis or concentrated in some area of the body. These are usually called **eyespots**. Multicellular photoreceptors may be classified into three general types, with some subdivisions. These types include **ocelli** (sometimes also called simple eyes or eyespots), **compound eyes** (found in most arthropods), and **complex eyes** (the "camera" eyes of cephalopod molluscs and vertebrates). In multicellular ocelli, the light-sensitive (retinular) cells may face outward; these ocelli are then said to be direct. Or the light-sensitive cells may be inverted. The inverted type is common among flatworms and nemerteans and is made up of a cup of reflective pigment and retinular cells (Figure 3.30A). The light-sensitive ends of these neurons face into the cup. Light entering the opening of the pigment cup is reflected back onto the retinular cells. Because light can enter only through the cup opening, this sort of ocellus gives the animal a good deal of information about light direction as well as variations in intensity.

Compound eyes are composed of a few to many distinct units called **ommatidia** (Figure 3.30B) and are described in more detail in Chapter 20. Although eyes of multiple units occur in certain annelid worms, they are best developed and best understood among the arthropods. Each ommatidium is supplied with its own nerve tract leading to a large optic nerve, and apparently each has its own discrete field of vision. The visual fields of neighboring ommatidia overlap to some degree, with the result that a shift in position of an object within the total visual field causes changes in the impulses reaching several ommatidial units; based in part on this phenomenon, compound eyes are especially suitable for detecting movement. Compound eyes nearly identical to those of living arthropods have been found in trilobite fossils and in numerous Cambrian stem-group arthropods. In fact, evidence

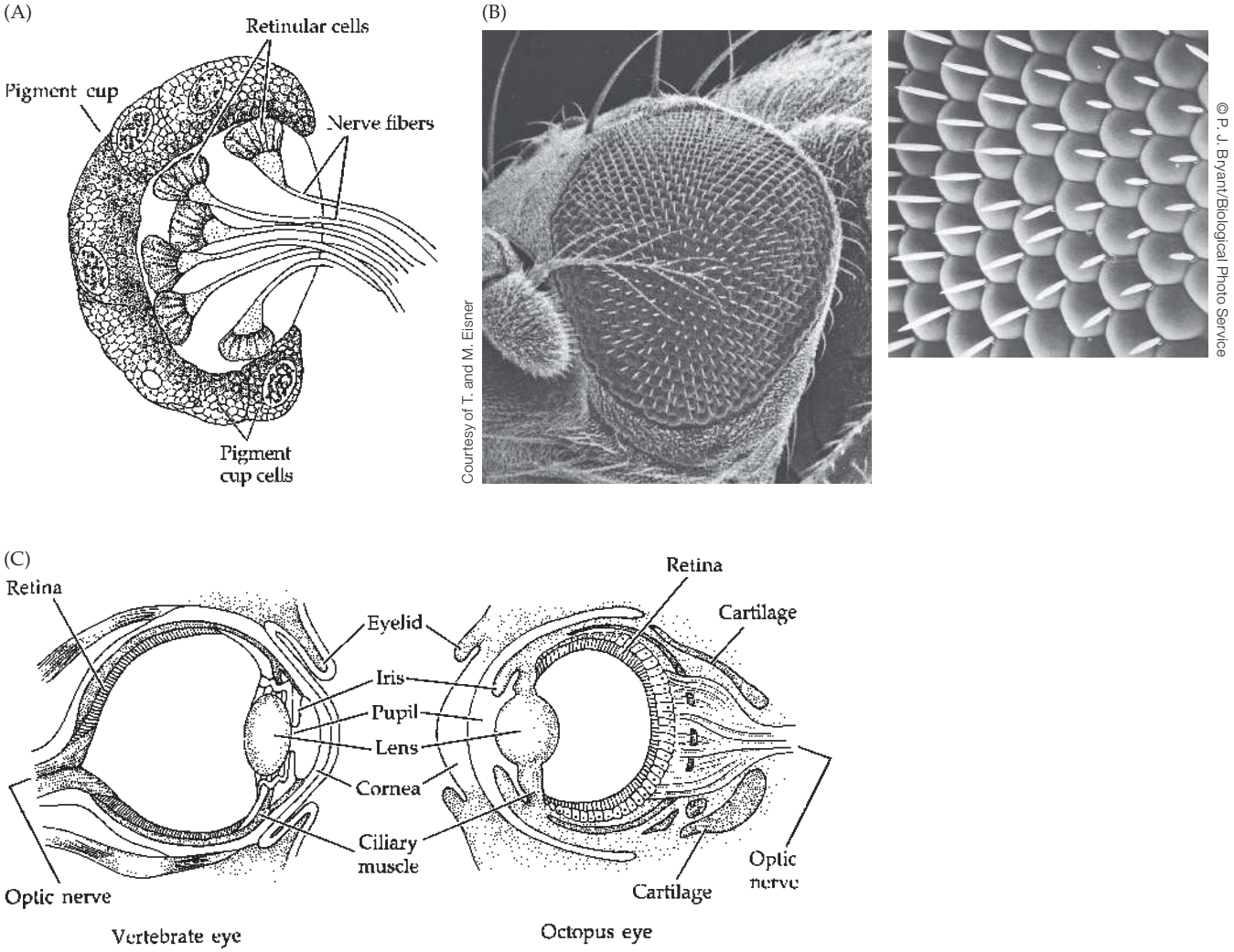

FIGURE 3.30 Some photoreceptors. (A) An inverted pigment-cup ocellus of a flatworm (section). (B) An insect's compound eye and a blown-up section of the eye. A single unit is called an ommatidium. (C) A vertebrate eye (left) and a cephalopod eye (right) (vertical cross-sections). Although many structural similarities are shared between vertebrate and cephalopod eyes (e.g., cornea, pupil, iris, ciliary muscle, lens, retina, optic nerve, etc.), their development differs. The cephalopod eye forms from an epidermal placode through a series of successive infoldings, whereas the vertebrate eye forms from the neural plate and induces the overlying epidermis to form the lens.

suggests that all of the arthropod eye types evolved out of an early arthropod compound eye architecture, even noncompound eyes such as the naupliar eyes of crustaceans and the ocelli of insects.

The complex eyes of squids and octopuses (Figure 3.30C) are probably the best image-forming eyes among the invertebrates. Cephalopod eyes are frequently compared with those of vertebrates, but they differ in many respects. The eye is covered by a transparent protective cornea. The amount of light that enters the eye is controlled by the iris, which regulates the size of the slitlike pupil. The lens is held by a ring of ciliary muscles and focuses light on the retina, a layer of densely packed photosensitive cells from which the neurons arise. The receptor sites of the retinal layer face in the direction of the light entering the eye. This direct eye arrangement is quite different from the indirect eye condition in vertebrates, where the retinal layer is inverted. Another difference is that in many vertebrates, focusing is accomplished by the action of muscles that change the shape of the lens, whereas in cephalopods it is achieved by moving the lens back and forth with the ciliary muscles and by compressing the eyeball.

A good deal of work suggests that metazoan photoreceptors evolved primarily along two lines. On one hand are photoreceptor units derived from or closely associated with cilia (e.g., in cnidarians, echinoderms, and chordates). These types of eyes are called **ciliary eyes**. On the other hand are photoreceptors derived from microvilli or microtubules and referred to as **rhabdomeric eyes** (e.g., in flatworms, annelids, arthropods, and molluscs). All animal photoreceptors may share a deep developmental homology with the *Pax-6* gene, which is known to initiate eye development (even in structurally nonhomologous eyes) in numerous distantly related phyla of both Protostomia and Deuterostomia.

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The evolution of blindness has occurred in many different phyla, although we still know very little about it. In situations like dark caves and the deep sea, there is an apparent selective advantage to eye loss, given that eyes are energetically expensive organs. However, studies have shown that in many, perhaps most, cases eyes that are dramatically degraded or reduced still retain remnants of the visual system (e.g., visual opsins). It might be that these are vestiges in the evolutionary process of disappearing. Or, it might be that they allow for sufficient photo-stimulation (in the "dark") to be an advantage to a species that might not need acute vision.

Thermoreceptors The influence of temperature changes on all levels of biological activity is well documented. Every student of general biology has learned about the basic relationships between temperature and rates of metabolic reactions. Furthermore, even the casual observer has noticed that many organisms' activity levels range from lethargy at low temperatures to hyperactivity at elevated temperatures and that thermal extremes can result in death. The problem is determining whether the organism is simply responding to the effects of temperature at a general physiological level, or whether discrete thermoreceptor organs are also involved.

There is considerable circumstantial evidence that at least some invertebrates are capable of directly sensing differences in environmental temperatures, but actual receptor units are for the most part unidentified. A number of insects, some crustaceans, and horseshoe crabs (Xiphosura) apparently can sense thermal variation. The only nonarthropod invertebrates that have received much attention in this regard are certain leeches, which apparently are drawn to warm-blooded hosts by some heat-sensing mechanism. Other ectoparasites (e.g., ticks) of warm-blooded vertebrates may also be able to sense the "warmth of a nearby meal," but little work has been done on this subject.

Independent Effectors

Independent effectors are specialized sensory response structures that not only receive information from the environment but also elicit a response to the stimulus directly, without the intervention of the nervous system per se. In this sense, independent effectors are like closed circuits. As discussed in later chapters, the stinging capsules (nematocysts) of cnidarians and the adhesive cells (colloblasts) of ctenophores are, at least under most circumstances, independent effectors.

Bioluminescence

Bioluminescence, the production of light by living creatures, occurs in a great variety of organisms in the sea and in some land animals, but it is, curiously, rare in fresh waters. On land, it is seen in a number of beetle groups, as well as some flies and springtails, centipedes and millipedes, a few earthworms, and at least one snail (as well as some fungi). In fresh water it has been reported from only a few insect larvae and a freshwater limpet. In the sea, bioluminescence plays a significant role in animal communication, and it has been recorded from various cnidarians, ctenophores, chaetognaths, annelids, molluscs, numerous arthropods, echinoderms, hemichordates, tunicates, at least one nemertean, and, of course, numerous fishes (as well as protists, bacteria, and fungi). Most bioluminescence commonly seen in the sea is produced by dinoflagellates emitting rapid (one-tenth of a second) flashes. But the patient nighttime observer will also discover that flashes of light are produced by some species of medusae, ctenophores, copepods, benthic ostracods, brittle stars, sea pansies and sea pens, chaetopterid and syllid polychaetes, limpets, clams, tunicates, and others.

Luminescence is the emission of light without heat. It involves a special type of chemical reaction in which the energy, instead of being released as heat, as occurs in most chemical reactions, is used to excite a product molecule that releases energy as a photon. In all cases, the reaction involves the oxidation of a substrate called **luciferin**, catalyzed by an enzyme called **luciferase**. The structures of these chemicals differ among taxa, but the reaction is similar. The color of light varies from deep blue (shrimp and dinoflagellates) to blue-green or green (certain millipedes, ostracods, and tunicates), to yellow and even red (fireflies). Bioluminescence serves several functions, including offense, defense (counter-illumination), prey attraction, and intraspecific communication. In some cases, the luminescence of metazoans (particularly bobtail squids and fishes) is not intrinsic but it is produced by symbiotic colonies of microorganisms hosted in a light organ. Some deep-sea fishes living at depths sunlight cannot reach have an extraordinary increase in the number of genes for rhodopsins, retinal proteins that detect dim light. Hence, despite the darkness of their habitat, they are able to see the faint bioluminescence of deep-sea shrimp, octopuses, bacteria, other fishes, etc.

Nervous Systems and Body Plans

The nervous systems of all animals are always receiving information by way of their associated receptors, processing this information, and eliciting appropriate responses. Nervous systems among Metazoa encompass a staggering diversity, from those in which a distinct system of identifiable neurons does not even exist (e.g., sponges and placozoans), to nerve nets of just a few hundred neurons, to the highly centralized systems of arthropods that may contain a million neurons, to cephalopods and vertebrates that can contain hundreds of millions or even billions of neurons. Yet all these architectures probably evolved out of a group of key components that were in place very early in

animal evolution, most having been retained since at least the Cambrian, if not earlier. Arthropods with well-preserved central nervous systems occur in Cambrian fossils more than 514 million years old.

The molecular components of nervous systems are also similar throughout the animal kingdom, with the same sets of proteins and signaling molecules being used again and again, though often in different contexts. Indeed, a compelling case is emerging that there exists a conserved suite of genes involved in molecular patterning of the nervous system across all Metazoa. Even in groups as distant as flies and vertebrates, similarities in the mechanisms that define the position of the central nervous system on either the dorsal or ventral side of the body reveals fundamental patterning similarities that define the formation of the neuroectoderm in both groups. Geoffroy Saint-Hilaire in 1822 originally proposed this dorsal-ventral axis inversion idea in his hypothesis that the dorsoventral axis of vertebrates and arthropods are essentially the same if arthropods were flipped over on their backs. The idea insinuates that the ventral nerve cords of nonvertebrates and the dorsal nerve cords of vertebrates are homologous.

The structure of the nervous system of any animal is related to its body plan and mode of life. Consider first a radially symmetrical animal with limited powers of locomotion, such as a planktonic jellyfish or a sessile sea anemone. In such animals the major receptor organs are more or less regularly (and radially) distributed around the body; the nervous system itself is a noncentralized, diffuse meshwork generally called a **nerve net** (Figure 3.31A). Radially symmetrical animals tend to be able to respond equally well to stimuli coming from any direction—a useful ability for creatures with either sessile or free-floating lifestyles. Interestingly, at least in cnidarians there are both polarized and nonpolarized synapses within the nerve net. Impulses can travel in either direction across the nonpolarized synapses because the neuronal processes on both sides are capable of releasing synaptic transmitter chemicals. This capability, coupled with the gridlike form of the nerve net, enables impulses to travel in all directions from a point of stimulation. From this brief description, it might be assumed that such a simple and "unorganized" nervous system would not provide enough integrated information to allow complex behaviors and coordination. In the absence of a structurally recognizable integrating center, the nerve net does not fit well with our earlier description of the sequence of events from stimulus to response. But many cnidarians are in fact capable of fairly intricate behavior, and the system works, often in ways that are not yet fully understood.

The tremendous evolutionary success of bilateral symmetry and unidirectional locomotion must have depended in large part on associated changes in the organization of the nervous system and the distribution of sense organs. The evolutionary trend among animals has been to centralize and concentrate the major coordinating elements of the nervous system. This central nervous system is usually made up of an anteriorly located neuronal mass (ganglion) from which arise one or more longitudinal nerve cords that often bear additional ganglia (Figure 3.31B). The anterior ganglion is referred to by a variety of names. Many authors have abandoned the term "brain" for such an organ because of the multifaceted implications of

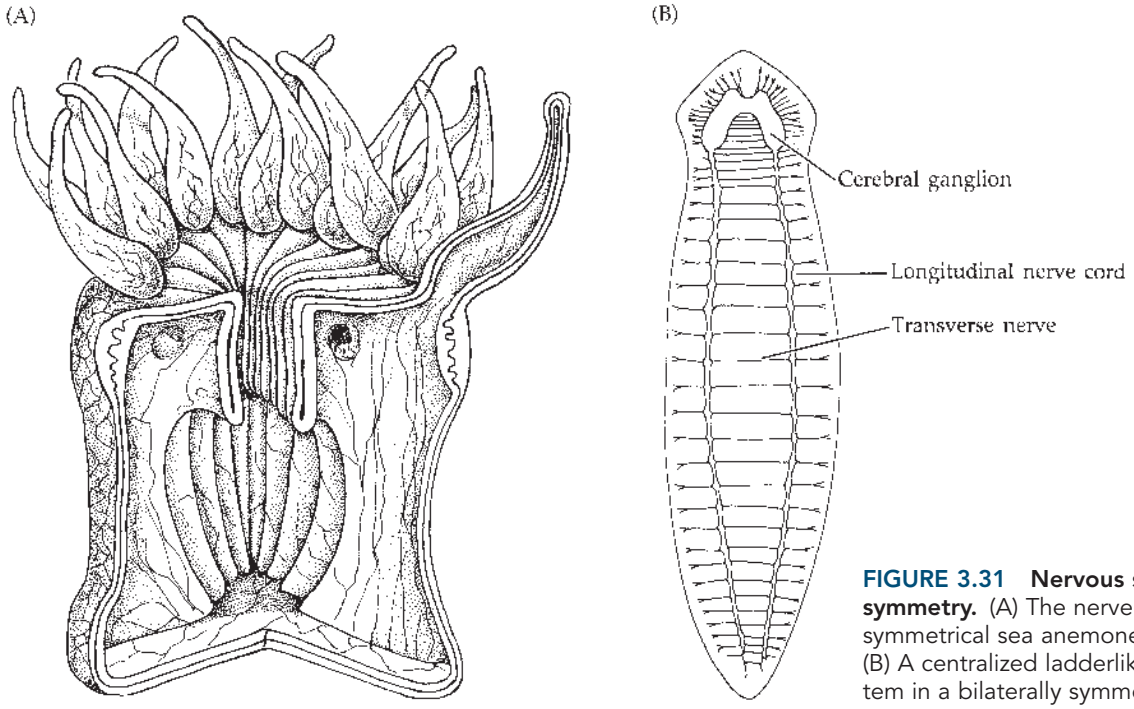

FIGURE 3.31 Nervous systems and symmetry. (A) The nerve net in a radially symmetrical sea anemone (cutaway view). (B) A centralized ladderlike nervous system in a bilaterally symmetrical flatworm.

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that word and adopt the more neutral term **cerebral ganglion** (or cerebral ganglia) for the general case. In many instances, a term denoting its relative position to some other organ is applied. For example, the cerebral ganglion commonly lies dorsal to the anterior portion of the gut and is thus a supraenteric (or supraesophageal, or suprapharyngeal) ganglion.

In addition to the cerebral ganglion, most bilaterally symmetrical animals have many of the major sense organs placed anteriorly. The concentration of these organs at the front end of an animal is called **cephalization**—the formation of a head region. Even though cephalization may seem an obvious and predictable outcome of bilaterality and mobility, it is nonetheless extremely important. It simply would not do to have information about the environment gathered by the trailing end of a motile animal, lest it enter adverse and potentially dangerous conditions unawares. Hunting, tracking, and other forms of food location are greatly facilitated by having the appropriate receptors placed anteriorly—toward the direction of movement.

In 1888, the brilliant Austrian zoologist Berthold Hatschek recognized three major groups of Bilateria, based largely on the structure and position of the central nervous system. He named these Zygoneura (what we now call Protostomia), Chordonia (what we now call Chordata), and Ambulacraria. Today, the central nervous system of Bilateria remains an important indicator of phylogenetic relatedness, not just in adults but also in larvae.

The central nervous system of bilaterians includes three principal elements: (1) the apical organ, present in almost all ciliated larvae but degenerating before or at metamorphosis; (2) at least a pair of cerebral ganglia that begin developing in the larval stage and persist into adulthood; and (3) an often paired longitudinal nerve cord.

Ciliated larvae are found in numerous lineages of Porifera, Cnidaria, Spiralia, and Ambulacraria, but they are absent in Ecdysozoa and Chordata (except for the nonfeeding amphioxus larva). These widespread ciliated larvae are thought to be homologues at some fundamental level and have been called **primary larvae**. One of the most characteristic organs of these larvae is the **apical organ**. This organ develops from the most apical embryonic blastomeres. The apical organ appears to be sensory, and it is probably involved in metamorphosis. Gene expression studies show that the apical poles of cnidarians and bilaterians are homologous. Protostome primary larvae have ganglia/nerve cords that are retained as an integral part of the adult central nervous system. These include two structures: (1) a pair of cerebral ganglia, which will form the major part of the adult brain; and (2) a circumblastoporal nerve cord, which becomes differentiated into a perioral loop, paired or secondarily fused ventral nerved cords, and a small perianal loop. Thus, in bilaterians the adult central nervous system begins to develop as ciliary structures during the larval state.

Although the origin of deuterostome central nervous system is more difficult to interpret, gene expression studies support the homology of echinoderm and enteropneust apical organs with those of other bilaterians. Even though the nerve cord is ventral in protostomes and dorsal in deuterostomes (in the phyla Hemichordata and Chordata), gene expression patterns during development are the same in both, suggesting homology. In echinoderms a consolidated cerebral ganglion does not exist, and instead there are radial nerves that develop from invaginations of the ectoderm along the developing radii. The radial nerves have been interpreted as homologues of the chordate neural tube, from which the chordate central nervous system develops and which is specialized in different ways in the three chordate phyla Cephalochordata, Urochordata, and Vertebrata.[6]

Longitudinal nerve cords receive information through peripheral sensory nerves from whatever sense organs are placed along the body, and they carry impulses from the cerebral ganglion to peripheral motor nerves to effector sites. Additionally, nerve cords and peripheral nerves often serve animals in reflex actions and in some highly coordinated activities that do not depend on the cerebral ganglion. The most primitive centralized nervous system may have been similar to that seen today in xenacoelomorph worms and some free-living flatworms, where pairs of longitudinal cords may attach to one another by transverse connectives in a ladderlike fashion (Figure 3.31B). Among those Metazoa that have developed active lifestyles (e.g., errant polychaetes, most arthropods, cephalopod molluscs, vertebrates), the nervous system has become increasingly centralized through a reduction in the number of longitudinal nerve cords. However, a number of invertebrates (e.g., ectoprocts, tunicates, echinoderms) have secondarily taken up sedentary or sessile modes of existence. Within these groups there has been a corresponding decentralization of the nervous system and a general reduction in and dispersal of sense organs.

In animals, two distinct strategies for achieving increased neuronal conduction speed evolved. In some clades, greatly increased axon diameter improves conduction speed and hence body speed and reaction time (e.g., cephalopod molluscs). The other strategy has been the evolution of myelinated sheaths around the axon of neurons. Cnidaria (and probably Xenacoelomorpha) have naked axons, while in Nephrozoa a glial plasma membrane covers both axons and somata of nerve cells. Although myelinated axons (in which a

[6]The "cydippid stage" of ctenophores is better interpreted as a juvenile, rather than a larva, because it lacks special larval organs and because it can, in certain cases, carry out sexual reproduction. Further, the "apical organ" of ctenophores is structurally different from that of cnidarians and bilaterians and is generally not considered homologous to the apical organ of those taxa.

glial layer is modified by great expansion into a myelinated sheath) are ubiquitous among the vertebrates, they are relatively rare among invertebrates, but they do occur in species of at least three phyla—chordates, annelids, and crustacean arthropods. Myelin forms as an enormously expanded glial plasma membrane, and the sheaths comprise multiple layers of the membrane. The myelinated sheaths in these three phyla differ in their fine anatomy and conduction velocity (vertebrate sheaths have the fastest conduction rate), and it has been suggested that myelin sheaths may have arisen independently in each of these groups. Myelin sheaths greatly increase the rate of nerve transmission, accommodating rapid body movements such as escape responses and retraction of vulnerable body parts (e.g., copepod first antennae, crab eyestalks).

Hormones and Pheromones

We have stressed the significance of the integrated nature of the parts and processes of living organisms and have discussed the general role of the nervous system in this regard. Organisms also produce and distribute within their bodies a variety of chemicals that regulate and coordinate biological activities. This very broad description of what may be called chemical coordinators obviously includes almost any substance that has some effect on bodily functions. One special category of chemical coordinators is **hormones**. This term refers to any chemical that is produced and secreted by some organ or tissue and then carried by the blood or other body fluid to exert its influence elsewhere in the body. In vertebrates, we associate this type of phenomenon with the endocrine system, which includes well-known glands as production sites. For our purposes we may subdivide hormones into two types. First are **endocrine hormones**, which are produced by more or less isolated glands and released into the circulatory fluid. Second are **neurohormones**, which are produced by special neurons called neurosecretory cells.

Much remains unknown concerning hormones in invertebrates. Most of our information comes from studies on insects and crustaceans, although hormonal activity has been demonstrated in a few other taxa and is suspected in most others. Among the arthropods, hormones are involved in the control of growth, molting, reproduction, eye pigment migration, and other phenomena; in at least some other taxa (e.g., annelids), hormones influence growth, regeneration, sexual maturation, and stolon formation in epitokes.

Hormones do not belong to any particular class of chemical compounds, nor do they all produce the same effects at their sites of action: some are excitatory, some are inhibitory. Because endocrine hormones are carried in the circulatory fluid, they reach all parts of an animal's body. The site of action, or target site, must be able to recognize the appropriate hormone(s) among the myriad other chemicals in its surroundings. This recognition usually involves an interaction between the hormone and the cell surface at the target site. Thus, under normal circumstances, even though a particular hormone is contacting many parts of the body, it will elicit activity only from the appropriate target organ or tissue that recognizes it.

In a general sense, pheromones are substances that act as "interorganismal hormones." These chemicals are produced by organisms and released into the environment, where they have an effect on other organisms. Most pheromone research has been on intraspecific actions, especially in insects, where activities such as mate attraction are frequently related to these airborne chemicals. We may view intraspecific pheromones as coordinating the activities of populations, just as hormones help coordinate the activities of individual organisms. There is also a great deal of evidence for the existence of interspecific pheromones. For example, some predatory species (e.g., some starfish) release chemicals into the water that elicit extraordinary behavioral responses on the part of potential prey species, generally in the form of escape behavior. We discuss examples of various pheromone phenomena for specific animal groups throughout the book.

Reproduction

The biological success of any species depends upon its members staying alive long enough to reproduce. The following account includes a discussion of the basic methods of reproduction among invertebrates and leads to the account of embryology and developmental strategies provided in Chapter 4.

Asexual Reproduction

Asexual reproductive processes do not involve the production and subsequent fusion of haploid cells but rely solely on vegetative growth through mitosis. Many invertebrates engage in various types of body fission, budding, or fragmentation, followed by growth to new individuals (Figure 3.32). These asexual processes depend largely on the organism's "reproductive exploitation" of its ability to regenerate (regrow lost parts). Even wound healing is a form of regeneration, but many animals have far more dramatic capabilities. The replacement of a lost appendage in familiar animals such as starfish and crabs is a common example of regeneration. However, these regenerative abilities are not "reproduction" because no new individuals result, and their presence does not imply that an animal capable of replacing a lost leg can necessarily reproduce asexually. Examples of organisms that possess regenerative abilities of a magnitude permitting asexual reproduction include

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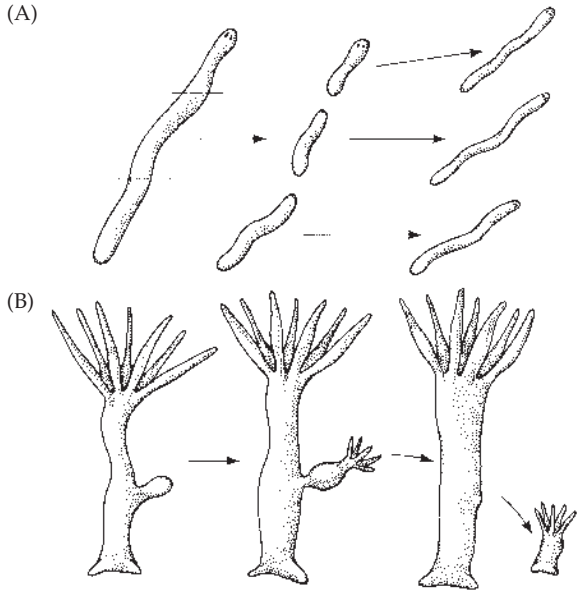

FIGURE 3.32 Some common asexual reproductive processes. (A) Fragmentation, followed by regeneration of lost parts. This process occurs in a number of vermiform invertebrates. (B) Budding may produce separate solitary individuals, as it does in *Hydra* (shown here), or it may produce colonies (see Figure 3.33).

sponges, many cnidarians (corals, anemones, and hydroids), many colonial animals, and certain types of worms. These animals have the property known as "whole body regeneration," meaning that they can regenerate any body part from a set of cells.

In many cases asexual reproduction is a relatively incidental process and is rather insignificant to a species' overall survival strategy. In others, however, it is an integral and even necessary step in the life cycle. There are important evolutionary and adaptive aspects to asexual reproduction. Organisms capable of rapid asexual reproduction can quickly take advantage of favorable environmental conditions by exploiting temporarily abundant food supplies, newly available living space, or other resources. This competitive edge is frequently evidenced by extremely high numbers of asexually produced individuals in disturbed or unique habitats, or in other unusual conditions. In addition, asexual processes are often employed in the production of resistant cysts or overwintering bodies, which are capable of surviving through periods of harsh environmental conditions. When favorable conditions return, these structures grow to new individuals.

A word about colonies A frequent result of asexual reproduction, particularly some forms of budding, is the formation of **colonies**. This phenomenon is especially common in certain taxa (e.g., cnidarians, ascidians, bryozoans) (Figure 3.33). The term "colony" is not easy to define. It may initially bring to mind ant

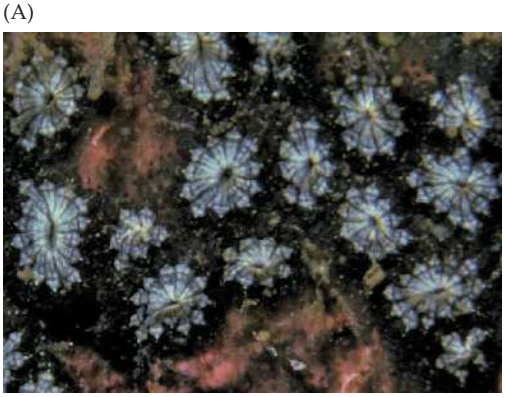

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FIGURE 3.33 Representative invertebrate colonies. (A) *Botryllus*, a colonial ascidian. (B) *Lophogorgia*, a colonial gorgonian. (C) Three species of coral. (D) *Aglaophenia*, a colonial hydroid.

or bee colonies, or even groups of humans; but these examples are more appropriately viewed as social units rather than as colonies, at least in the context of our discussions. For our purposes, we define colonies as associations in which the constituent individuals are not completely separated from each other, but organically connected together, either by living extensions of their bodies or by material that they have secreted. While occasional mixed colonies may exist (usually due to fusion of two separate colonies, as in some tunicates and bryozoans), most colonies are composed of genetically identical individuals. We describe the nature of numerous examples of colonial life in later chapters.

The formation of colonies not only may enhance the benefits of asexual reproduction in general, but also produces overall functional units that are much greater in size than mere individuals; thus this growth habit may be viewed as a partial solution to the surface-to-volume dilemma. Increased functional size through colonialism can result in a number of advantages for animals: it can increase feeding efficiency; facilitate the handling of larger food items; reduce chances of predation; increase the competitive edge for food, space, and other resources; and allow groups of individuals within the colony to specialize for different functions. Colonies of many animals can use fragmentation as a form of propagation.

Sexual Reproduction

Although reproduction is critical to a species' survival, it is the one major physiological activity that is not essential to an individual organism's survival. In fact, when animals are stressed, reproduction is usually the first activity that ceases, but others release large amounts of gametes to maximize output under severe stress. Sexual reproduction is especially energy costly, yet it is the characteristic mode of reproduction among multicellular organisms.[7]

Given the advantages of asexual reproduction, one might wonder why all animals do not employ it and abandon costly and complicated sexual activities entirely. The most frequently given explanation for the popularity of sexual reproduction (aside from anthropomorphic views, of course) focuses on the long-term benefits of genetic variation. Recombination allows for the maintenance of high genetic heterozygosity in individuals and high polymorphism in populations. Through regular meiosis and recombination, a level of genetic variation is maintained generation after generation, within and among populations; thus species are thought to be more "genetically prepared" for environmental changes, including both shifts in the physical environment and the changing milieu of competitors, predators, prey, and parasites.

Although this advantage must surely be real, does it satisfactorily explain the role of sex in short-term selection (i.e., generation by generation)? Presumably even in the short term an advantage lies in the maintenance of genetic variability. That is, genetic variability in individuals may increase their chances of quickly adapting to environmental fluctuations, predators, parasites, and disease. In 1973, Leigh Van Valen proposed the idea that in order just to "keep up" with changing environments, populations must continually access new and different allele combinations through the process of natural selection—a notion called the "red queen hypothesis" after the Red Queen in *Alice in Wonderland*, who commanded her courtiers to run continuously just to stay in the same place.

Sexual reproduction involves the formation of haploid cells through meiosis and the subsequent fusion of pairs of those cells to produce a diploid zygote (Figure 3.34). The haploid cells are **gametes**—sperm and eggs—and their fusion is the process of fertilization, or **syngamy**. The production of gametes is accomplished by the gonads—**ovaries** in females and **testes** in males—or their functional equivalents. The gonads are frequently associated with reproductive systems that may include various arrangements of ducts and tubes, accessory organs such as yolk glands or shell glands, and structures for copulation or transferring gametes. The different levels of complexity of these systems are related to the developmental strategies used by the organisms in question, as discussed in Chapter 4 and described in the coverage of each phylum. The variation in such matters is immense, but at this point we introduce some basic terminology of structure and function.

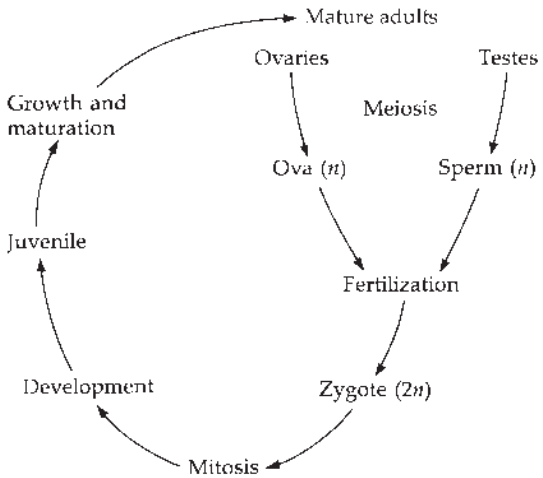

FIGURE 3.34 **A generalized metazoan life cycle.**

[7] In thinking of animals, we typically view "sex" and "reproduction" as one and the same. However, at the cellular level these two processes are opposites: reproduction is the division of one cell to form two, whereas the sexual process incudes two cells fusing to form one! Conventional sex is the alternation of meiosis and fertilization events.

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Many invertebrates simply release their gametes into the water in which they live (**broadcast spawning**), where external fertilization occurs. In such animals the gonads are usually simple, often transiently occurring structures associated with some means of getting the eggs and sperm out of the body. This release is accomplished through a discrete plumbing arrangement (coelomoducts, metanephridia, or gonoducts—sperm ducts and oviducts) or by temporary pores in, or rupture of, the body wall. In such animals, synchronous spawning is critical, and marine species rely largely on this synchrony and the water currents to achieve fertilization. Water temperature, light, phytoplankton abundance, lunar cycle, and the presence of conspecifics have all been implicated in synchronized spawning events of invertebrates.

On the other hand, invertebrates that pass sperm directly from the male to the female, where fertilization occurs internally, must have structural features to facilitate such activities. Figure 3.35 illustrates stylized male and female reproductive systems. A general scenario leading to internal fertilization in such systems is as follows: Sperm are produced in the testes and transported via the **sperm duct** to a precopulatory storage area called the **seminal vesicle**. Prior to mating, many invertebrates incorporate groups of sperm cells into sperm packets, or **spermatophores**. Spermatophores provide a protective casing for the sperm and facilitate transfer with minimal sperm loss. In addition, many spermatophores are themselves motile, acting as independent sperm carriers. Some sort of male copulatory or intromittent organ (e.g., penis, cirrus, or some other modified appendages in arthropods, such as pedipalps or legs, often called gonopods) is inserted through the female's gonopore and into the vagina. Sperm are passed through the male's ejaculatory duct directly, or by way of a copulatory organ, into the female system, where they are received and often stored by a **seminal receptacle**.

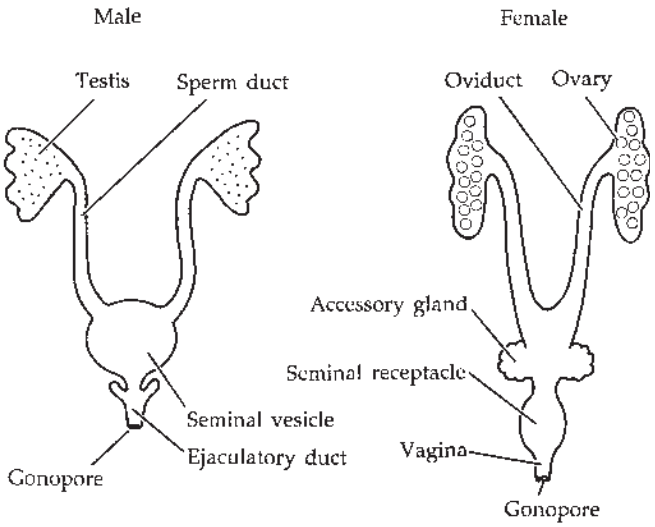

FIGURE 3.35 Schematic and generalized male and female reproductive systems. See text for explanation.

In the female, eggs are produced in the ovaries and transported into the region of the **oviducts**. Sperm eventually travel into the female's reproductive tract, where they encounter the eggs; fertilization often takes place in the oviducts. Among invertebrates, the sperm may move by flagellar or ameboid action or by locomotor structures on the spermatophore packet; they may be aided by ciliary action of the lining of the female reproductive tract. Various accessory glands may be present both in males (such as those that produce spermatophores or seminal fluids) and in females (such as those that produce yolk, egg capsules, or shells). This simple sequence is typical (although with many elaborations) of most invertebrates that rely on internal fertilization, but many others exist, including not uncommon strategies in which the sperm is injected through the epidermis of a female individual.

Animals in which the sexes are separate, each individual being either male or female, are termed **gonochoristic** (or **dioecious**, especially in plants). However, many invertebrates are **hermaphroditic** (or **monoecious,** especially in plants): each animal contains both ovaries and testes and thus is capable of producing both eggs and sperm (though not necessarily at the same time).[8] Although self-fertilization may seem to be a natural advantage in this condition, such is not the case. In fact, with some exceptions, self-fertilization in hermaphrodites is usually prevented. Fertilizing one's self would be the ultimate form of inbreeding and would presumably result in a dramatic decrease in potential genetic variation and heterozygosity (as with asexual reproduction). The rule for many hermaphroditic invertebrates is mutual cross-fertilization, wherein two individuals function alternately or simultaneously as males and exchange sperm and then use the mate's sperm to fertilize their own eggs. The real advantage of hermaphroditism now becomes clear: a single sexual encounter results in the impregnation of two individuals, rather than only one as in the gonochoristic condition.

A common phenomenon among hermaphroditic invertebrates is **protandric hermaphroditism**, or simply **protandry** (Greek *proto*, "first"; *andro*, "male"), where an individual is first a functional male but later in life changes sex to become a functional female. The less common reverse situation, female first and then male, is called **protogynic hermaphroditism**, or simply **protogyny** (Greek *gynos*, "female"). At least some invertebrates alternate regularly between being

[8]Hermaphroditus, the beautiful son of Hermes and Aphrodite, was united with a water nymph at a Carian fountain. Thus his body became both male and female.

functional males and females, as explained by Jerome Tichenor (*Poems in Contempt of Progress*, 1974):

Consider the case of the oyster,
Which passes its time in the moisture;
Of sex alternate,
It chases no mate,
But lives in self-contained cloister.

In addition to the clever oysters immortalized by Professor Tichenor (aka Joel W. Hedgpeth), some other taxa in which the hermaphroditic condition is common include barnacles, arrow worms (Chaetognatha), flatworms, clitellate annelids, tunicates, many gastropods, and cymothoid isopods (Crustacea).

The sexual conditions include myriad variations on the themes described above, including the reproductive systems of nematodes, which may involve three sexes (**trioecy**)—females, males, and hermaphrodites—and the two sexes of *Caenorhabditis elegans*, which include a male and a hermaphrodite. Colonial organisms may include one sex or both sexes, or all individuals may be hermaphroditic.

Parthenogenesis

Parthenogenesis (Greek *parthenos*, "virgin"; *genesis*, "birth") is a special reproductive strategy in which unfertilized eggs develop into viable adult individuals. Parthenogenetic species are known in many invertebrate (and vertebrate and plant) groups, including gastrotrichs, rotifers, tardigrades, nematodes, gastropods, certain insects, and various crustaceans. The taxonomic distribution of parthenogenesis is spotty; it is rare to find a whole genus, let alone any higher taxon, that is wholly parthenogenetic. Some higher taxa that are largely parthenogenetic (e.g., aphids, cladocerans) are cyclically parthenogenetic, and they punctuate their life histories with sex.[9] Among the invertebrates, parthenogenesis usually occurs in small-bodied species that are parasites or that are free-living but inhabit extreme or highly variable habitats such as temporary freshwater ponds. There is a general trend for parthenogenesis to become more prevalent as one moves toward higher latitudes or into harsher environments. Overall, it appears that parthenogenetic taxa arise from time to time and succeed in the short run due to certain immediate advantages, but in the long run they might be condemned to extinction through competition with their sexual relatives.

In most species that have been studied, parthenogenetic periods alternate with periods of sexual reproduction. In temperate freshwater habitats, parthenogenesis often occurs during summer months, with the population switching to sexual reproduction as winter approaches. In some species, parthenogenesis takes place for many generations, or several years, eventually to be punctuated by a brief period of sexual reproduction. In some rotifers, parthenogenesis predominates until the population attains a certain critical size, at which time males appear and a period of sexual reproduction ensues. One whole clade of rotifers (the bdelloids) appears to persist and evolve completely without conventional sex, but it may sustain genetic diversity through high levels of horizontal gene transfer within and between species, including the incorporation of nonrotifer metazoan and nonmetazoan genes. Cladocerans switch from parthenogenesis to sexual reproduction under a number of conditions, such as overcrowding, adverse temperature, or food scarcity, or even when the nature of the food changes. Many parasitic species alternate between a free-living sexual stage and a parasitic parthenogenetic one; this arrangement is seen in some nematodes, thrips (Thysanoptera), gall wasps, aphids, and certain other hemipterans.

One of the most interesting examples of parthenogenesis occurs in honeybees; in these animals the queen is fertilized by one or more males (drones) at only one period of her lifetime, in her "nuptial flight." The sperm are stored in her seminal receptacles. If sperm are released when the queen lays eggs, fertilization occurs and the eggs develop into females (queens or workers). If the eggs are not fertilized, they develop parthenogenetically into males (drones).

The question of the existence or prevalence of purely parthenogenetic species has been debated for decades. Many species once thought to be entirely parthenogenetic have proved, upon closer inspection, to alternate between parthenogenesis and brief periods of sexual reproduction. In some species purely parthenogenetic populations apparently exist only in some localities. In other species, parthenogenetic lineages have been traced to sexual ancestral populations occupying relictual habitats. Nevertheless, for some parthenogenetic animals, males have yet to be found in any population, and these may indeed be purely clonal species. One cannot help but wonder how long such species can exist in the face of natural selection without the benefits of any genetic exchange. One would predict that, as with any form of asexual reproduction, obligatory parthenogenesis would eventually lead to genetic stagnation and extinction. There may, however, be some as yet unexplained genetic mechanisms to avoid this, because some parthenogenetic animals (e.g., some earthworms, insects, and lizards) are capable of inhabiting a wide range of habitats. Presumably they either have a significant level of genetic adaptability or possess "general purpose genotypes."

[9] A number of fishes and amphibians are parthenogenetic, but none seem to have overcome the need for their eggs to be fused with sperm in order to initiate development. The parthenogenetic females usually mate with males of another species, which provide sperm that trigger development (a behavior called **pseudogamy**). A few lizards apparently have no need for a sperm to trigger parthenogenetic development. No parthenogenetic wild birds or mammals have been documented.

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Chapter Summary

In this chapter, we explore fundamentals of animal architecture and body plans. Most animal phyla exhibit bilateral symmetry, with associated cephalization. However, some phyla (Cnidaria, Ctenophora, Echinodermata) have various forms of radial symmetry. And a few phyla express no symmetry at all; that is, they are asymmetrical (most Porifera, Placozoa). All animals have some form of locomotion, though sometimes limited to a larval stage. Smaller aquatic animals must contend with Reynolds number effects as they move their body, or body parts, through water. Cilia/flagella play important roles in almost all larger aquatic animal groups, either in direct locomotion or by moving the "environment" closer to their feeding and gas exchange surfaces. Most animals have musculature and a skeleton of some kind, often hydrostatic but usually rigid. Most animals have a complete (through) gut, with both mouth and anus. A few have no gut at all (Porifera, Placozoa, tapeworms, acanthocephalans), while some others have an incomplete gut, lacking an anus (Cnidaria, Xenacoelomorpha, Platyhelminthes).

Many aquatic taxa are suspension feeders, removing particulate food matter from the surrounding water through filter feeding, contact suspension feeding, scan-and-trap feeding, or mucous net feeding. Other animals are deposit feeders. Animals can also be categorized as herbivores, carnivores, or scavengers. In addition to eating particle-sized or larger food matter, many invertebrates can also absorb dissolved organic matter (DOM) directly from the water in which they live. Finally, a good number of animals rely on symbiotic relationships with various microbes, which provide all or part of their nutrition, such as chemoautotrophic bacteria or different types of algae. One group of bone-eating annelid worms (*Osedax*) are carnivorous scavengers that cultivate and consume bacterial endosymbionts that are capable of digesting the bones of dead vertebrates on the seafloor. Other invertebrates rely on a symbiotic aerobic bacterium to break down cellulose in wood that the animals can then digest (e.g., shipworm bivalves).

Almost all animals must osmoregulate and deal with toxic byproducts of protein digestion (e.g., ammonia). Many, especially the Bilateria, use various forms of nephridia for these purposes (e.g., protonephridia or metanephridia). Large-bodied metazoans rely on open or closed circulatory systems for internal transport of nutritional products, oxygen and carbon dioxide, and toxins to be expelled. Pumping structures or general body movement keep the blood or hemolymph circulating in the body. Many invertebrates rely on integumentary or cutaneous gas exchange, but others have external organs (e.g., gills, book lungs), internal organs (e.g., lungs, tracheae), or restricted areas of the body specialized for this. Oxygen binding and transport are usually by special respiratory pigments (e.g., hemoglobins, hemocyanins, hemerythrins, chlorocruorins).

Except in sponges and placozoans, structural nervous systems are found in all metazoan phyla. A wide range of sense organs have evolved among animals, including tactile receptors, georeceptors, proprioceptors, phonoreceptors, baroreceptors, chemoreceptors, thermoreceptors, and photoreceptors—including several types of eyes.

Asexual reproduction occurs in many metazoan phyla, and in some cases this leads to the formation of colonies. Sexual reproduction occurs in every animal phylum and involves the generation and fusion of male and female gametes. Animals may be gonochoristic (dioecious) or hermaphroditic (monoecious), and parthenogenesis is also known from some species in several phyla.

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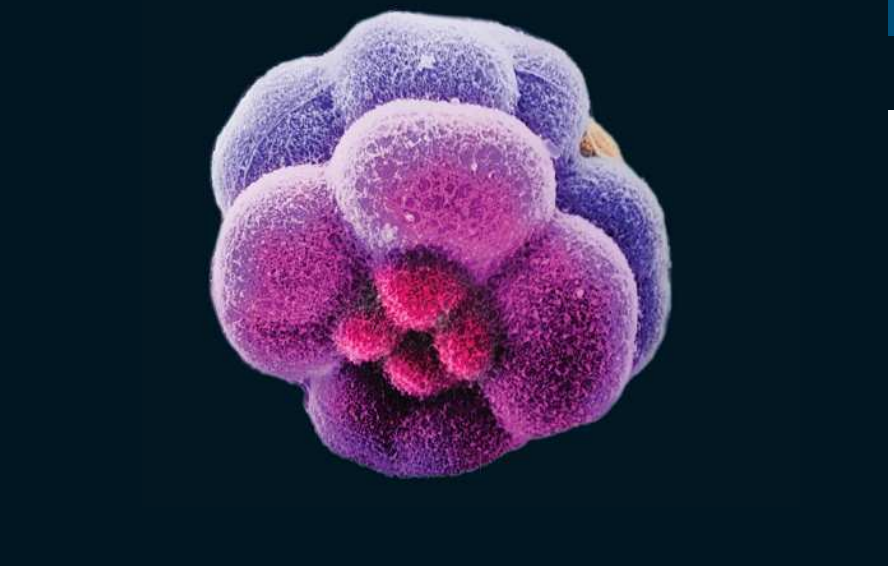

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CHAPTER 4

Introduction to the Animal Kingdom

Development, Life Histories, and Origin

The process by which unicellular zygotes transform themselves into multicellular individuals and eventually into reproducing adults is called **ontogeny**. At the core of metazoan ontogeny is **embryogenesis**—the growth and development of the embryo. The embryo is that stage of an organism between fertilization and birth. It is the principal phase of life history that mediates between genotype and phenotype.

As we saw in Chapter 3, the cells of animals are organized into functional units, generally as tissues and organs, with specific roles that support the whole animal. These different cell types are interdependent, and their activities are coordinated in predictable patterns and relationships. The tissues and organs develop through a series of events early in an organism's embryogeny. The embryonic tissues, or **germ layers**, form the framework upon which metazoan body plans are constructed. Thus, the cells of animals (Metazoa) are specialized, interdependent, coordinated in function, and develop through a genetically orchestrated tissue-layering process during embryogeny.

The influence of yolk on early zygotic divisions, as well as on the differentiation of embryonic tissues, is one of the best established principles of zoology, yet one that is more labile than previously believed. So it is not surprising that a large body of detailed descriptive research on animal embryos has accumulated, leading to a strong focus on structure and physical processes in the field of developmental biology. Because particular developmental schemes characterize different animal lineages, developmental biology has compiled detailed descriptions of cell divisions, cell fates, embryonic germ layers, and larval or adult structures in the search for shared evolutionary patterns among animal phyla. Among the most detailed studies in biology are the meticulous accounts of early metazoan development by Wilhelm Roux, Hans Driesch, Edmund Beecher Wilson, Hans Spemann, and others. The apparent tendency for progressive stages of embryonic development to reveal the evolutionary history of animals is what inspired Ernst Haeckel, Karl von Baer, Walter Garstang, and others to formulate their versions of the **recapitulation hypothesis**, or "**biogenetic law**" (see the end of this chapter). And, despite some ongoing philosophical debate, from a morphological perspective ontogeny does appear to recapitulate many aspects of animal phylogeny, at least in some animal groups.

However, the recent emergence of *molecular* developmental biology (a field known as evo-devo) has changed some long-standing embryological principles in subtle but compelling ways. Haeckel's biogenetic law is no longer seen to govern the development of metazoan embryos in the ways embryologists once thought that it did. Taxon-specific patterns, and deviations of those patterns

in animal development, have revealed more complicated interactions than could ever have been anticipated from morphological descriptions alone. For these reasons, developmental biology can no longer consist primarily of descriptions of ova, early cell divisions, and the formation of increasingly complex balls of cells and cell layers, although these classic patterns are still a major part of this field. A modern approach to the study of animal development includes molecular as well as morphological studies with a great deal of experimental biology.

Evolutionary Developmental Biology: Evo-Devo

Molecular biology has had an explosive impact on the study of development and animal phylogenetics and evolution. "**Evo-devo**," the catchy abbreviation for the field of evolutionary developmental biology, is also used for the burgeoning discipline of comparative developmental genetics—the evolutionary study of the spatial and temporal expression of genes that control body architecture among metazoans. Much of evo-devo focuses on the roles of **transcription factors** (**TF**s), which are the products of the genes involved in controlling early development. These genes and TFs define the primary embryonic body axes (e.g., the oral–aboral, anterior–posterior, and dorsal–ventral axes), the directionality of structures developing along these axes, and the appearance of particular structures or organizations such as body cavities, segments, or appendages. Evo-devo investigates the genetic underpinnings of nearly every process described within classical studies of developmental biology. The focus of developmental biology has thus shifted, from the ontogenetic study of animal structural organization, to the comparative ontogenetic study of gene functions and their roles in body organization.

As genomic methods become less expensive and more widely explored, the number of animal species whose full genome is known has dramatically increased, with high-quality genomes now available for nearly all animal phyla. Therefore, the old separation between "model organisms," for which unlimited genomic resources were available, and non-model organisms has blurred, and the ability to sequence whole genomes for a few thousand U.S. dollars has "democratized" the field of evo-devo, with growing opportunities for evolutionary comparison of the different patterns and mechanisms for virtually any animal that can be grown in the laboratory. The use of developmental genomics has therefore become more than the mere determination of whether ontogeny recapitulates phylogeny, an idea that is now seen to be an oversimplification. Instead, the comparison of developmental similarities and differences, as well as how the differences play out in adult organisms, has led to a much more subtle and discerning understanding of how animals are organized and how that organization unfolds within individual lifespans. Although the breadth of these changes is beyond the scope of this book, some general patterns are now apparent, as summarized below.

Developmental Tool Kits

If animals arose from among the Protista, a basic set of genetic factors are likely to have existed in that ancestry that supported multicellularity (which arose several times in the Eukaryota), facilitated its expression, and allowed these traits to be favored by selection. Likely genetic factors may have included a tendency for cells to aggregate rather than disperse after mitosis, the biochemical ability for cells to remain together as a group, and the movement or differentiation of cells bearing one set of specializations in response to proximity with cells bearing another set of specializations.

The possibility that such traits existed implies they were mediated in some way by the transcription products of genes borne by the protistan ancestors of animals. Sets of functional genes that control ontogenetic processes have been called **developmental tool kits**, and with respect to the evolution of multicellularity, they are likely to have been associated with three processes: (1) the adhesion of cells to one another, (2) the transduction of biochemical signals within and between cell types (i.e., **cell signaling pathways**), and (3) differentiation of cells from primordial to specialized states.

The transition to multicellularity from a unicellular state was a fundamental event in metazoan evolution. However, until recently, there were few avenues available for investigating this transition. The possibility that developmental tool kits underlying multicellularity existed at the origin of the Metazoa suggests that recognizable homologous gene sequences in different species, or **orthologs**, and their transcription factors might be found in predictable ways within close relatives of metazoans, as it has been shown for groups including choanoflagellates, ichthyosporeans, and filastereans, as well as throughout the metazoans themselves. Recent genomic studies have shown that despite some of the shared developmental tool kit, a large number of gene families were acquired at the stem of Metazoa, while other genes have been loss at that branch.

The structural organization of choanoflagellates, as well as their similarity to metazoans such as sponges, have made these creatures compelling candidates as metazoan ancestors, and molecular phylogenetic methods have allowed this hypothesis to be directly tested. Analyses of genomic data from diverse metazoan lineages strongly support the idea of animals and choanoflagellates having a common ancestor, and as predicted, a majority of choanoflagellate-expressed genes have homologous sequences (orthologs) in animal genotypes.

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Noteworthy too are observations that choanoflagellates express a surprising diversity of adhesion and cell signaling homologues. Thus, by identifying genes shared among animals and their apparent most recent living relatives, tests of specific developmental hypotheses regarding genome evolution in early animals have become increasingly possible. However, things aren't always as easy as they seem.

The Relationship Between Genotype and Phenotype

A search for genetically conserved tool kits underlying particular events or morphological landmarks in animal development seems exciting indeed. Unfortunately, evidence now suggests that a direct correspondence between genotype and phenotype in metazoan development is rare—things are usually more complicated. Early studies were lured in this direction by the striking degree to which **Hox clusters** (groups of homeotic genes that control the body plan and limb organization of developing embryos along their anterior–posterior axis) seemed to exhibit organizational and functional consistency throughout the Metazoa. The discovery in the late 1970s that animals as diverse as vertebrates and arthropods had structurally and functionally related Hox genes led to the assumption that all animals would contain similar gene clusters. And some gene sequences, including Hox clusters and other similar genes, confirmed this assumption. The developmental gene *brachyury* (*bra*) is a good example. The transcription products of *bra* define the midline of bilaterians, and the gene also is expressed in the notochord of species belonging to the phylum Chordata. Its expression pattern confirms the homologies suggested by morphology, in that its expression in the notochord of chordates provides an example of a homologous gene with a homologous function in a homologous morphological character—the notochord (which is a synapomorphy of the phylum).

The use of gene sequences and gene products for phylogenetic analysis has proven to be more complicated than expected. For example, Hox genes that are apparently homologous in their sequences may not be identical or even necessarily similar in their expression in different taxa, even among closely related taxa. Gene sequence homology, it seems, does not guarantee that the specific functions of the genes will be similar. And, Hox genes have been found to be linearly arranged only in certain taxa, despite their linear representation in most review papers and textbooks (Figure 4.1).

Despite their presumed role as an evolutionary "magic bullet," developmental genes now seem every bit as likely as morphological characters are to exhibit homoplasy (e.g., convergent evolution), not only in their sequence but also in their function! While developmental genetic programs may at first appear to contain phylogenetic information, observed patterns are likely to represent patterns shaped by the needs of the developmental program in different lineages. Because such difficulties are widespread, using particular genes to establish homology of certain anatomical features in different metazoan lineages can be challenging.

The Evolution of Novel Gene Function

New functional roles appear to routinely evolve in developmental genetic systems. Developmental genes, despite being under strong stabilizing selection to perform precise functions, can evolve in unexpected ways. This tendency is called **developmental system drift** or **DSD**. The existence of DSD can be useful for tracking the evolution of particular structures (e.g., visual elements) but can cause confusion because DSD itself often leads to morphological divergences.

DSD appears to occur in two ways. First, a gene that performs a function in one taxon may be co-opted for another use in a different taxon. The process often begins with **gene duplication**, when replication errors create multiple copies of functional genes. Redundancy in regulatory function allows continuation of normal metabolism, but it also allows duplicated gene products to be used elsewhere. For example, the gene *Pax6* is expressed in a range of both eyed and eyeless bilaterians, suggesting that this patterning gene has been co-opted for multiple functions in the regulation of eye development. Large gene expansions have now been mapped to key nodes in animal evolution, including the base of Metazoa, but massive gene loss has also been important in clades such as Deuterostomia and Ecdysozoa.

A second DSD mechanism occurs when differences in gene expression arise due to genetic interactions, or epistasis, occurring within different genetic backgrounds. Identical sequences can produce different phenotypic effects in different species, or even among members of the same species. Although the magnitude of these effects can become increasingly pronounced as species divergence increases, the complexities of epistatic interactions are seldom predictable.

Gene Regulatory Networks

A major contribution of genomic analyses to developmental biology is the conclusion that individual genes do not control cellular or development function. That is, there is no one gene "for" a particular phenotype or structure. Instead, groups of genes, usually called **gene regulatory networks**, are responsible for producing functional traits. Four major groups of these regulatory clusters exist: (1) cell differentiation networks, which appear to allow groups of cells to differentiate in particular ways; (2) subcircuits, developmental gene networks that are repeatedly used in general cell function; (3) switches, regulatory gene networks that turn

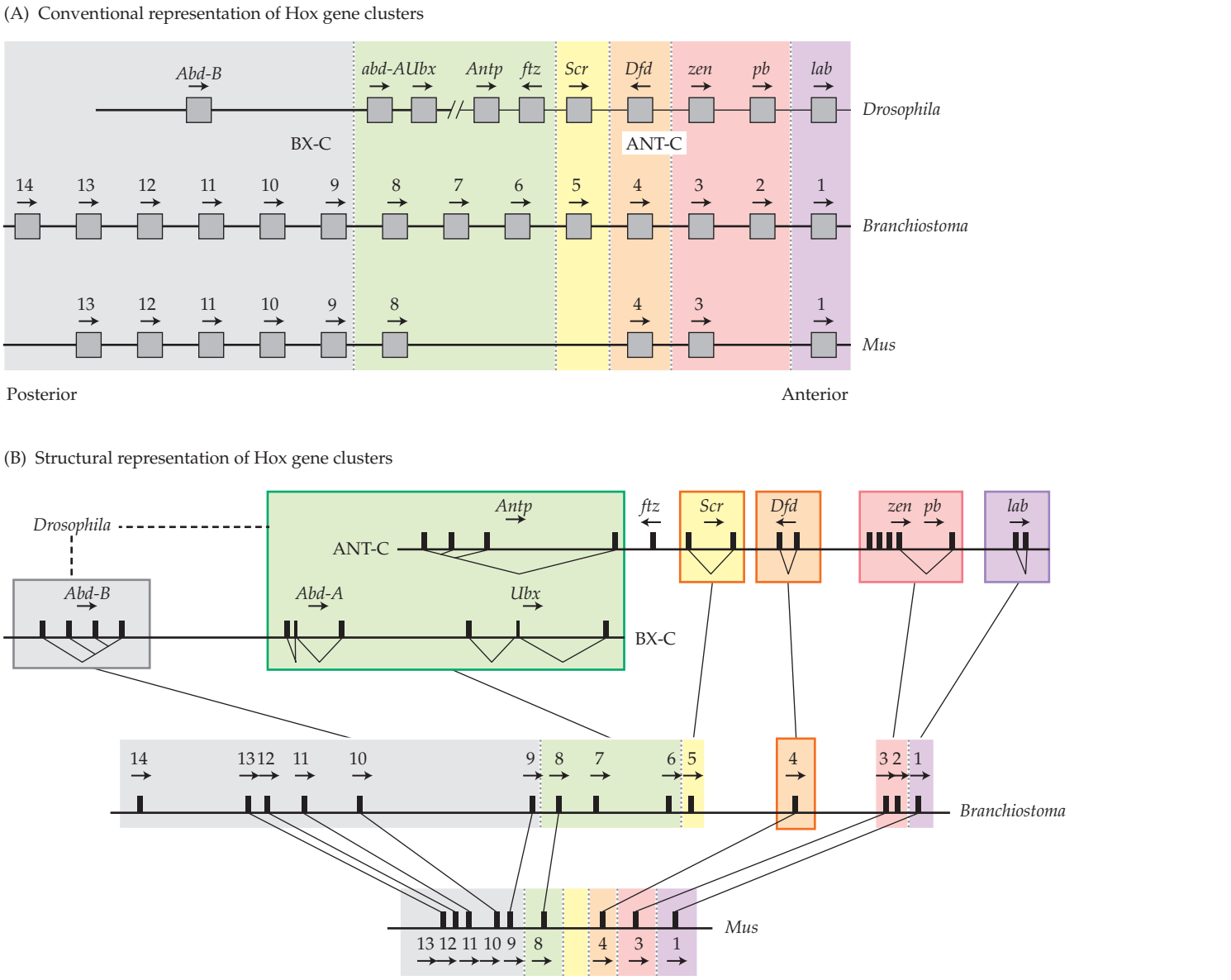

FIGURE 4.1 Representations of Hox genes in textbooks are often oversimplified and thus can lead to erroneous views of metazoan phylogenetic relationships. In this figure, the horizontal lines represent chromosomes. The colored boxes represent Hox gene "clusters," those genes that are related in their sequences and thus appear to be derived from a common ancestral Hox gene, in an insect (*Drosophila melanogaster*), a cephalochordate (amphioxus, *Branchiostoma lanceolatum*), and a vertebrate (mouse, *Mus musculus*). The arrows represent gene orientation, that is, the direction in which transcription of the DNA coding strand proceeds. (A) Hox "clusters" 1 through 14 as they are often represented in textbooks and some scientific articles. In such oversimplified representations, Hox genes, including BX-C (the bithorax complex of *Drosophila* that controls development of abdominal and posterior thoracic segments) and ANT-C (the antennipedia complex of *Drosophila* that controls the formation of legs), are incorrectly shown as being located in close proximity, with clusters that are similar in nucleotide sequence length, and with gene clusters that are arranged in a linear order on chromosomes. (B) A more accurate representation of Hox clusters as they actually exist within *Drosophila*, *Branchiostoma*, and *Mus*, shown to scale with regard to the actual size of the genes (the number of nucleotides involved, including noncoding sequences), the relative distances between the genes (the degree to which genes form "clusters"), and clearer spatial and gene orientation arrangements of Hox elements with respect to one another on the chromosomes. Note that in *Drosophila*, the BX-C and ANT-C complexes are "split" (spatially separated as indicated by the dashed line) on chromosome III, in contrast to the less spatially dispersed arrangements characteristic of chordates (*Branchiostoma* and *Mus*). Note also that while *Drosophila* gene orientations are variable (indicated by arrows), they are consistently unidirectional in *Branchiostoma* and *Mus*. While Hox clusters in chordates (*Branchiostoma* and *Mus*) tend to be more spatially condensed than in other metazoans, they are especially "organized" in this way in vertebrates (e.g., *Mus*). Accurate physical representations of Hox genes are needed to inform the discussion on the structural and functional evolution of Hox clusters.

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cell functions off or on to regulate the timing of particular developmental events; and (4) kernels, complex and tightly conserved gene networks designed to specify the fields of cells from which particular body parts will eventually arise.

Because kernels appear to be the type of network most important for organizing lineage-specific development (e.g., there are likely to be bilaterian, protostome, spiralian, and ecdysozoan kernels), these are considered most likely useful for phylogenetic analyses of the kind originally conceived of for Hox clusters. Nevertheless, it is still possible for gene regulatory networks to undergo substantial evolution within lineages. Thus, as with all such analyses, care must be used in choosing which networks to include.

Eggs and Embryos

The physical (and physiological) attributes that distinguish the Metazoa are the result of their embryonic development. Stated differently, adult phenotypes result from specific sequences of developmental stages. Therefore, both animal unity and diversity are as evident in patterns of development as they are in the body architecture of adults. The patterns of development discussed here reflect this unity and diversity, and serve as a basis for understanding the sections on embryology in later chapters.

Eggs

Biological processes in general are cyclical. Successive generations illustrate this generality, as the term "life cycle" implies, and where the description of a process begins is only a matter of convenience. Here, we begin with the egg, or **ovum**, a single remarkable cell capable of developing into a new individual. Once fertilized, all of the different cell types of an adult animal are derived during embryogenesis from this single totipotent entity. A fertilized ovum contains not only the genetic information necessary to direct development but also some quantity of nutrient material called **yolk**, which sustains the early stages of life. In a few animals, unfertilized eggs can also undergo development through parthenogenesis.

Eggs are polarized along an **animal–vegetal axis**. This polarity may be apparent in the egg itself, or it may be recognizable as development proceeds. The **vegetal pole** is associated with the formation of nutritive organs (e.g., the digestive system), whereas the **animal pole** (often illustrated at the top of the egg) produces other regions of the embryo. Animal ova are categorized primarily by the amount and location of yolk within the cell (Figure 4.2), two factors that greatly influence certain aspects of development. **Isolecithal** eggs contain a relatively small amount of yolk that is more or less evenly distributed throughout the cell. Ova in which the yolk is concentrated at one end (toward the vegetal pole) are termed **telolecithal** eggs; those in which the yolk is concentrated in the center are called **centrolecithal** eggs.

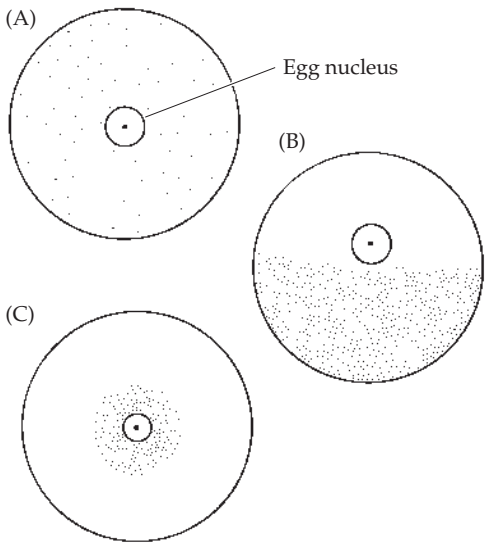

FIGURE 4.2 Types of ova. Stippling denotes the distribution and relative concentration of yolk within the cytoplasm. (A) An isolecithal ovum has a small amount of yolk distributed evenly. (B) The yolk in a telolecithal ovum is concentrated toward the vegetal pole. The amount of yolk in such eggs varies greatly. (C) A centrolecithal ovum has yolk concentrated at the center of the cell.

The actual amount of yolk in telolecithal and centrolecithal eggs is highly variable. Yolk production (**vitellogenesis**) is typically the longest phase of egg production, although its duration varies by orders of magnitude among species. Rates of yolk production depend on the specific vitellogenic mechanism used. In general, opportunistic (so-called *r*-selected) species have evolved vitellogenic pathways for the rapid conversion of food into egg production, while more specialist (so-called *K*-selected) species utilize slower pathways.

Cleavage

The penetration of an ovum by a sperm cell and the subsequent fusion of the male and female nuclei initiate the transformation of an ovum into a **zygote** or fertilized egg. We use the term **cleavage** for the initial cell divisions of a zygote, and the resulting cells are called **blastomeres**. Certain aspects of the pattern of early cleavage are determined by the amount and placement of yolk, whereas other features are inherent in the genetic programming of the particular organism. Isolecithal and weakly to moderately telolecithal ova generally undergo **holoblastic** cleavage. That is, the cleavage planes pass completely through the cell, producing blastomeres that are separated from one another by thin cell membranes (Figure 4.3A).

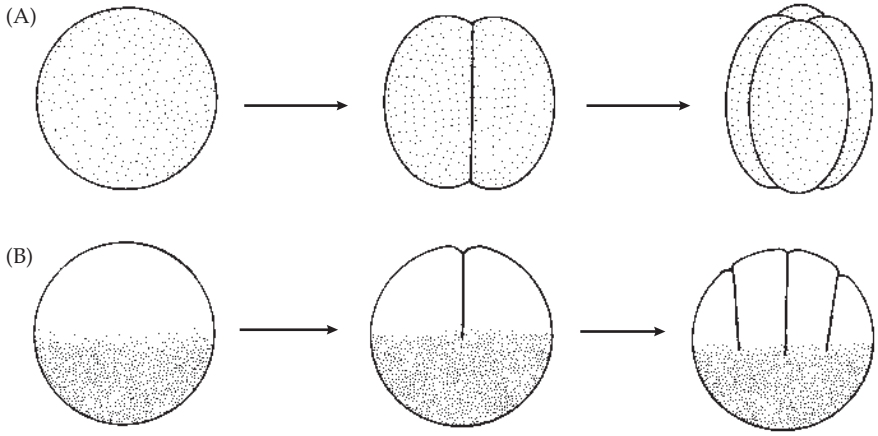

FIGURE 4.3 Types of early cleavage in developing zygotes. (A) Holoblastic cleavage. The cleavage planes pass completely through the cytoplasm. (B) Meroblastic cleavage. The cleavage planes do not pass completely through the yolky cytoplasm. The stippling represents yolk distribution in the egg and early zygote.

Whenever very large amounts of yolk are present (as in strongly telolecithal eggs), the cleavage planes do not pass readily through the dense yolk, so the blastomeres are not fully separated from one another by cell membranes. This pattern of early cell division is called **meroblastic** cleavage (Figure 4.3B). The pattern of cleavage in centrolecithal eggs is dependent on the amount of yolk and varies from holoblastic to various modifications of meroblastic.

Orientation of Cleavage Planes

A number of terms describe the relationship of cleavage planes to the animal–vegetal axis of the egg and the relationships of the resulting blastomeres, one to another (Figure 4.4). Cell divisions during cleavage may be **equal** or **unequal**, indicating the comparative sizes of the resulting groups of blastomeres. The term **subequal** is used when blastomeres are only slightly different in size. When cleavage is distinctly unequal, the larger cells lying at the vegetal pole are called **macromeres.** The smaller cells located at the animal pole are called **micromeres**.

Cleavage planes that pass through or parallel to the animal–vegetal axis produce **longitudinal** (= meridional) divisions; those that pass at right angles to the axis produce **transverse** divisions. Transverse divisions may be equatorial, when the embryo is separated equally into animal and vegetal halves, or simply latitudinal, when the division plane does not pass through the "equator" of the embryo.

Radial and Spiral Cleavage

Most invertebrates display one of two cleavage patterns defined on the basis of the orientation of the blastomeres about the animal–vegetal axis. These patterns are called **radial** cleavage and **spiral** cleavage and are illustrated in Figure 4.5. Radial cleavage involves strictly longitudinal and transverse divisions. Thus, the blastomeres are arranged in rows either parallel or perpendicular to the animal–vegetal axis. The placement

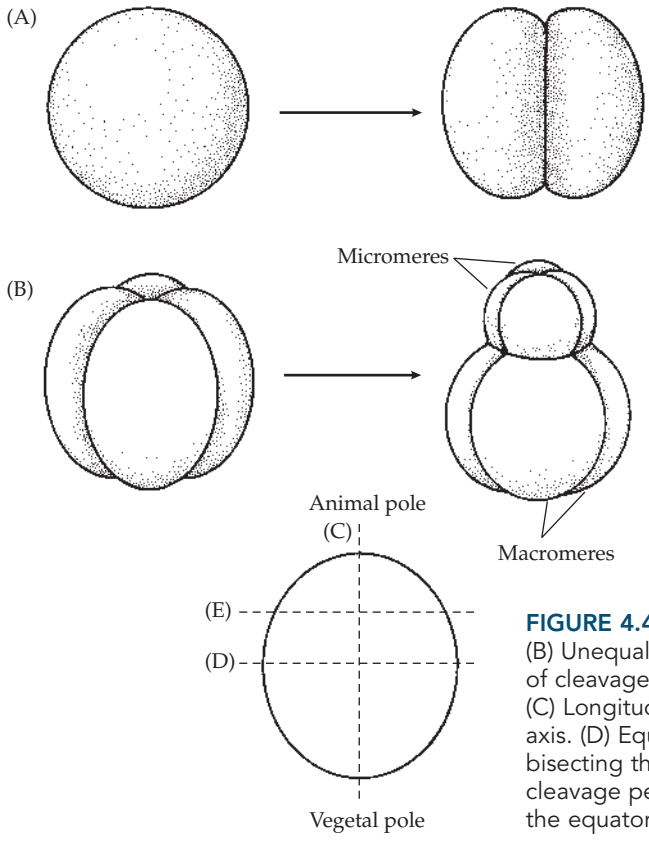

FIGURE 4.4 Planes of holoblastic cleavage. (A) Equal cleavage. (B) Unequal cleavage produces micromeres and macromeres. (C–E) Planes of cleavage relative to the animal–vegetal axis of the egg or zygote. (C) Longitudinal (= meridional) cleavage parallel to the animal–vegetal axis. (D) Equatorial cleavage perpendicular to the animal–vegetal axis and bisecting the zygote into equal animal and vegetal halves. (E) Latitudinal cleavage perpendicular to the animal–vegetal axis but not passing along the equatorial plane.

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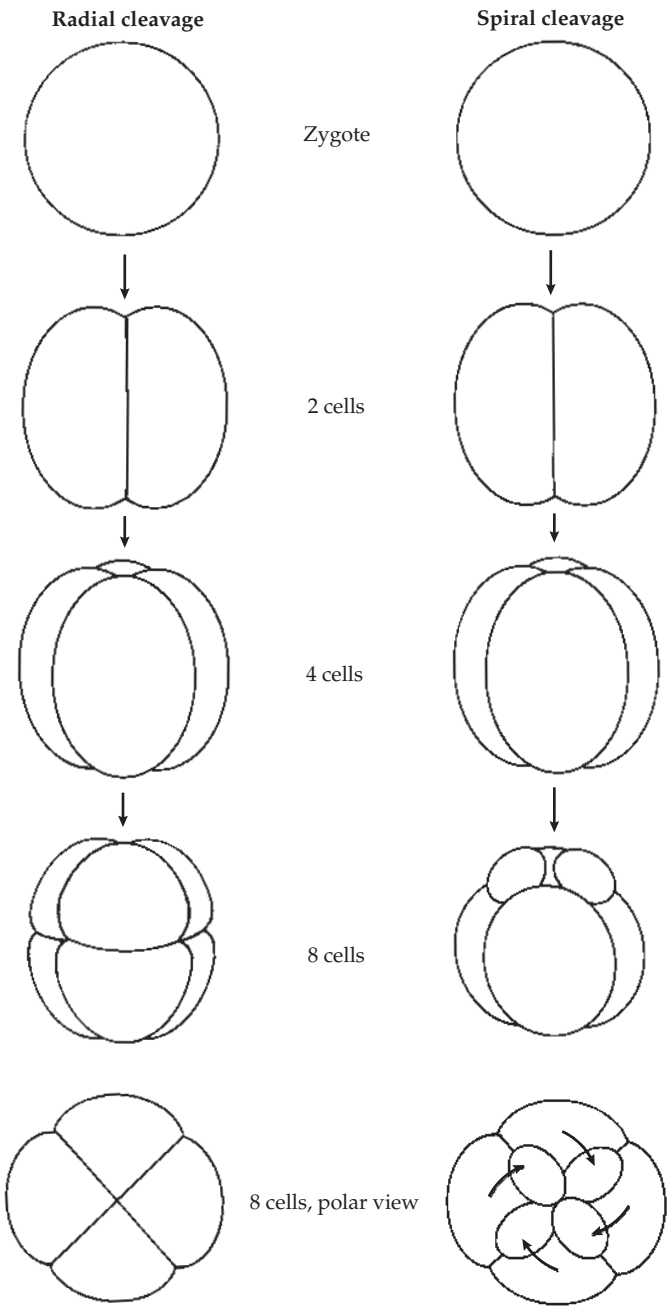


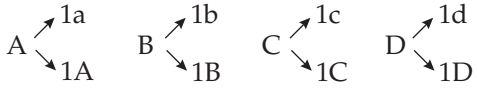
FIGURE 4.5 Comparison of radial versus spiral cleavage through the 8-cell stage. During radial cleavage, the cleavage planes all pass either perpendicular or parallel to the animal–vegetal axis of the embryo. Spiral cleavage involves a tilting of the mitotic spindles, commencing with the division from 4 to 8 cells. The resulting cleavage planes are neither perpendicular nor parallel to the axis. The polar views of the resulting 8-cell stages illustrate the differences in blastomere orientation.

of the blastomeres shows a radially symmetrical pattern in polar view. The chapter opening photo shows the 16-cell-stage embryo of a radially cleaving echinoderm (*Lytechinus pictus*), with 4 large macromeres behind 4 smaller micromeres (and 8 "mesomeres" behind the macromeres).

Spiral cleavage is quite another matter. Although not inherently complex, it can be difficult to describe. The first two divisions are longitudinal, generally equal or subequal. Subsequent divisions, however, displace the blastomeres laterally so that they lie within the furrows between previously divided cells. This condition is a result of the formation of the mitotic spindles at oblique angles rather than parallel to the axis of the embryo; hence the cleavage planes are neither perfectly longitudinal nor perfectly transverse. The division from 4 to 8 cells involves a displacement of the cells near the animal pole in a clockwise (**dextrotropic**) direction (viewed from the animal pole). The next division, from 8 to 16 cells, occurs with a displacement in a counterclockwise (**levotropic**) direction; the next is clockwise, and so on—alternating back and forth until approximately the 64-cell stage. We hasten to add that divisions are frequently not synchronous; not all of the cells divide at the same rate. Thus, a particular embryo may not proceed from 4 cells to 8, to 16, and so on, as neatly as in our generalized description.

During his extensive studies on the polychaete worm *Alitta succinea*, conducted at the Marine Biological Laboratory at Woods Hole, E. B. Wilson established an elegant coding system for spiral cleavage, one that allows us to follow the developmental lineage of every embryonic cell. Wilson's system, published in 1892, is usually applied to spiral cleavage in order to trace cell fates and compare development among species. Our account of spiral cleavage is a general one, but it provides a point of reference for later consideration of the patterns in different groups of animals.

At the 4-cell stage, following the initial longitudinal divisions, the cells are given the codes of A, B, C, and D and are labeled clockwise in that order when viewed from the animal pole (Figure 4.6A). These 4 cells are referred to as a **quartet** of macromeres, and they may be collectively coded as simply Q. The next division is more or less unequal, with the 4 cells nearest the animal pole being displaced in a fashion, as explained previously. These 4 smaller cells are called the first quartet of micromeres (collectively the lq cells) and are given the individual codes of 1a, 1b, 1c, and 1d. The numeral "1" indicates that they are members of the first micromere quartet to be produced; the letters correspond to their respective macromere origins. The capital letters designating the macromeres are now preceded with the numeral "1" to indicate that they have divided once and produced a first micromere set (Figure 4.6B). We may view this 8-celled embryo as four pairs of daughter cells that have been produced by the divisions of the 4 original macromeres as follows:



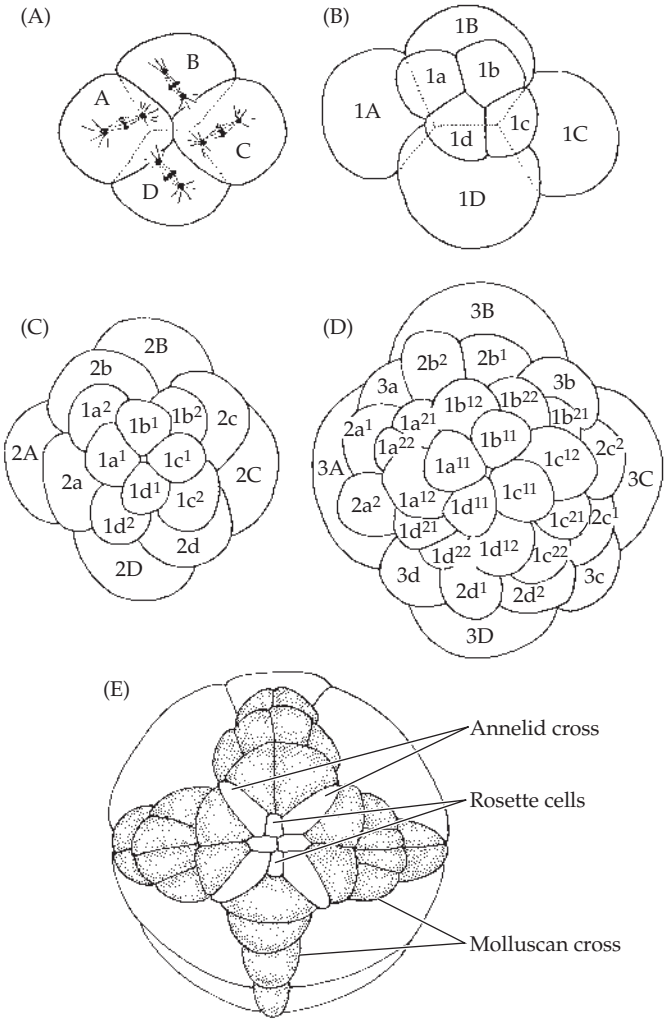


FIGURE 4.6 Spiral cleavage. (A–D) Spiral cleavage through 32 cells (assumed synchronous) labeled with E. B. Wilson's coding system (all diagrams are surface views from the animal pole). (E) Schematic diagram of a composite embryo at approximately 64 cells showing the positions of the rosette, annelid cross, and molluscan cross.

Note that although the macromeres and micromeres are sometimes similar in size, these terms are nonetheless always used in describing spiral cleavage. Much of the size discrepancy depends upon the amount of yolk present at the vegetal pole in the original egg; this yolk tends to be retained primarily in the larger macromeres.

The division from 8 to 16 cells occurs levotropically and involves cleavage of each macromere and micromere. Notice that the only code numbers that are changed through subsequent divisions are the prefix numbers of the macromeres. These are changed to indicate the number of times these individual macromeres have divided and to correspond to the number of micromere quartets thus produced. So at the 8-cell stage, we can designate the existing blastomeres as the 1Q (= 1A, 1B, 1C, 1D) and the lq (= 1a, 1b, 1c, 1d). The macromeres (1Q) divide to produce a second quartet of micromeres (2q = 2a, 2b, 2c, 2d), and the prefix numeral of the daughter macromeres is changed to "2." The first micromere quartet also divides and now comprises 8 cells, each of which is identifiable not only by the letter corresponding to its parent macromere but now by the addition of superscript numerals. For example, the 1a micromere (of the 8-cell embryo) divides to produce two daughter cells coded as $1a^1$ and the $1a^2$ cells. The cell that is physically nearer the animal pole of the embryo receives the superscript "1," the other cell the superscript "2." Thus, the 16-cell stage (Figure 4.6C) includes the following cells:

$$\text{Derivatives of the 1q} \begin{cases} 1a^1 & 1b^1 & 1c^1 & 1d^1 \\ 1a^2 & 1b^2 & 1c^2 & 1d^2 \end{cases}$$

$$\text{Derivatives of the 1Q} \begin{cases} 2q = 2a & 2b & 2c & 2d \\ 2Q = 2A & 2B & 2C & 2D \end{cases}$$

The next division (from 16 to 32 cells) again involves dextrotropic displacement. The third micromere quartet (3q) is formed, the daughter macromeres are now given the prefix "3" (3Q), and all of the 12 existing micromeres divide. Superscripts are added to the derivatives of the first and second micromere quartets according to the rule of position as stated previously. Thus, the $1b^1$ cell divides to yield the $1b^{11}$ and $1b^{12}$ cells; the $1a^2$ cell yields the $1a^{21}$ and $1a^{22}$ cells; the 2c yields the $2c^1$ and $2c^2$, and so on. Do not think of these superscripts as double-digit numbers (i.e., "twenty-one" and "twenty-two"), but rather as two-digit sequences reflecting the precise lineage of each cell ("two-one" and "two-two").

The elegance of Wilson's system is that each code tells the history as well as the position of the cell in the embryo. For instance, the code $1b^{11}$ indicates that the cell is a member (derivative) of the first quartet of micromeres, that its parent macromere is the B cell, that the original 1b micromere has divided twice since its formation, and that this particular cell rests uppermost in the embryo relative to its sister cells. The 32-cell state (Figure 4.6D) is composed of the following:

$$\text{Derivatives of the 1q} \begin{cases} 1a^{11} & 1b^{11} & 1c^{11} & 1d^{11} \\ 1a^{12} & 1b^{12} & 1c^{12} & 1d^{12} \\ 1a^{21} & 1b^{21} & 1c^{21} & 1d^{21} \\ 1a^{22} & 1b^{22} & 1c^{22} & 1d^{22} \end{cases}$$

$$\text{Derivatives of the 2q} \begin{cases} 2a^1 & 2b^1 & 2c^1 & 2d^1 \\ 2a^2 & 2b^2 & 2c^2 & 2d^2 \end{cases}$$

$$\text{Derivatives of the 2Q} \begin{cases} 3q = 3a & 3b & 3c & 3d \\ 3Q = 3A & 3B & 3C & 3D \end{cases}$$

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The division to 64 cells follows the same pattern, with appropriate coding changes and additions of superscripts. The displacement is levotropic and results in the following cells:

Derivatives of the 1q

$1a^{111}$	$1b^{111}$	$1c^{111}$	$1d^{111}$
$1a^{112}$	$1b^{112}$	$1c^{112}$	$1d^{112}$
$1a^{121}$	$1b^{121}$	$1c^{121}$	$1d^{121}$
$1a^{122}$	$1b^{122}$	$1c^{122}$	$1d^{122}$
$1a^{211}$	$1b^{211}$	$1c^{211}$	$1d^{211}$
$1a^{212}$	$1b^{212}$	$1c^{212}$	$1d^{212}$
$1a^{221}$	$1b^{221}$	$1c^{221}$	$1d^{221}$
$1a^{222}$	$1b^{222}$	$1c^{222}$	$1d^{222}$

Derivatives of the 2q

$2a^{11}$	$2b^{11}$	$2c^{11}$	$2d^{11}$
$2a^{12}$	$2b^{12}$	$2c^{12}$	$2d^{12}$
$2a^{21}$	$2b^{21}$	$2c^{21}$	$2d^{21}$
$2a^{22}$	$2b^{22}$	$2c^{22}$	$2d^{22}$

Derivatives of the 3q

$3a^{1}$	$3b^{1}$	$3c^{1}$	$3d^{1}$
$3a^{2}$	$3b^{2}$	$3c^{2}$	$3d^{2}$

Derivatives of the 3Q

4q =	4a	4b	4c	4d
4Q =	4A	4B	4C	4D

Notice that no two cells share the same code, so exact identification of individual blastomeres and their lineages is always possible. This is not the case with some other types of embryos.

Late in the spiral cleavage of certain animals, distinctive cell patterns appear, formed by the orientation of some of the apical first-quartet micromeres (Figure 4.6E). The topmost cells ($1q^{111}$ micromeres) lie at the embryo's apex and form the **rosette**. In some groups (e.g., annelids), other micromeres ($1q^{112}$ micromeres) produce an **annelid cross** roughly at right angles to the rosette cells. In molluscs, the annelid cross may appear (often called peripheral rosette cells in these groups), but an additional **molluscan cross** forms from the $1q^{12}$ cells and their derivatives. The arms of the molluscan cross lie between the cells of the annelid cross (Figure 4.6E), and this configuration is not known to occur in any other metazoan phylum. Some phylogenetic significance has been given to the appearance of these crosses, as we discuss in later chapters.

Cell Fates

Tracing the fates of cells through development has been a popular and productive endeavor of embryologists for over a century. Such studies have played a major role in allowing researchers to describe development as well as propose homologies among the attributes in different animals. The cells of embryos eventually become established as functional parts of tissues or organs, but before they do, there is much variation in the timing and degree to which cell fates become firmly fixed. Although under normal conditions their functions are specialized, even in adults, the cells of some animals (e.g., sponges) retain the ability to change their structure and function. Other animal taxa have remarkable power to regenerate lost parts or entire bodies, wherein cells dedifferentiate and then generate new tissues and organs. In still other taxa, cell fates are relatively fixed and cells are able only to produce more of their own kind.

Carefully watching the development of any animal makes it clear that certain cells predictably form certain structures. Here too, the emerging field of molecular developmental biology has shown that many molecular components of development are also widely conserved throughout the animal kingdom. For example, some transcription factors and cell signaling systems from widely divergent phyla are clearly homologous and evidently operate in much the same way. On the other hand, these highly conserved molecular components can also be used in diverse ways by embryos. The pattern of orthologous gene expression in early metazoan embryos illustrates both aspects of this relationship. Even such basic developmental features as adult body axis formation and cleavage geometry differ among the metazoan phyla (Figure 4.7). Such fundamental developmental variations appear to have been essential in fabricating the highest levels of animal body plans.

In some cases, cell fates are determined very early during cleavage—as early as the 2- or 4-cell stage. If one experimentally removes a blastomere from the early embryo of such an animal (as Roux did), then that embryo will fail to develop normally; the fates of the cells have already become fixed, and the missing cell cannot be replaced. Animals whose cell fates are established very early are said to have **determinate cleavage**. On the other hand, the blastomeres of some animals can be separated at the 2-cell, 4-cell (as Driesch did), or even later stages (as Spemann did), and each separate cell will develop normally; in these cases the fates of the cells are not fixed until relatively late in development. Such animals are said to have **indeterminate cleavage**. Eggs that undergo determinate cleavage are often called **mosaic ova** because the fates of regions of undivided cells can be mapped. Eggs that undergo indeterminate cleavage are called **regulative ova**, in that they can "regulate" to accommodate lost blastomeres and thus cannot easily be predictably mapped prior to division.

In any case, formation of the basic body plan is generally determined by the time the embryo comprises about 104 cells (usually after one or two days). By this time, all available embryonic material has been apportioned into specific cell groups, or "founder regions." These regions are relatively few, each forming

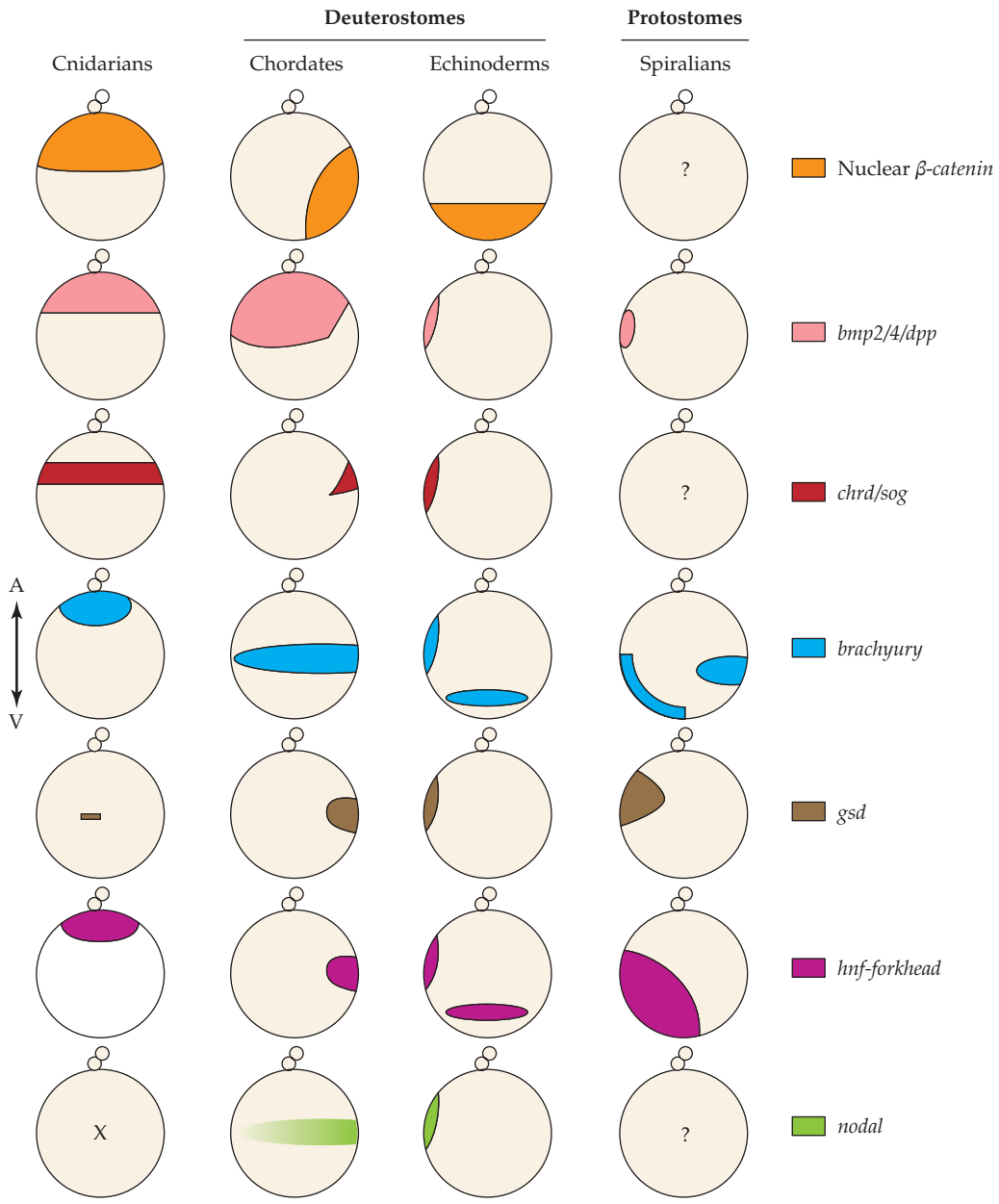

FIGURE 4.7 Locations and patterns of expression in some genes at the beginning of gastrulation in diverse metazoan embryos (cnidarians, chordates, echinoderms, spiralians). A↔V represents the animal–vegetal axis. All but one of the genes shown (*nodal*) are present in cnidarians as well as in chordates. While some genes (e.g., nuclear *β-catenin*) seem to track the changing location of gastrulation across taxa, other genes (e.g., *chordin* [*chrd*] and *goosecoid* [*gsd*] in echinoderms) are associated with gastrulation in some species and disassociated from such activity in others. The two circles at the animal pole represent polar bodies, X indicates that the gene is not present in the genome of a lineage, and ? indicates that the gene has not been recovered in a lineage. Gene abbreviations: *bmp*, bone morphogenetic protein; *dpp*, decapentaplegic; *sog*, short gastrulation; *hnf-forkhead*, hepatocyte nuclear factor, a forkhead homolog. (After M. Q. Martidale. 2005. *Nat Rev Genet* 6: 917–927. https://www.nature.com/articles/nrg1725)

a territory within which still more intricate developmental patterns unfold. As these zones of undifferentiated tissue are established, the unfolding genetic code drives them to develop into their "preassigned" body tissues, organs, or other structures. Graphic representations of these regions are called **fate maps**.

In the past, mosaic eggs and determinate cleavage have been equated with spirally cleaving embryos, and regulative ova and indeterminate cleavage with radially cleaving embryos. However, surprisingly few actual tests for determinacy have been performed, and what evidence is available suggests that there are many exceptions to this generalization. That is, some embryos with radial cleavage appear determinate.

In spite of the variations and exceptions, there is a remarkable underlying consistency in the fates of

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blastomeres among embryos that develop by typical spiral cleavage. Many examples of these similarities are discussed in later chapters, but we illustrate the point by noting that the germ layers of spirally cleaving embryos tend to arise from the same groups of cells. The first three quartets of micromeres and their derivatives give rise to **ectoderm** (the outer germ layer); the 4a, 4b, 4c, and 4Q cells to **endoderm** (the inner germ layer); and the 4d cell to **mesoderm** (the middle germ layer). Many students of embryology view this uniformity of cell fates as strong evidence that taxa sharing this pattern are related to one another in some fundamental way and that they share a common evolutionary heritage. We will have much more to say about this idea throughout this book.

Evo-devo analyses, for their part, provide an objective means for assessing germ layer homology by identifying genes that are transcribed at different developmental times, rather than identifying pools of cells by eventual fate (Figure 4.7). Genes that have proven useful for such analyses include *GATA 4*, *5*, and *6*, genes associated with mucus production in endodermal tissue; *twist*, a gene associated with mesodermal development; *snail*, a repressor of E-cadherin, and thus important for downregulating ectodermal genes within mesoderm and allowing mesenchymal development; and *brachyury*, a gene important in defining the midline of many bilaterians. However, this approach is complicated by the fact that even among closely related taxa, similar structures may be derived from different germ layers (e.g., Malpighian tubules are derived from ectoderm in insects but arise from endoderm in chelicerates). As we have explained, traits used for evolutionary comparative analyses, even at the molecular level, must be selected with caution.

Blastula Types

The product of early cleavage is called the **blastula**, which may be defined developmentally as the embryonic stage preceding the formation of embryonic germ layers. Several types of blastulae are recognized among invertebrates. Holoblastic cleavage generally results in either a hollow or a solid ball of cells. A **coeloblastula** (Figure 4.8A) is a hollow ball of cells, the wall of which is usually one cell layer thick. The space within the sphere of cells is the **blastocoel**, or primary body cavity. A **stereoblastula** (Figure 4.8B) is a solid ball of blastomeres; obviously there is no blastocoel at this stage. Meroblastic cleavage sometimes results in a cap or disc of cells at the animal pole over an uncleaved mass of yolk. This arrangement is appropriately termed a **discoblastula** (Figure 4.8C). Some centrolecithal ova undergo odd cleavage patterns to form a **periblastula**, similar in some respects to a coeloblastula that is centrally filled with noncellular yolk (Figure 4.8D).

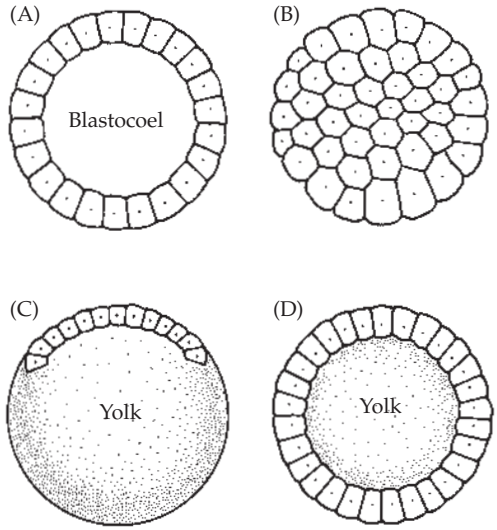

FIGURE 4.8 Types of blastulae. These diagrams represent sections along the animal–vegetal axis. (A) Coeloblastula. The blastomeres form a hollow sphere with a wall one cell layer thick. (B) Stereoblastula. Cleavage results in a solid ball of blastomeres. (C) Discoblastula. Cleavage has produced a cap of blastomeres that lies at the animal pole, above a solid mass of yolk. (D) Periblastula. Blastomeres form a single cell layer enclosing an inner yolky mass.

Gastrulation and Germ Layer Formation

Through one or more of several methods the blastula develops toward a multilayered form, a process called **gastrulation** (Figure 4.9). The structure of the blastula dictates to some degree the nature of the process and the form of the resulting embryo, the **gastrula**. Gastrulation is the formation of the embryonic germ layers, the tissues on which all subsequent development eventually depends. In fact, we may view gastrulation as the embryonic analogue of the transition from protistan to metazoan grades of complexity. It achieves separation of those cells that must interact directly with the environment (i.e., locomotor, sensory, and protective functions) from those that process materials ingested from the environment (i.e., nutritive functions).

The initial inner and outer sheets of cells are the **endoderm** and **ectoderm**, respectively; in most animals a third germ layer, the **mesoderm**, is produced between the ectoderm and the endoderm. One striking example of the unity among the Metazoa is the consistency of the fates of these germ layers. For example, ectoderm always forms the nervous system, the outer skin and its derivatives; endoderm forms the main portion of the gut and associated structures; mesoderm forms the coelomic lining, the circulatory system, most of the internal support structures, and the musculature. The process of gastrulation, then, is a critical one in establishing the basic materials and their locations for building the whole organism.

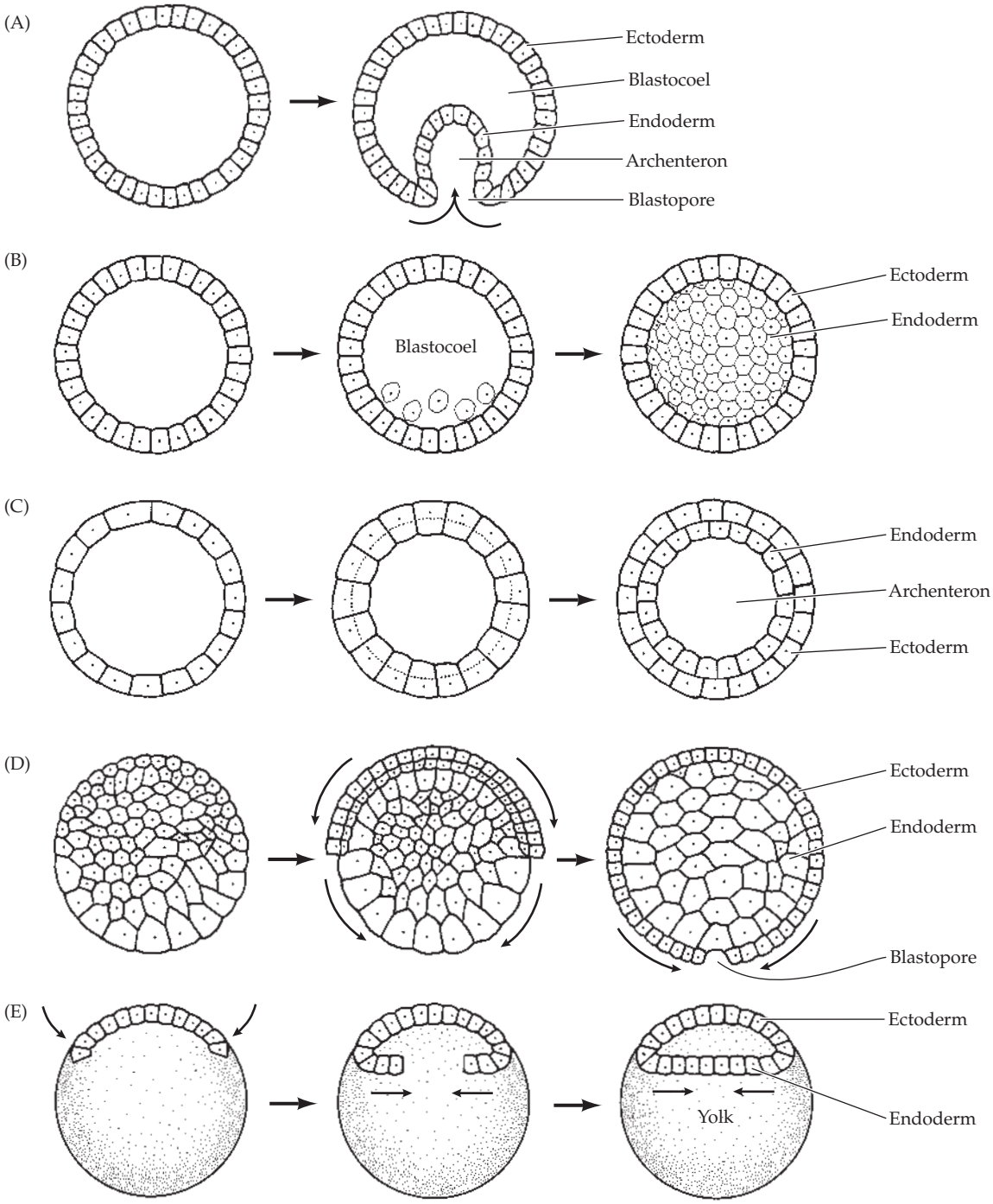

FIGURE 4.9 Forms of gastrulation. (A) Invagination of a coeloblastula to form a coelogastrula. (B) Unipolar ingression of a coeloblastula to form a stereogastrula. (C) Delamination of a coeloblastula to form a double-layered coelogastrula. (D) Epiboly of a stereoblastula to form a stereogastrula. (E) Involution of a discoblastula to form a discogastrula.

Coeloblastulae often gastrulate by **invagination**, a process commonly used to illustrate gastrulation in general zoology classes. The cells in one area of the surface of the blastula (frequently at or near the vegetal pole) pouch inward as a sac within the blastocoel (Figure 4.9A). These invaginated cells are now called the endoderm, and the sac thus formed is the embryonic gut, or **archenteron**; the opening to the outside is the **blastopore**. The outer cells are now called ectoderm, and a double-layered hollow coelogastrula has been formed. The blastopore may become the primordial mouth or anus, depending on the animal lineage. If this structure becomes the mouth, the ectoderm lining the interior of the blastopore is considered **stomodeal**. If the blastopore becomes the anus, the ectoderm lining the interior of this structure is

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considered **proctodeal**. Note that the diagrams in Figure 4.9 represent cross sections of three-dimensional embryos. Thus, the **coelogastrula** (Figure 4.9A) actually resembles a balloon with an invisible finger poking into it at the vegetal pole.

The coeloblastulae of many cnidarians undergo a gastrulation process that results in a solid gastrula (**stereogastrula**). Usually the cells of the blastula divide such that the cleavage planes are perpendicular to the surface of the embryo. Some of the cells detach from the wall and migrate into the blastocoel, eventually filling it with a solid mass of endoderm. This process is called **ingression** (Figure 4.9B) and may occur only at the vegetal pole (**unipolar** ingression) or more or less over the whole blastula (**multipolar** ingression). In a few instances (e.g., certain hydroids), the cells of the blastula divide with cleavage planes that are parallel to the surface, a process called **delamination** (Figure 4.9C). This process produces a layer or a solid mass of endoderm surrounded by a layer of ectoderm.

Stereoblastulae that result from holoblastic cleavage generally undergo gastrulation by **epiboly**. Because there is no blastocoel into which the presumptive endoderm can migrate by any of the methods mentioned earlier, gastrulation of this form involves a rapid growth by a sheet of presumptive ectodermal cells around the presumptive endoderm (Figure 4.9D). Cells of the animal pole proliferate rapidly, growing down and over the vegetal cells to enclose them as endoderm. The blastopore forms where the edges of this ectodermal sheet converge from all sides upon a single point at the vegetal pole. The archenteron typically forms secondarily as a space within the developed endoderm.

Figure 4.9E illustrates gastrulation by **involution**, a process that usually follows the formation of a discoblastula. The cells around the edge of the disc divide rapidly and grow beneath the disc, thus forming a double-layered gastrula with ectoderm on the surface and endoderm below. There are several other types of gastrulation, mostly variations or combinations of the processes just described. These gastrulation methods are discussed in later chapters.

During gastrulation, subtle shifts in the timing of regulatory gene expression, in the timing of cell fate specification, or in the movement of cells relative to one another can generate distinct developmental pathways. Such developmental divergences may dramatically shift larval or even adult formation within a lineage. For example, sea urchin larvae appear to have switched from **planktotrophy** (feeding larvae) to **lecithotrophy** (nonfeeding larvae) at least 20 times within the history of this echinoderm clade. Among nonfeeding larvae, egg size is often greater, cleavage is significantly altered, and the average larval life span is shorter.

Mesoderm and Body Cavities

During or soon after gastrulation, a middle layer forms between the ectoderm and the endoderm. This middle layer may be derived from ectoderm, as it is in members of the diploblastic phylum Cnidaria, or from endoderm, as it is in members of the triploblastic phyla. In the first case the middle layer is sometimes called **ectomesoderm**, and in the latter case it is called **endomesoderm** (or "true mesoderm"). Thus, the triploblastic condition, by definition, includes endomesoderm. In this text, and most others, the term "mesoderm" in a general sense refers to endomesoderm rather than ectomesoderm. Although endomesoderm is characteristic of triploblastic metazoans, in many lineages some ectomesoderm is also produced.

In diploblastic and certain triploblastic phyla (the acoelomates), the middle layer does not form thin sheets of cells; rather it produces a more-or-less solid but loosely organized mesenchyme consisting of a gel matrix (the **mesoglea**) containing various cellular and fibrous inclusions. In a few cases (e.g., the hydrozoans) a virtually noncellular mesoglea lies between the ectoderm and endoderm (see Chapter 6).

In most animals, the area between the inner and outer body layers includes a fluid-filled space. As discussed in Chapter 3, this space may be either a **blastocoelom**, a cavity not completely lined by mesoderm, or a true **coelom**, a cavity fully enclosed within thin sheets of mesodermally derived tissue. Endomesoderm generally originates in one of two basic ways (Figure 4.10), although modifications of these processes are discussed in later chapters. In most phyla that undergo spiral cleavage (e.g., flatworms, annelids, molluscs), a single micromere—the 4d cell, called the **mesentoblast**—proliferates as mesoderm between the developing archenteron (endoderm) and the body wall (ectoderm) (Figure 4.10A). The other cells of the 4q (the 4a, 4b, and 4c cells) and the 4Q cells generally contribute to endoderm. But exceptions exist, for

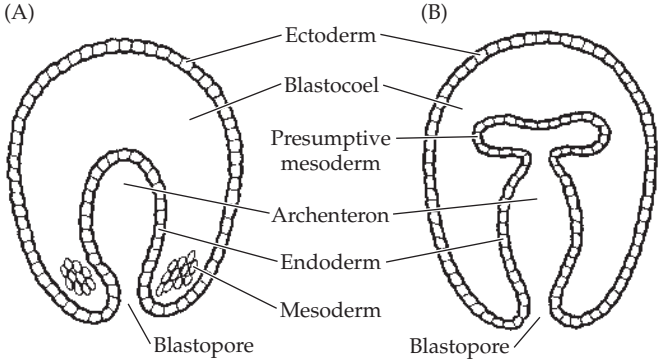

FIGURE 4.10 Methods of mesoderm formation in late gastrulae (frontal sections). (A) Mesoderm formed from derivatives of a mesentoblast. (B) Mesoderm formed by archenteric pouching.

example among the annelids, as in *Capitella teleta*, in which the mesoderm arises from 3c and 3d instead of 4d. In some other taxa (e.g., echinoderms and chordates) the mesoderm arises from the wall of the archenteron itself (i.e., from preformed endoderm), either as a solid sheet or as pouches (Figure 4.11B).

In addition to giving rise to other structures (such as the muscles of the gut and body wall), in coelomate animals mesoderm is intimately associated with the formation of the body cavity. In those instances where mesoderm is produced as solid masses derived from a mesentoblast, the body cavity arises through a process called **schizocoely**. Normally in such cases, bilaterally paired packets of mesoderm gradually enlarge, split internally, and then expand to simultaneously line the body wall, support viscera, and create thin-walled coelomic spaces (Figure 4.11A,B). The number of such paired coeloms varies among different animals and is frequently associated with segmentation, as it is in annelid worms (Figure 4.11C).

The other general method of coelom formation is called **enterocoely**; it accompanies the process of mesoderm formation from the archenteron. In the most direct sort of enterocoely, mesoderm production and coelom formation are one and the same process. Figures 4.10 and 4.12A illustrate this process, which is called **archenteric pouching**. A pouch or pouches form in the gut wall. Each pouch eventually pinches off from the gut as a complete coelomic compartment. The walls of these pouches are defined as mesoderm. In some cases the mesoderm arises from the wall of the archenteron as a solid sheet or plate that later becomes bilayered and hollow (Figure 4.12B). Some authors consider this process to be a form of schizocoely (because of the "splitting" of the mesodermal plate), but it is in fact a modified form of enterocoely. Enterocoely frequently results in a tripartite arrangement of the body cavities, which are designated **protocoel**, **mesocoel**, and **metacoel** (Figure 4.12C).

Following germ tissue establishment, cells begin to specialize and sort themselves out to form the organs and tissues of the body—a poorly understood process known as **morphogenesis**. Cell movements are an essential part of morphogenesis. In addition, in order to sculpt the organs and systems of the body, cells need to "know" when to stop growing and even die. For example, in nematode worms the vas deferens first develops with a closed end; the cell that blocks the end of this tube helps the vas deferens link up to the cloaca. Once the connection has been made, this terminal cell dies and disassociates, creating the opening to the cloaca.

Recent research suggests that the same families of molecules that guide the earliest stages of embryogenesis—setting up the elements of body patterning (Figure 4.7)—also play vital roles during morphogenesis. Communication among adjacent cells is also critical to morphogenesis, and there are three ways cells "talk" to one another during this process, known as **induction**. The first is via diffusible signaling molecules released from one cell and detected by the adjacent cell. These molecules include hormones, growth factors, and special substances called **morphogens**. A second method involves actual contact between the surfaces of adjacent cells, allowing cell surface molecules to interact. Cells selectively recognize other cells, adhering to some and migrating over others. A third method involves the movement of substances through gap junctions between cells. Of all the stages of ontogeny, we know least about morphogenesis.

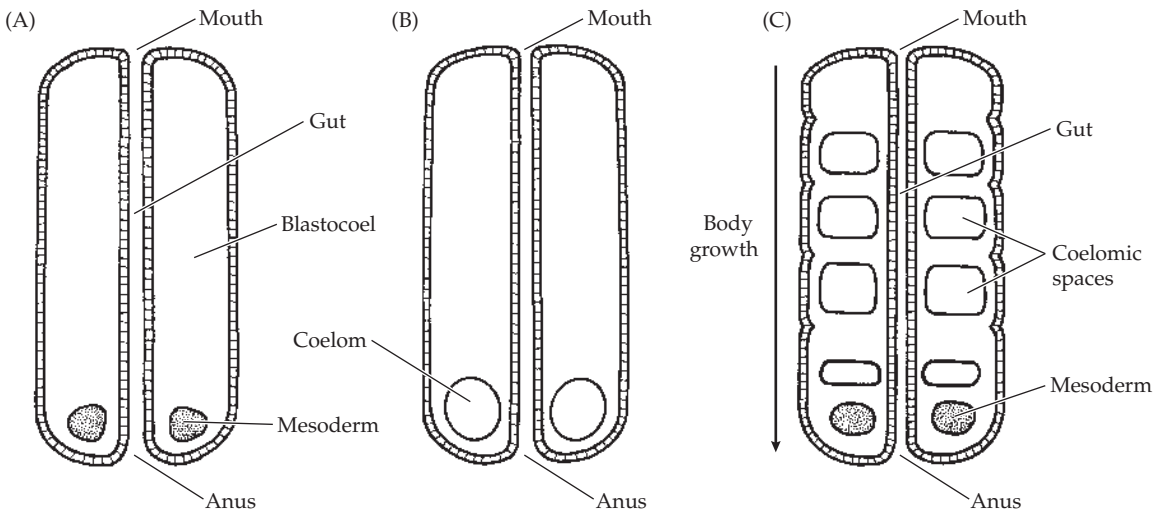

FIGURE 4.11 Coelom formation by schizocoely (frontal sections). (A) Precoelomic conditions with paired packets of mesoderm. (B) Hollowing of the mesodermal packets to produce a pair of coelomic spaces. (C) Progressive proliferation of serially arranged pairs of coelomic spaces. This process occurs in metameric annelids.

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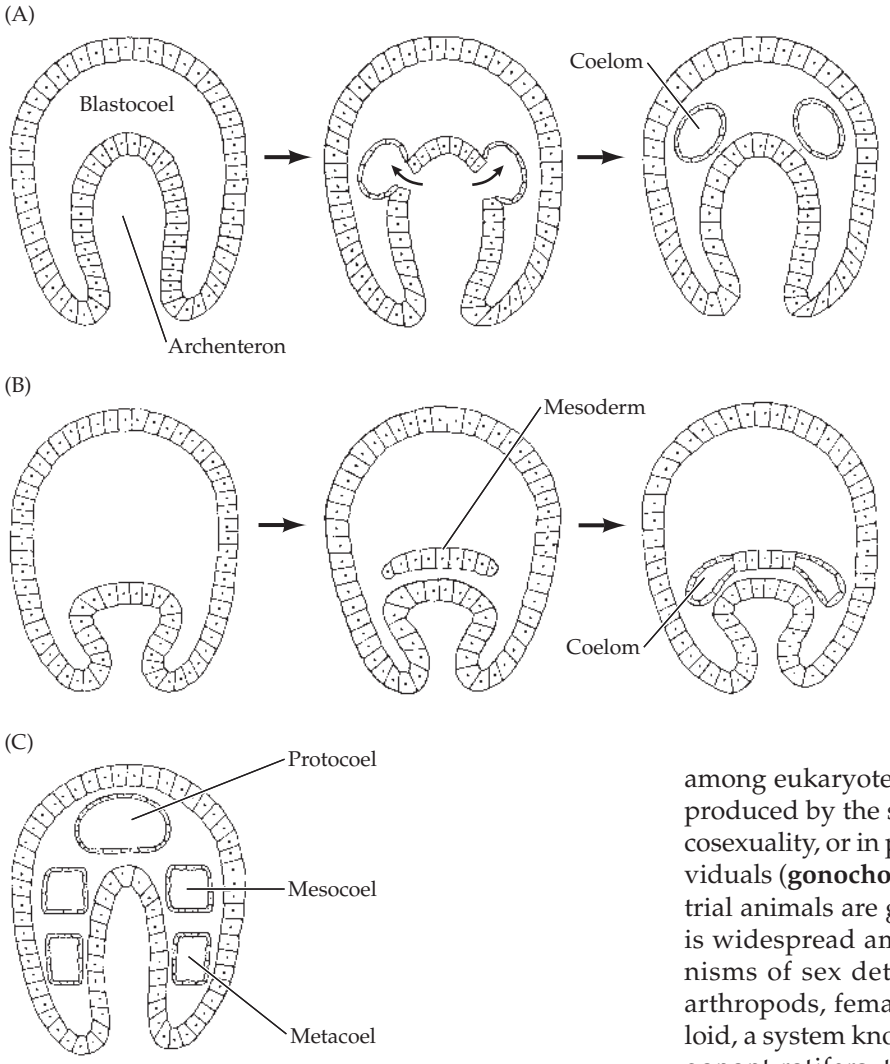

FIGURE 4.12 Coelom formation by enterocoely (frontal sections). (A) Archenteric pouching. (B) Proliferation and subsequent hollowing of a plate of mesoderm from the archenteron. (C) The typical tripartite arrangement of coeloms in a deuterostome embryo.

Life Cycles: Sequences and Strategies

The patterns of early development just described are not isolated sequences of events but are related to the mode of reproduction, the presence or absence of larval stages in the life cycle, and the ecology of the adult. Efforts to classify various invertebrate life cycles and to explain the evolutionary forces that gave rise to them have produced a large number of publications and a great deal of controversy. Most of these studies concern marine invertebrates, on which we center our attention first, and a selection of these are provided in the references for this chapter. We then present some comments on the special adaptations of terrestrial and freshwater forms.

Classification of Life Cycles

Our discussion of life cycles focuses on sexually reproducing animals. Sexual reproduction with some degree of gamete dimorphism is nearly universal among eukaryotes. Male and female gametes may be produced by the same individual (**hermaphroditism**, cosexuality, or in plants, monoecy) or by separate individuals (**gonochory**, or in plants, dioecy). Most terrestrial animals are gonochoristic, but hermaphroditism is widespread among marine invertebrates. Mechanisms of sex determination are diverse; in certain arthropods, females may be diploid and males haploid, a system known as **haplodiploidy**, and in monogonont rotifers, the males are also haploid, derived from an unfertilized egg. Other forms of sex determination involve structurally distinct sex chromosomes. In **male heterogamety**,[1] males carry X and Y sex chromosomes and females are XX, as in some vertebrates. In **female heterogamety**, females are ZW and males ZZ, as seen in many crustaceans. There is typically little or no recombinational exchange between X and Y chromosomes (or between Z and W) because there is almost no genetic homology between the sex chromosomes. Most of the Y (or W) chromosome is devoid of functional gene loci, other than a few RNA genes and some genes required for male (or female) fertility and sex determination. In any event, it is the fusion of male and female gametes that initiates the process of ontogeny and a new cycle in the life history of an organism.

A number of classification schemes for life cycles have been proposed over the past few decades (see papers by Thorson, Mileikovsky, Chia, Strathmann, Jablonsky, Lutz, and McEdward). We have generalized

[1]Not to be confused with heterogamy, the alternation of generations, especially between sexual and parthenogenetic generations.

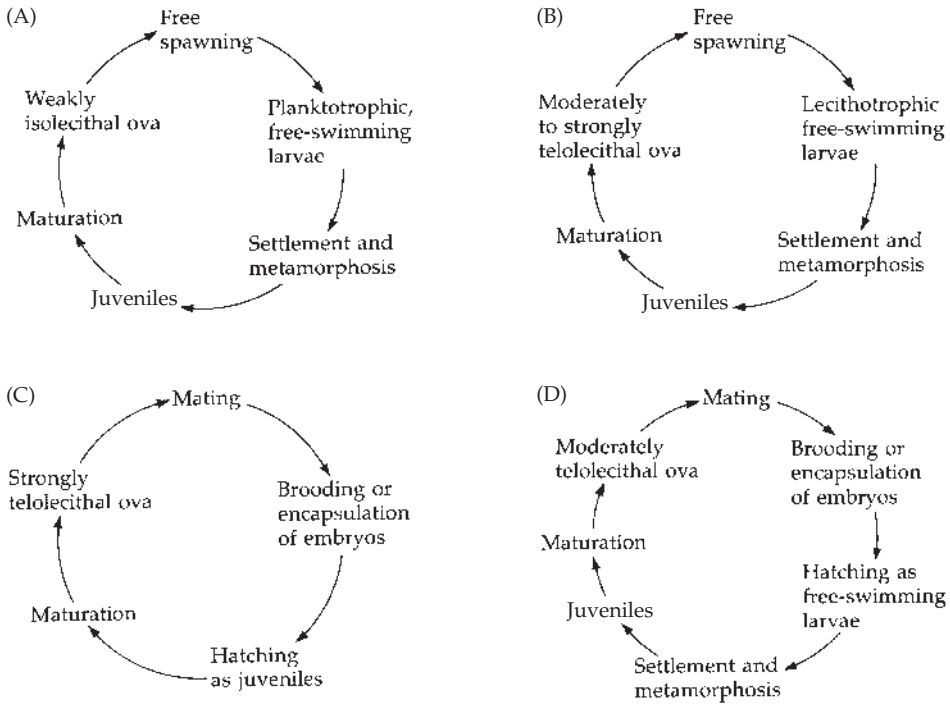

FIGURE 4.13 Some generalized invertebrate life cycle strategies. (A) Indirect development with planktotrophic larvae. (B) Indirect development with lecithotrophic larvae. (C) Direct development. (D) Mixed life cycle. Note that in many marine invertebrates the sperm is broadcast and taken up by the female.

from the works of various authors and suggest that most animals display some form of one of the three following basic patterns (Figure 4.13).

1. **Indirect development** The life cycle includes free spawning of gametes followed by the development of a free larval stage (usually a swimming form), which is distinctly different from the adult and must undergo a more or less drastic metamorphosis to reach the juvenile or young adult stage. The equivalent in terrestrial invertebrates is seen in insects with holometabolous development. In aquatic groups, two basic larval types can be recognized.
   a. Indirect development with **planktotrophic** larvae. The larva survives primarily by feeding, usually on plankton. (The feeding larvae of some deep-sea species are demersal and feed on detrital matter, never swimming very far off the bottom.)
   b. Indirect development with **lecithotrophic** larvae. The larva survives primarily on yolk supplied to the egg by the mother.
2. **Direct development** The life cycle does not include a free larva. In these cases the embryos are often cared for by the parents in one way or another (generally by brooding or encapsulation) until they emerge as juveniles. The equivalent in terrestrial invertebrates is seen in insects with ametabolous or hemimetabolous development.
3. **Mixed development** The life cycle involves brooding or encapsulation of the embryos at early stages of development and subsequent release of free planktotrophic or lecithotrophic larvae. The initial source of nutrition and protection is the adult.

Not every species can be conveniently categorized into just one of these developmental patterns. For example, some species have free larvae that depend on yolk for a time but begin to feed once they develop the ability to do so. Some species actually display different developmental strategies under different environmental conditions—convincing evidence that embryogeny, like so many other aspects of a species or population, is subject to selection pressures and can readily evolve.

These life cycle patterns provoke three basic questions. First, how do different developmental sequences relate to other aspects of reproduction such as egg types and mating or spawning activities? Second, how do overall developmental sequences relate to the survival strategies of larvae and adults? Third, what evolutionary mechanisms are responsible for the patterns seen in any given species? Given the large number of interacting factors to be considered, these are complex questions, and our understanding of them is still incomplete. However, by first examining cases of indirect and direct development, we can illustrate some of the principles that underlie their relationships to different ecological situations. Then we will briefly address some ideas about mixed development.

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Indirect Development

Consider first a life cycle with planktotrophic larvae (Figure 4.13A). The metabolic expense incurred on the part of the adults involves only the production and release of gametes. Animals with fully indirect development generally do not mate; instead, they shed their eggs and sperm into the water, thus divorcing the adults from any further responsibility of parental care. Such animals typically undergo **synchronous (epidemic) broadcast spawning** of large numbers of gametes, thereby ensuring some level of successful fertilization. This pattern of development is relatively common in opportunistically settling and colonizing (*r*-selected) marine species that make use of tides or ocean currents to disperse their progeny and that are capable of rapid production of high numbers of gametes.

The eggs of animals expressing such traits are usually isolecithal and individually inexpensive to produce. The overall cost—and it is a significant one to each potential parent—is in the production of very large numbers of eggs. Being supplied with little yolk, the embryos must develop quickly into feeding larvae to survive. Mortalities among the embryos and larvae are extremely high and can result from a variety of factors, including lack of food, predation, or adverse environmental conditions. Each successful larva must accumulate enough nutrients from feeding to provide for its immediate survival, as well as for the processes of settling and metamorphosis from larva to juvenile or subadult. That is, it must feed to excess as it prepares for a new lifestyle as a juvenile. Survival rates from zygote to settled juvenile are often less than one percent. Such high mortalities are offset by the initial high production of gametes. But by the same token, high larval mortalities offset the high production of gametes—if all of these zygotes survived, the Earth would quickly be covered by the offspring of animals with indirect development.

What are the advantages and limitations of such a life history, and under what circumstances might it be successful? This sort of planktotrophic development is most common among benthic marine invertebrates in relatively shallow water and the intertidal zones of tropical and warm temperate seas. Here the planktonic food sources are more consistently available (although often in low concentration) than they are in colder or deeper waters, thus reducing the danger of starvation of the larvae. Such **meroplanktonic life cycles** allow animals to take advantage of two distinct resources (plankton in the upper water column as larvae; benthos and bottom plankton as adults). This arrangement reduces or eliminates competition between larvae and adults. Indirect development also provides a mechanism for dispersal, a particularly important benefit to species that are sessile or sedentary as adults. There is good evidence to suggest that animals with free-swimming larvae are likely to recover more quickly from damage to the adult population than those engaging in direct development. A successful set of larvae is a ready-made new population to replace lost adults.

The disadvantages of planktotrophic development result from the unpredictability of larval success. Excessive larval deaths can result in poor recruitment and the possibility of invasion of suitable habitats by competitors. Conversely, unusually high survival rates of larvae can lead to overcrowding and intraspecific competition upon settling.

Animals that produce fully lecithotrophic larvae (Figure 4.13B) must produce yolky and thus more metabolically expensive eggs. This built-in nutrient supply releases the larvae from dependence on environmental food supplies and generally results in reduced mortalities. It is not surprising that these animals produce somewhat fewer ova than those with planktotrophic larvae. The eggs are either spawned directly into the water or are fertilized internally and released as zygotes. Again, the adults' parental responsibility ends with the release of gametes or zygotes into the environment. Although survival rates of lecithotrophic larvae are generally higher than those of planktotrophic types, they are low compared with those of embryos that undergo direct development.

Marine invertebrates that live in relatively deep benthic environments tend to produce lecithotrophic larvae. Here, some of the advantages of indirect development are realized, but larvae do not require environmental food supplies and therefore avoid the intense predation commonly encountered in surface water. The trade-off is clear: in deeper water fewer, more expensive zygotes are produced, but they can survive where more numerous, less expensive planktotrophic larvae cannot.

Settling and Metamorphosis

Of particular importance to the successful completion of animal life cycles with free larval stages are the processes of settlement and metamorphosis. These are crucial and dangerous events in an animal's life cycle because they often require rapid and dramatic changes in individual habitats and lifestyle. Free-swimming larvae usually metamorphose into benthic juveniles, a process that involves the shedding of larval structures and the rapid growth or mobilization of juvenile ones. Surviving this transformation in form and function and adopting a new mode of life, often sessile or more sedentary, require adequate stored resources, appropriate responses to internal and external conditions, and considerable luck.

Throughout their free-swimming lives larvae "prepare" for these events, until they reach a condition in which they are physiologically capable of metamorphosis. Such larvae are termed **competent**. The duration of the free-swimming period varies greatly among

metazoan larvae and depends on factors such as original egg size, yolk content, and the availability of food for planktotrophic forms. Once a larva becomes competent, it generally begins to respond to certain environmental cues that induce settling behavior, a fascinating field of inquiry that includes chemical as well as physical cues, such as the noise of waves in reef environments. Metamorphosis is often preceded by settling, although some species metamorphose prior to settling and still others engage in both processes simultaneously. In any case, larvae typically become negatively phototactic and/or positively geotactic and move toward the bottom to settle. In species that are planktonic both as larvae and as adults (**holoplanktonic species**), the larvae obviously do not settle on the benthos.

Once contact with a substratum is made, a larva tests it, to determine its suitability as a habitat. This act of substratum selection may involve processing physical, chemical, and biological information. A number of studies show that important factors include substratum texture, composition, and particle size; presence of conspecific adults (or dominant competitors); presence of key chemical cues; presence of appropriate food sources; sound; and the nature of bottom currents or turbulence. Contact with the substrate includes risks. Previously settled planktivores and predators are likely to be common in many potentially suitable habitats. Once again, larval mortalities at this stage are high.

Many invertebrate larvae touch down on the bottom for a few minutes, then launch themselves back up into the current again and again until a suitable substratum is found. Assuming an appropriate situation is encountered, metamorphosis is induced and proceeds to completion. Interestingly, some feeding larvae are able to postpone metamorphosis and resume planktonic life if they initially encounter an unsuitable substratum. In such cases, however, the larvae become gradually less selective; eventually, metamorphosis ensues regardless of the availability of a proper substratum. The ability to prolong the larval period until conditions are favorable for settlement has obvious survival advantages, and invertebrates differ greatly in this capability. Those that can postpone settlement may do so by several hours, days, or even months (based on laboratory experiments).

Direct Development

Direct development avoids some of the disadvantages but also misses some of the advantages of indirect development. A typical scenario involves the production of relatively few, very yolky eggs, followed by some sort of mating activity and internal fertilization (Figure 4.13C). The embryos receive prolonged parental care, either directly (by brooding in or on the parent's body) or indirectly (by encapsulation in egg cases provided by the parent). Animals that simply deposit their fertilized eggs, either freely or in capsules, are said to be **oviparous**. A great number of invertebrates as well as some vertebrates (amphibians, many fishes, reptiles, birds, and monotremes) display oviparity. Animals that brood their embryos internally and nourish them directly, such as placental mammals or peracarid crustaceans, are described as **viviparous**. **Ovoviviparous** animals brood their embryos internally but rely on the yolk within the eggs to nourish their developing young. Most internally brooding invertebrates are ovoviviparous, but in velvet worms, in addition to oviparity, multiple types of viviparity are found.

The large, yolky eggs of most invertebrates with direct development are metabolically expensive to produce, and they are a rich source of food for potential predators. But while only a few eggs are possible, the investment is protected though parental effort, and survival rates are relatively high. The dangers of planktonic larval life and metamorphosis are avoided, and the embryos eventually hatch as juveniles.

What sorts of environments and lifestyles might result in selection for such a developmental sequence? At the risk of overgeneralizing, we can say that there is a tendency for specialist (e.g., *K*-selected) species to display direct development. Another situation in which direct development occurs is when the adults have no dispersal problems. We find, for example, that holoplanktonic species with pelagic adults (e.g., arrow worms, phylum Chaetognatha; pelagic gastropods) often undergo direct development, either by brooding or by producing floating egg cases. A second situation is one in which critical environmental factors (e.g., food, temperature, water currents) are highly variable. There is a trend among benthic invertebrates to switch from planktotrophic indirect development to direct development at increasingly higher latitudes. The relatively harsh conditions and strongly seasonal occurrence of planktonic food sources in polar and subpolar areas partially explain this tendency for the high proportion of direct developing (and brooding) species.

In addition to avoiding some of the danger of larval life, direct development has another distinct advantage. The juveniles hatch in suitable habitats where the adults brooded them or deposited the eggs in capsules. Thus, there is a reasonable assurance of appropriate food sources and other environmental factors for the young.

Mixed Development

As defined earlier, mixed life histories involve some period of brooding prior to release of a free larval stage. Costly, yolky zygotes are protected for some time and then are released as larvae, exploiting the advantages of dispersal. This developmental pattern is often ignored when classifying life histories, but in fact it is

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widespread among gastropods, insects, crustaceans, sponges, cnidarians, and a host of other animal groups. Some workers view mixed development as either the "best" or the "worst" of both worlds (i.e., fully indirect or direct). Others suggest that such sequences are evolutionarily unstable and that local environmental pressures are driving them toward direct or indirect development. There are, however, other possible explanations. It may very well be that under some environmental situations a brooding period followed by a larval phase is adaptive and stable.

Furthermore, at least some species show population variability in the relative lengths of time embryos exist in a brooded versus a free larval phase. If this variability responds to local environmental pressures, then clearly such a species might adapt quickly to changing conditions or even exploit this ability by extending its geographic range to live under a variety of settings. In this regard, mixed life histories may represent **developmental polymorphism**, in which the frequency and intensity of particular environmental cues influence the proportion of the population that expresses or does not express a particular larval phenotype. Such **phenotypic plasticity** in life history expression is an area in need of further investigation.

Our short description of life history strategies certainly does not explain all observable patterns in nature. The historical and evolutionary forces acting on invertebrates (and their larvae) are highly complex. For example, larvae are subject to all manner of oceanographic variables (e.g., diffusion, lateral and vertical transport, sea floor topography, storms) as well as their self-directed vertical movements, seasonality, and biotic factors (predators, prey, competition, nutrient availability). Life history predictions based strictly on environmental conditions do not always hold true. Invertebrates living in the deep sea and at the poles do not always brood (as was once thought), although many echinoderms in Antarctic waters do brood. We now know that all life history strategies occur in these regions, and many deep-sea and polar species release free-swimming larvae, and even planktotrophic larvae. Even some invertebrates of deep-sea hydrothermal vent communities produce free-swimming larvae. In many cases, this may be due to evolutionary constraints: vent gastropods, for example, belong to lineages that are almost strictly lecithotrophic, regardless of latitude or habitat. Thus, vent gastropods are apparently constrained by their phylogenetic histories. Other vent species that release free larvae, however, are not so constrained: mytilid bivalves, for example, possess a wide range of reproductive modes and tend to release planktotrophic larvae in deep-sea and vent environments. Furthermore, reproductive cycles in many abyssal invertebrates appear to be seasonal, perhaps cued by annual variations in surface water productivity. There is still much to be learned.

Adaptations to Land and Fresh Water

The foregoing account of life cycle strategies applies largely to marine invertebrates. Many invertebrates, however, have invaded land or fresh water, and their success in these habitats requires not only adaptation of the adults to special problems, but also adaptation of the developmental forms. As discussed in Chapter 1, terrestrial and freshwater environments are more rigorous and unstable than the sea, and they are generally unsuitable for reproductive strategies that involve free spawning of gametes or the production of delicate larval forms. Most groups of terrestrial and freshwater invertebrates have adopted internal fertilization followed by direct development, while their marine counterparts often exhibit external fertilization and produce free-swimming larvae.

Parasite Life Cycles

The evolutionary success of parasites is clear. Every animal species examined for symbionts appears to provide habitat for at least one, and usually many, associated species. These symbionts often draw benefits from their hosts at their hosts' expense, and thus they are parasites. Most parasites have rather complicated life cycles, and specific examples are given in later chapters. For now, we will examine parasitic lifestyles in a general way to understand their central features and to introduce some basic terminology.

As outlined in Chapter 1, parasites may be classified as **ectoparasites** (living upon the host), **endoparasites** (living internally, within the host), or **mesoparasites** (living in some cavity of the host that opens directly to the outside, such as the oral, nasal, anal, or gill cavities). While associated with a host, a parasite may engage in sexual or asexual reproduction, but the eggs or embryos are usually released to the outside via some avenue from the host's body. The problems at this point are very similar to those encountered during indirect larval development: some mechanism must be provided to ensure adequate survival through the developmental stages, and some sequence of events must bring the parasite back to an appropriate host (the proper "substratum") for maturation and reproduction. As explained earlier, habitat transitions are risky. Thus, many parasites are **parthenogenetic**—a form of reproduction in which the ovum undergoes embryonic development and produces a new individual without fertilization. Parthenogenesis produces offspring that are genetically identical to their parent. Other parasites may be capable of asexual reproduction by way of fission or budding. The production of asexual progeny appears to be one mechanism by which parasites offset the high mortality that attends transitions from one host to the next.

Parasites exploit at least two different habitats in their life cycles. This practice is essential because when hosts die, their parasites usually die with them. Thus,

the developmental period from zygote to adult parasite involves either the invasion of another host, or a free-living period between host invasions. When more than one host species is utilized for the completion of the life cycle, the organism harboring the adult parasite is called the **primary** or **definitive** host. Hosts in which developmental or larval forms reside are called **intermediate** hosts. The completion of complex life cycles often requires elaborate methods of transfer from one host to the other (this could involve more than two hosts), and again, surviving the changes from one habitat to another can be problematic. Losses are routinely high. Thus, we find that many parasites enjoy some of the benefits of indirect development (e.g., dispersal and exploitation of multiple resources) while being subjected to accompanying high mortalities and the dangers of very specialized lifestyles.

We emphasize again that our discussions of life cycles are generalities to which there are many exceptions. But given these basic patterns, you should recognize and appreciate the adaptive significance of life history patterns of the different invertebrate groups discussed later. You might also be able to predict the sorts of sequences that would be likely to occur under different conditions. For example, given a situation in which a particular species is known to produce very high numbers of free-spawned, isolecithal ova, what might you predict about cleavage pattern, blastula and gastrula type, presence or absence of a larval stage, type of larva, adult lifestyle, and ecological settings in which such a sequence would be advantageous? We hope you will develop the habit of asking these kinds of questions and thinking in this way about all aspects of your study of invertebrates.

The Relationships Between Ontogeny and Phylogeny

Of the many fields of study from which we draw information used in phylogenetic investigations, embryology has been one of the most important and productive. The construction of phylogenies may be accomplished and subsequently tested by several different methods (Chapter 2). But regardless of method, one of the principal problems of phylogeny reconstruction—in fact, central to the process—is separating true homologies from similar character traits that are the result of evolutionary convergence. Even when these problems involve comparative adult morphology, one must often seek answers in studies of the development of the organisms and structures in question. The search is for developmental processes or structures that are homologues and thus demonstrate relationships between ancestors and descendants. Changes that take place in developmental stages are not trivial evolutionary events. It has been effectively argued that developmental phenomena may themselves provide the evolutionary mechanisms by which entire new lineages originated (Chapter 1). As Stephen Jay Gould (1977) noted,

> *Evolution is strongly constrained by the conservative nature of embryological programs. Nothing in biology is more complex than the production of an adult . . . from a single fertilized ovum. Nothing much can be changed very radically without discombobulating the embryo.*

Indeed, the persistence of distinctive body plans throughout the history of life is testimony to the resistance to change of complex developmental programs. (See Hall 1996 for an excellent analysis of these issues.)

Although few workers would argue against a significant relationship between ontogeny and phylogeny, the exact nature and extent of the relationship have historically been subjects of considerable controversy, a good deal of which continues today. (Gould 1977 presents a fine analysis of these debates.) Central to much of the controversy is the concept of recapitulation.

The Concept of Recapitulation

In 1866 Ernst Haeckel, a physician who found a higher calling in zoology and never practiced medicine, introduced his **law of recapitulation** (or the **biogenetic law**), most commonly stated as "ontogeny recapitulates phylogeny." Haeckel suggested that a species' embryonic development (ontogeny) reflects the adult forms of that species' evolutionary history (phylogeny). According to Haeckel, this was no accident but a result of a close mechanistic relationship between the two processes: phylogenesis is the actual cause of embryogeny. Restated, animals have an embryogeny *because* of their evolutionary history. Evolutionary change over time has resulted in a continual adding on of morphological stages to the developmental process of organisms. The implications of Haeckel's proposal are immense. Among other things, it means that to trace the phylogeny of an animal, one need only examine its development to find therein a sequential or "chronological" parade of the animal's adult ancestors.

Ideas and disagreement concerning the relationship between ontogeny and phylogeny were by no means new even at Haeckel's time. Over 2,000 years ago Aristotle described a sequence of "souls" or "essences" of increasing quality and complexity through which animals pass in their development. He related these conditions to the adult "souls" of various lower and higher organisms, a notion suggestive of a type of recapitulation.

Descriptive embryology flourished in the nineteenth century, stimulating vigorous controversy regarding the relationship between development and evolution. Many of the leading developmental biologists of the time were in the thick of things, each proposing his own explanation (Meckel 1811; Serres 1824; von Baer 1828; and others). It was Haeckel, however, who really stirred

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the pot with his discourse on the "law" of recapitulation. He offered a focal point around which biologists argued pro or con for 50 years; sporadic skirmishes still erupt periodically. Walter Garstang critically examined the biogenetic law and gave us a different line of thinking. His ideas, presented in 1922, are reflected in many of his poems (published posthumously in 1951). Garstang made clear what a number of other biologists had suggested: evolution must be viewed not as a succession of ancestral adult forms, but as a succession of ontogenies. Each animal is a result of its own developmental processes, and any change in an adult must represent a change in its ontogeny. So what we see in the embryogeny of a particular species are not tiny replicas of its adult ancestors, but rather an evolved pattern of development in which clues or traces of ancestral ontogenies, and thus phylogenetic relationships to other organisms, may be found.

Arguments over these matters did not end with Garstang, and they continue today in many quarters. In general, we tend to agree with the approach (if not all of the details) of Gosta Jägersten in *Evolution of the Metazoan Life Cycle* (1972). Recapitulation per se should not categorically be accepted or dismissed as an "always" or "never" phenomenon. The term must be clearly defined in each case investigated, not locked into Haeckel's original definition and implications. For instance, similar, distinctive, homologous larval types within a group of animals reflect some degree of shared ancestry (e.g., crustacean nauplii or molluscan veligers). And we may speculate on such matters at various taxonomic levels, even when the adults are quite different from one another (e.g., annelids and molluscs are very different but have similar trochophore larvae). These phenomena may be viewed as developmental evidence of relatedness through shared ancestry, and thus they are examples of "recapitulation" in a broad sense.

Jägersten's example of vertebrate gill slits is particularly appropriate because, to him, it provides a case in which Haeckel's strict concept of recapitulation is manifest. In writing of this feature Jägersten (1972) stated:

> *The fact remains . . . that a character which once existed in the adults of the ancestors but was lost in the adults of the descendants is retained in an easily recognizable shape in the embryogenesis of the latter. This is my interpretation of recapitulation (the biogenetic "law").*

Hyman (1940) perhaps put it most reasonably when she wrote:

> *Recapitulation in its narrow Haeckelian sense, as repetition of adult ancestors, is not generally applicable; but ancestral resemblance during ontogeny is a general biological principle. There is no need to quibble over the word recapitulation; either the usage of the word should be altered to include any type of ancestral reminiscence during ontogeny, or some new term should be invented.*

Other authors, however, are not comfortable with such flexibility and have made great efforts to categorize and define the various possible relationships between ontogeny and phylogeny, of which strict recapitulation is considered only one (see especially chapter 7 of Gould 1977). Although much of this material is beyond the scope of this book, we discuss a few commonly used terms here because they bear on topics in later chapters. We have drawn on a number of sources cited in this chapter to mix freely with our own ideas in explaining these concepts.

Heterochrony and Paedomorphosis

When comparing two ontogenies, one often finds that some features appear earlier or later in one sequence than in the other. Such temporal displacement during development is called **heterochrony**. When comparing suspected ancestral and descendant embryogenies, for example, we may find the very rapid (accelerated) development of a particular feature and thus its relatively early appearance in a descendant species or lineage. Conversely, the development of a trait may be slower (retarded) in a descendant than in an ancestor and thus appear later in the descendant's ontogeny. This retardation may be so pronounced that a structure may never develop to more than a rudiment of its ancestral condition. (For excellent reviews of heterochrony and its impact on phylogeny see Gould 1977, and McKinney and McNamara 1991.)

Particular types of heterochrony result in a condition known as **paedomorphosis**, wherein sexually mature adults possess features characteristically found in early developmental stages of related forms (i.e., juvenile or larval features). Paedomorphosis results when adult reproductive structures develop before completion of the development of all the adult nonreproductive (somatic) structures. This condition can result from two different heterochronic processes. These are **neoteny**, in which somatic development is retarded, and **progenesis**, in which reproductive development is accelerated. These two terms are frequently used interchangeably because it is not always possible to know which process has given rise to a particular paedomorphic condition. Recognition of paedomorphosis may play a significant role in examining evolutionary hypotheses concerning the origins of certain lineages. For example, the evolution of precocious sexual maturation of a planktonic larval stage (that would "normally" continue developing to a benthic adult) might result in a new diverging lineage in which the descendants pursue a fully pelagic existence. Such a scenario, for example, may have been responsible for the origin of some small planktonic crustaceans. Paedomorphosis has also played major roles in theories regarding the origin of the vertebrates.

Myriad questions about the role of embryogenesis in evolution and the usefulness of embryology in

constructing and testing phylogenies persist. As the following accounts show, different authors continue to hold a variety of opinions about these matters.

The Origin of the Metazoa

One theme we develop throughout this book is the evolutionary relationships within and among the invertebrate taxa (see Chapters 8 and 28). Life has probably existed on this planet for nearly 4 billion years; humans have been observing it scientifically for only a few thousand years, and evolutionarily for only about 150 years. Thus, the thread of evolutionary continuity we actually see around us today looks a bit like frazzled ends, representing the many successful animal lineages that survive today, but omitting the legions of extinct species and lineages whose identities could provide a clearer understanding of the history of life on Earth. It is only through conjecture, study, inference, and the testing of hypotheses that we are able to trace phylogenetic strands back in time, joining them at various points to produce hypothetical pathways of evolution. We do not operate blindly in this process but use rigorous scientific methodology to draw upon information from many disciplines in attempts to make our evolutionary hypotheses meaningful and (we hope) increasingly closer to the truth—to the actual biotic history of Earth (Chapter 2).

In Chapter 1 we briefly reviewed the history of life, in part inferred from the fossil record, and in Chapter 28 we present a phylogenetic tree of the animal kingdom. However, many workers have not been satisfied to develop phylogenetic analyses based solely upon known (extant and extinct) animal groups but have felt compelled to speculate on hypothetical ancestors that might have occurred along the evolutionary road to modern life. A variety of evolutionary stories have been proposed to describe these sequences of hypothetical metazoan ancestors. We discuss some of these next, and some key works are cited in the references at the end of this book.

Origin of the Metazoan Condition

The origin of the metazoan condition has received attention for more than a century. One of the most spectacular phenomena in the fossil record is the seeming sudden appearance of nearly all of the metazoan phyla living today in a brief span of 30 million years, at the Precambrian–Cambrian transition (approximately 541 million years ago). There is now little doubt that animals—the Metazoa—arose as a monophyletic group from a protist ancestor shared with choanoflagellates 650 million years ago or earlier (Chapter 1). The debates now concern what these first animals were like, what oceanic habitats they inhabited, and how the changes from unicellularity to multicellularity took place.

Historical Perspectives on Metazoan Origins

What intermediate forms might have linked protists and metazoans? Some authors have chosen to design logical but hypothetical creatures for this purpose. Others rummage among extant types, arguing the advantages of using "real" organisms. Although it is probable that the actual precursor of the Metazoa is long extinct, the existence of modern-day forms that combine protist and metazoan traits keeps this debate alive, although it is well established that the closest living relatives are choanoflagellates, ichthyosporeans, and filastereans. Figure 4.14 illustrates some creatures that were once proposed to be "intermediates" between protists and metazoans, even though today we know that many of them are actually derived metazoans (thus illustrating the flaw in nonempirical narratives of "hypothetical ancestor" scenarios).

Before molecular tools convincingly linked protists to metazoan ancestry, several theories of metazoan evolution enjoyed support. In 1892, Johannes Frenzel described one such organism collected from salt pans in Argentina (Figure 4.14F). Tiny *Salinella* possessed a mouth and an anus, fed on organic detritus, and a single layer of cells formed its entire body wall. Although this creature lacked the layered cellular construction of the Metazoa, it displayed a higher level of organization than colonial protists, and the phylum Monoblastozoa was erected for it. Sadly, *Salinella* has not been seen since the original report, and many zoologists, including some who went sampling in the same purported salt pans, suspect that Frenzel seriously misinterpreted whatever creature he saw. Other so-called "mesozoan" phyla, Dicyemida and Orthonectida (Figure 4.14G,H), are also structurally simple, but these animals are endoparasites of invertebrates and have complex life cycles. While possibly resembling early metazoans, their body organization, life cycles, and phylogenetic position have all shown them to be more derived than ancestral.

The **colonial theory** of metazoan evolution was first expressed by Ernst Haeckel (1874), who proposed that a colonial flagellated protist gave rise to a planuloid metazoan ancestor (the planula is the basic larval type of cnidarians; see Chapter 7). The ancestral protist in this theory was a hollow sphere of flagellated cells that developed anterior–posterior locomotor orientation, and specialization of cells into separate somatic and reproductive functions. Similar conditions are common in living colonial protists, including freshwater, colonial, photosynthetic flagellates such as *Volvox* (Figure 4.14A). Haeckel called this hypothetical protometazoan ancestor a **blastea** (Figure 4.15A) and supported its validity by noting the widespread occurrence of coeloblastulae among modern animals.

In Haeckel's scenario, the first Metazoa arose by invagination of the blastea; the resulting animals had a double-layered, gastrula-like body (a **gastrea**) with a

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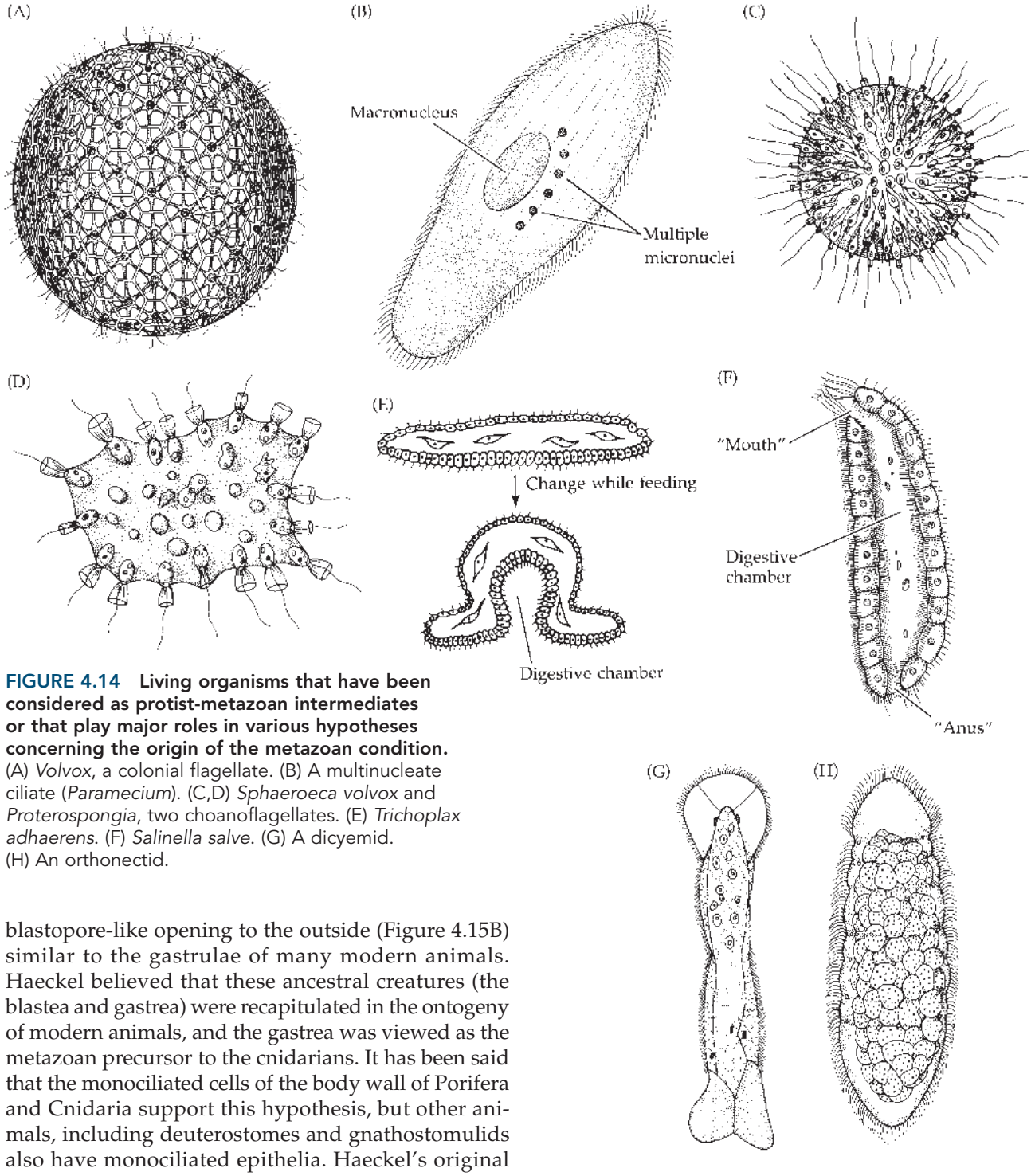

FIGURE 4.14 Living organisms that have been considered as protist-metazoan intermediates or that play major roles in various hypotheses concerning the origin of the metazoan condition. (A) *Volvox*, a colonial flagellate. (B) A multinucleate ciliate (*Paramecium*). (C,D) *Sphaeroeca volvox* and *Proterospongia*, two choanoflagellates. (E) *Trichoplax adhaerens*. (F) *Salinella salve*. (G) A dicyemid. (H) An orthonectid.

blastopore-like opening to the outside (Figure 4.15B) similar to the gastrulae of many modern animals. Haeckel believed that these ancestral creatures (the blastea and gastrea) were recapitulated in the ontogeny of modern animals, and the gastrea was viewed as the metazoan precursor to the cnidarians. It has been said that the monociliated cells of the body wall of Porifera and Cnidaria support this hypothesis, but other animals, including deuterostomes and gnathostomulids also have monociliated epithelia. Haeckel's original ideas were somewhat modified over the years by various authors (e.g., Elias Metschnikoff, Libbie Hyman). Some have argued that the transition to a layered construction occurred by ingression rather than by invagination and that the original Metazoa were solid, not hollow, based in large part on the view that ingression is the primitive form of gastrulation among cnidarians (Figure 4.15C).

In 1883, Otto Bütschli presented another variant of the colonial theory, a bilaterally symmetrical, flattened creature consisting of two cell layers, which fed by crawling over its food and using its ventral layer as a digestive surface. Bütschli called this creature a **plakula**. In amazing support of the plakula hypothesis, a tiny, flagellated, multicellular creature was discovered in a marine aquarium at the Graz Zoological Institute (Austria) in the late nineteenth century. *Trichoplax adhaerens* was placed in its own phylum, the Placozoa (see Chapter 6), and like Bütschli's plakula has an outer, partly flagellated epithelium surrounding an inner mesenchymal cell mass. Its body margins

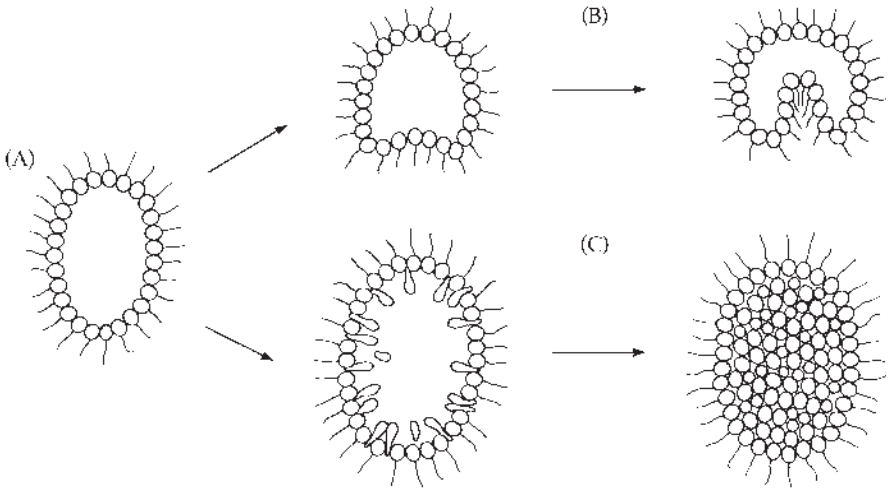

FIGURE 4.15 Two versions of the colonial theory of the origin of the Metazoa. (A) The hypothetical colonial flagellate ancestor, Haeckel's "blastea" (section). (B) According to Haeckel, the transition to a multicellular condition occurred by invagination, a developmental process that resulted in a hollow "gastrea." (C) According to Metschnikoff, the formation of a solid "gastrea" occurred by ingression.

are irregular, its cells show some specialization for somatic and reproductive function, and when feeding, *Trichoplax* "hunches up" to form a temporary digestive chamber on its underside (Figure 4.14E)—producing a form strikingly similar to Bütschli's hypothetical creature. While this hypothesis is compelling, molecular phylogenetic analyses do not place *Trichoplax* at the base of the metazoan tree.

In the 1950s and 60s J. Hadži and E. D. Hanson envisioned the metazoan ancestor as a multinucleate, bilaterally symmetrical, benthic ciliate, crawling about with its oral groove directed toward the substratum. This **syncytial theory** proposed that a cellular epidermis surrounding an inner syncytial mass could form if this creature's surface nuclei partitioned themselves off from one another with cell membranes, producing an acoel wormlike creature. Arguments in support of this hypothesis rested upon similarities between modern ciliates and acoels (Chapter 9), including shape, symmetry, mouth location, surface ciliation, and size; large ciliates are larger than small acoels. However, objections to this hypothesis were more convincing. Acoels undergo complex embryonic development; nothing of this sort occurs in ciliates. Acoel guts are cellular, not syncytial. And molecular phylogenetics has shown acoels to be basal bilaterians, not primitive metazoans. Not surprisingly, the syncytial theory enjoys little support today.

The Origin of Multicellularity

Molecular phylogenetic studies have revealed that multicellularity likely evolved in a dozen or more eukaryotic clades and has led to monophyletic lineages of such disparate groups as plants, animals, several different groups of amoebas, and others. Conditions favoring unicellularity persisted for protists for over 1.5 billion years, by most accounts, until two events occurred. First, atmospheric oxygen of sufficient concentration to support multicellular organization became available due to the activities of photosynthetic algae. Second, predation pressure from heterotrophic protists, capable of phagocytizing or otherwise devouring other unicellular individuals, appears to have favored aggregation of cells after mitosis.

Once a tendency to aggregate arose, there appears to have been competition within individuals for certain functions. If, as appears likely, the first multicellular animals were flagellated, these individuals faced a trade-off between the ability to swim and the ability to engage in mitotic division. The cellular machinery for the two functions appears to compete, as is evidenced even today by the fact that animal cells bearing flagella or cilia never replicate until they have retracted and inactivated their flagellar or ciliary apparatus. In xenacoelomorphs, worn-out ciliated epidermal cells are simply reabsorbed (Chapter 9). A balance may have arisen between the ability to move and the ability to replicate cells, favoring a tendency toward cellular specialization. If selection favored a shift in the location of nonflagellated cells toward the interior of the individual, with flagellated cells remaining outside, further specialization of internal cells may have become possible, necessitating the evolution of layers of cells with flexible ontogenetic fates, as well as biochemical mechanisms that distinguished or allowed particular cellular interactions.

Most evidence today points to the protist phylum Choanoflagellata as the likely ancestral group from which the Metazoa arose. Choanoflagellates possess collar cells essentially identical to those found in sponges. Choanoflagellate genera such as *Proterospongia*, *Sphaeroeca*, and others are animal-like colonial protists (Figure 4.14C,D) and are commonly cited as typifying a potential metazoan precursor. However, some recent molecular evidence suggests that ctenophores, not sponges, lie at the base of the metazoan tree. Clearly, debate on the emergence of Metazoa from

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their protist ancestor will continue for some time to come (Chapter 28).

The Origin of the Bilateral Condition and the Coelom

We discussed the functional significance of bilaterality briefly in Chapter 3. The evolution of an anterior–posterior body axis, unidirectional movement, and cephalization almost certainly coevolved to some degree, and it probably coincided with the invasion of benthic environments and the development of creeping locomotion. Furthermore, the origin of the triploblastic condition likely took place soon after the appearance of the first bilateral forms. Among modern-day invertebrates, bilaterality and triploblasty generally co-occur.

Various hypotheses concerning the origin of the coelom are summarized in R. B. Clark's fine book *Dynamics in Metazoan Evolution* (1964). Clark's personal approach was a functional one that emphasized the adaptive significance of the coelom as the central criterion for evaluating ideas concerning its origin. When early soft-bodied, bilaterally symmetrical animals larger than a few millimeters assumed a benthic, crawling, or burrowing lifestyle, a fluid (hydrostatic) skeleton was essential for certain types of movement. The evolution of a body cavity filled with fluid against which muscles could operate would have offered a tremendous locomotory advantage in addition to providing a circulatory medium and space for organ development. How might such spaces have originated?

Most of the ideas concerning the evolutionary origin of the coelom were developed from the mid-nineteenth to early twentieth century, during the heyday of comparative embryology. Most of these hypotheses shared the premise of monophyly—that the coelomic condition arose only once. The inherent problem with a monophyletic approach is the difficulty of relating existing coelomate animals to a single common coelomate ancestor. Considering the advantages of possessing a coelom, the very different methods of embryonic development (schizocoely and various forms of enterocoely), and the variety of adult coelomic body plans, it may be more biologically reasonable to suggest that the coelomic condition arose twice. There are several current ideas about how this might have happened, and a number of others have mostly been discarded as being incompatible with existing evidence or with our standard definition of the coelom.

The coelom may have originated by the pinching off and isolation of embryonic gut diverticula, as occurs in the development of many extant enterocoelous animals (Figure 4.16). This so-called **enterocoel theory** (in several versions) enjoyed relatively strong support by many authors since it was originally proposed by Sir E. Ray Lankester in 1877. An obvious point in favor of this general idea is that enterocoely does occur in many living animals, thus retaining the hypothetical ancestral process. In addition, various authors cite examples of noncoelomate animals (anthozoans and flatworms) in which gut diverticula exist in arrangements that resemble possible ancestral patterns.

Another popular idea concerning coelom origin is the **gonocoel theory** (see publications by Bergh, Hatschek, Meyer, Goodrich, and others). This hypothesis suggests that the first coelomic spaces arose by way of mesodermally derived gonadal cavities that persisted subsequent to the release of gametes (Figure 4.17). The serial arrangement of gonads, as seen in animals such as flatworms and nemerteans, could have resulted in serially arranged coelomic spaces and linings such as occurs in annelids, where they often still produce and store gametes. A major argument against this hypothesis is that in no modern-day coelomate animals do gonads develop before coelomic spaces. As we have seen, however, heterochrony can account for such turnabouts.

Another idea on coelom origin is called the **nephrocoel theory** (see publications by Lankester, Ziegler, Faussek, Snodgrass, and others). The association

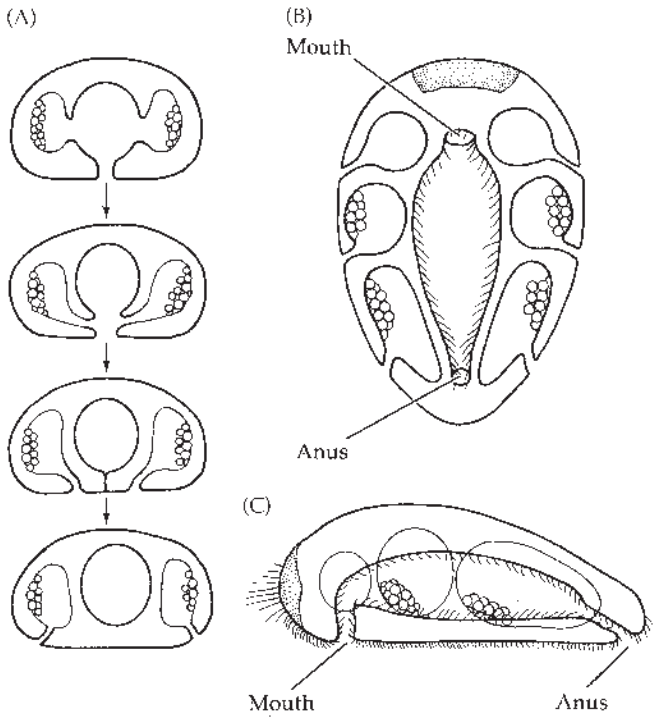

FIGURE 4.16 Jägersten's bilaterogastrea theory, according to which the coelomic compartments arise by enterocoelic pouching. (A) The formation of paired coeloms from the wall of the archenteron. The slitlike blastopore of the bilaterogastrea closes midventrally, leaving mouth and anus at opposite ends (B). (B,C) The tripartite coelomic condition in Jägersten's hypothetical early coelomate animal (ventral and lateral views).

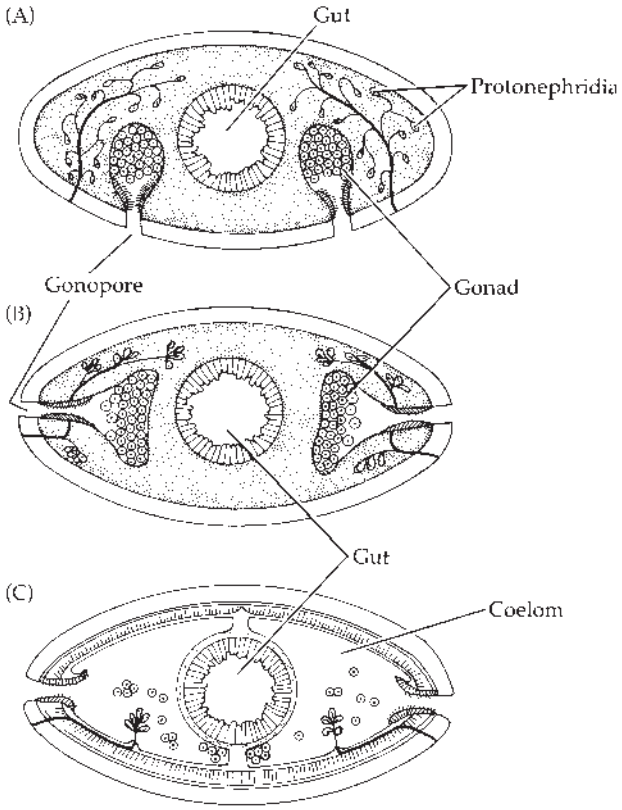

FIGURE 4.17 A version of the gonocoel theory (schematic cross sections). (A) The condition in flatworms, which have mesodermally derived gonads leading to ventral gonopores. (B) The condition in nemerteans, which have serially arranged gonadal masses leading to laterally placed gonopores. (C) The condition in polychaetes, in which the linings of the gonads have expanded to produce coelomic spaces with coelomoducts to the outside.

between the coelom and excretion has prompted different versions of this hypothesis over the years. One idea is that the protonephridia of flatworms expanded to coelomic cavities, arguing that the coelom first arose from ectodermally derived structures. Another view is that coelomic spaces arose as cavities within the mesoderm and served as storage areas for waste products. Certainly the coelomic cavities of many animals are related to excretory functions, but there is no convincing evidence that this relationship was the primary selective force in the origin of the coelomate condition.

Clark (1964) speculated that schizocoely, as we know it today, could have evolved by the formation of spaces within the solid mesoderm of acoelomate animals and then have been retained in response to the positive selection for the resulting hydrostatic skeleton. This is a very straightforward view, in part because, like the enterocoel theory, it accommodates a real developmental process.

As we mentioned earlier, these hypotheses share the fundamental constraint of arguing a monophyletic origin to all coelomate animals. The basic developmental differences between the two great clades of coelomate animals (the Protostomia and the Deuterostomia) suggest that the coelom may have arisen separately in these two lineages. Given the strong similarities between the coelomate Protostomia and acoelomorph worms, it is easy to envision the protostome clade arising from a triploblastic acoelomate ancestor. Hollowing of the mesoderm in such a precursor to produce fluid-filled hydrostatic spaces can be easily explained both developmentally (modern-day schizocoely) and functionally (peristaltic burrowing, increased size, and so on).

To derive the Deuterostomia and Protostomia from an immediate coelomate ancestor creates a complicated scenario. The simplest hypothesis might be to view the deuterostome ancestor as a diploblastic animal, perhaps a planuloid form, in which enterocoely occurred. Deriving the Deuterostomia separately from the evolution of spiral cleavage and the other features of protostomes avoids many of the complications inherent in a monophyletic view of coelom origin. Imagine a hollow, invaginated, gastrula-like metazoan swimming with its blastopore trailing, as do the planula larvae of some cnidarians. Enterocoely may have accompanied a tendency toward benthic life, giving the animal a peristaltic burrowing ability. The archenteron may have then opened anteriorly as a mouth, with the new coelomate creature adopting a deposit-feeding lifestyle. If such a story began at the level of diploblastic Metazoa (e.g., cnidarians), then the radial cleavage seen today in the Bilateria was also present in the ancestor to that group.

The Trochaea Theory

The Danish zoologist Claus Nielsen has envisioned the two major bilaterian clades, Protostomia and Deuterostomia, arising from an ancient common ancestor that conforms to Haeckel's radially symmetrical gastrea. Nielsen's theory proposes that Protostomia arose by way of at least two hypothetical ancestral forms, called the **trochaea** and the **gastroneuron**. The deuterostome line was originally believed to have led to the Deuterostomia by way of a hypothetical **notoneuron** ancestor. (The names "gastroneuron" and "notoneuron" referred to the ventral versus dorsal positions of the major nerve cords in most protostomes and deuterostomes, respectively.)

The theory provided a scenario of the evolution of the ancestral Protostomia, which possessed a trochophore larva and a ventral nervous system. The early ancestor in this model was a holopelagic planktotrophic gastraea with a ring of compound cilia (the **archaeotroch**) around the blastopore, which was used in swimming and particle collection by the downstream method (Figure 4.18A). It was presumed that after settling, the adult form of this animal would creep on the bottom, collecting detritus, using monociliated cells around the blastopore. An anterior–posterior axis evolved along with

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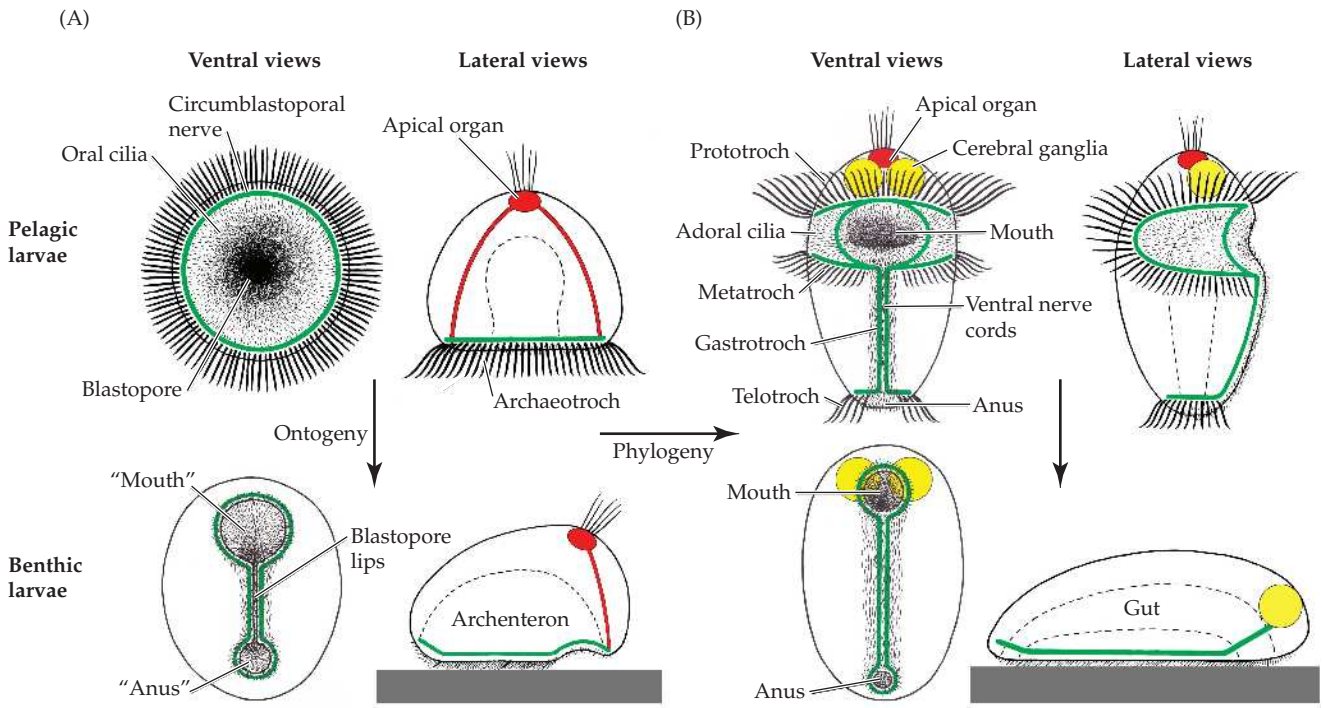

FIGURE 4.18 The trochaea theory. Ventral and lateral views of pelagic larvae and benthic adults predicted by Claus Nielsen's trochaea theory. (A) The upper drawings show the morphology of the holopelagic trochaea; the lower drawings illustrate the pelago-benthic life cycle of an early protostomian ancestor. (B) The upper drawings show the pelagic phase of the life cycle of the fully differentiated ancestral protostomian with a trochophore larva; the lower drawings show the benthic form of this animal. Apical organ is in red; cerebral ganglia, yellow; blastoporal nervous system, green.

the establishment of a creeping lifestyle. Transport of food particles into and out of the archenteron may have become enhanced by compression of the lateral blastopore lips, which were fused in the adult, leaving an anterior mouth and a posterior anus (i.e., a through gut). This fusion of the blastopore lips may soon have become established in the larval stage. The archaeotroch was lost in the creeping adult but retained in the pelagic larva.

The anterior part of the archaeotroch around the mouth could have become laterally extended, with the anterior region becoming the **prototroch** and the posterior region the **metatroch**, bordering a lateral extension of the perioral ciliary area, the **adoral ciliary zone** (Figure 4.18B). Over evolutionary time, this may have created the characteristic trochophore ciliary feeding and swimming structures seen in modern protostomes, wherein the posterior part of the archaeotroch became the **telotroch**. The ciliary bands of the trochophores rely on downstream ciliary feeding, in which the larvae capture food particles from the water on the downstream side of the ciliary feeding bands, and these particles then are transported to the mouth by the adoral ciliary band. The lateral blastopore closure may have resulted in a differentiation of a circumblastoporal ring nerve into an anterior loop around the mouth, the paired (or secondarily fused) ventral nerve cords, and a small loop around the anus (in both the trochophore larva and the adult). The brain of the trochophore and the adult ancestor consisted of the anterior-most part of the perioral nerve loop and a new paired structure, the large cerebral ganglion developing from the **episphere** of the larva, that is, from the area in front of the prototroch.

Owing to the realization that Deuterostomia have the neural tube morphologically ventral, and that deuterostomy occurs in several phyla of Protostomia, Nielsen has revised his views on the origin of the former, and in the latest version of his theory the gastroneuron is seen as the latest common ancestor of *all* bilaterians.

Closing Thoughts

As you can see, when one attempts to describe hypothetical ancestors, evolutionary analysis at the level of phyla can be convoluted and problematical. Many different viewpoints of the same phenomena will inevitably arise. We trust, however, that you have gained some insights into the particular hypotheses discussed here. A fundamental caveat should be kept in mind: any number of evolutionary pathways can be proposed and made to appear convincing on paper by imagining appropriate hypothetical ancestors or intermediates, but one must always ask whether these marvelous hypothetical creatures would have worked as functional organisms and whether rigorous phylogenetic

analyses support the hypotheses. Clark (1964: p. 258) spends a good deal of time on this point and emphasizes it in his conclusion with the following passage:

> *The most important and least considered of these [principles] is that hypothetical constructs which represent ancestral, generalized forms of modern groups, or stem forms from which several modern phyla diverge, must be possible animals. In other words, they must be conceived as living organisms, obeying the same principles that we have discovered in existing animals.*

In such terms, evolutionary hypotheses can be evaluated. From a phylogenetic point of view, it may be best to avoid initial speculation on what a hypothetical ancestor might have looked like and to instead rely on the analysis of known taxa to establish genealogical relationships or branching patterns. Once a tree has been constructed, the pattern of features associated with the taxa on the tree will themselves predict the nature (character combination) of the ancestor for each branch. This method attempts to avoid the potential problem of circular reasoning, in which a hypothetical ancestor is established first and hence constrains and foretells the nature of the taxa descended from it. In either case, for the hypotheses to be truly scientific, they must be testable with new data gathered outside the framework of that used in their initial formulation.

Chapter Summary

This chapter introduced you to some fundamental aspects of invertebrate development and life history and to the role these fields have played in understanding animal evolution. Many discussions on invertebrate biology and evolution have relied on these data and biological patterns since the earliest days of embryology, and today the field of evo-devo has integrated key components, taking a step forward toward the goal of connecting genotype to phenotype. Fundamental concepts of evo-devo and embryology presented in this chapter will help you better understand the origin of mesoderm and body cavities in metazoans, as well as the anatomical features that have long been central to discussions of animal relationships. You have learned that there are several types of animal life cycles, including direct development, indirect development (with metamorphosis), and complex parasitic life cycles that may include multiple hosts and habitats (marine, freshwater, terrestrial), and about the evolutionary consequences of adopting one or another lifestyle. Finally, we explored some theories related to animal evolution and the putative connection between ontogeny and phylogeny, concluding with a brief discussion on the origin of metazoans and some key aspects relevant to animal phylogeny.

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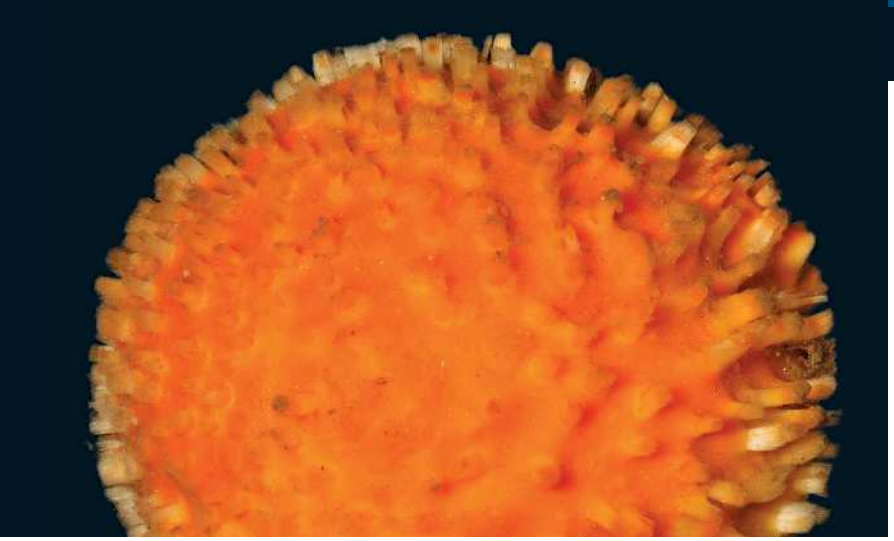

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CHAPTER 5

Phylum Porifera

The Sponges

Chapters 1 through 4 provide a detailed introduction to the animal kingdom, Metazoa, or Animalia. Metazoans are a clade (monophyletic group) of eukaryotes, those creatures whose cells contain membrane-enclosed organelles and have a membrane-enclosed nucleus. However, animals differ from other eukaryotes (i.e., fungi, plants, and the myriad protist clades) in their combination of multicellularity, heterotrophic and ingestive nutrition, and unique style of tissue formation through embryonic germ layering. Thus, **metazoans are heterotrophic multicellular eukaryotes that undergo embryogenesis by way of tissue layering.** Metazoan synapomorphies include: gastrulation; unique modes of oogenesis and spermatogenesis; a unique sperm structure; mitochondrial gene reduction; epidermal epithelia with septate, tight, or zonula adherens junctions; striate myofibrils; actin-myosin contractile elements; type IV collagen; and the presence of a basal lamina or basement membrane beneath epidermal layers (of course, some of these features have been secondarily lost in a few groups). The formation of embryonic germ layers takes place through a process called gastrulation, and even the primitive living metazoans (e.g., sponges) undergo this process. Gastrulation is a process that achieves separation of those cells that must interact directly with the environment (e.g., locomotor, sensory, and protective functions) from those that process materials obtained from the environment (e.g., nutritive functions). Evidence is strong that Metazoa share a common ancestor with the choanoflagellate protists.

However, despite these fundamental shared similarities, there are four phyla of Metazoa that are so ancient and possess such a simple body construction that their relationships to other animals continue to

This chapter was revised by Ana Riesgo.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

challenge us—these are the four nonbilaterian phyla: Cnidaria, Ctenophora, Placozoa, and Porifera. Porifera, the sponges, are covered in this chapter, the other three in the following chapters. In addition to lacking bilateral symmetry, these four phyla lack true mesoderm development. The current consensus of phylogenetic analyses suggests that either Porifera or Ctenophora are the first offshoot of all living animal phyla.

Phylum Porifera: The Sponges

The phylum Porifera (Latin *porus*, "pore"; *ferre*, "to bear") comprises those odd but fascinating animals called sponges. At first glance, sponges may seem difficult to reconcile within the animal kingdom—adults lack a gut, muscles, nerves and conventional neuronal signaling systems, typical metazoan organs, gap junctions between cells, an obvious anterior–posterior polarity (except in larvae), and some of the key metazoan developmental genes, such as a ParaHox cluster. In addition, they have cross-striated ciliary rootlets in larval cells and choanocytes—a feature characteristic of many protists. However, they do possess the metazoan-defining attributes of multicellularity derived by embryonic layering, specialized junctions between cells, actin-myosin contractile elements, and type IV collagen. In addition, recent genomic analyses of species spanning the four extant classes of Porifera reveal the presence of certain homeobox genes and representatives of most higher metazoan molecules involved in cell–cell communication, signaling pathways, postsynaptic processes, complex "sealing" epithelia (impermeable or selectively permeable and regulating epithelia), reproduction, and immune recognition. Sponges also undergo typical animal-like sexual reproduction and the development of embryos through a structured series of cellular divisions (cell cleavages) that result in a spatially organized larva with multiple cell layers and sensory capabilities. Most larvae have an obvious anterior–posterior polarity, and many adult sponges possess an apical–basal polarity, defined by the presence of a large osculum at one end (although the positions of oscula are often dictated purely by hydrodynamic forces in the environment). Others show such polarity by virtue of their pedunculate or pinnate growth form, often even with stems/stalks and rootlike structures. Molecular genetic analyses indicate Porifera is monophyletic and clearly within Metazoa. In fact, sponge genes have been recently discovered that are implicated in regulating anterior–posterior polarity and specifying particular tissues during the development of other basal metazoans, supporting the contention that sponges undergo true gastrulation during embryogenesis. Figures 5.1 and 5.2 illustrate a variety of sponge body forms and some sponge anatomy. Box 5A lists the major characteristics of sponges.

Sponges are sessile, primarily suspension-feeding, multicellular animals that utilize flagellated cells called choanocytes to circulate water through a unique system of water canals. Most rely on an internal skeleton of calcium carbonate or silicon dioxide spicules to support their body, which can be quite large. It was long thought that Porifera lacked distinct embryological germ layering that leads to definable tissues, a condition sometimes referred to as "the parazoan grade of body construction." However, we now know that sponges undergo distinct gastrulation events from which the adult tissues derive, and the old concept of "Parazoa" is finally laid to rest. However, some of the adult tissues in sponges are somewhat transmutable and not fixed, due to a degree of cellular pluripotency—most cells are capable of changing form (although pinacocytes and sclerocytes cannot do so), and two cellular lineages are kept in a totipotent state to be recruited "on demand" (archaeocytes and choanocytes). So, despite the fact that sponges are large-bodied multicellular animals typically supported by an internal skeleton of spicules or stiffened collagen (spongin), in some ways they function like organisms at the unicellular grade of complexity. In fact, as you will discover in this chapter, their nutrition, gas exchange, and response to environmental stimuli are

BOX 5A Characteristics of the Phylum Porifera

1. Metazoans partly at the cellular grade of construction, with simple tissues, but with a high degree of cellular pluripotency; adults asymmetrical or with a distinct apical–basal polarity (often superficially appearing as radially symmetrical); larvae usually have anterior–posterior polarity
2. Cells have adherens junctions in some species, but no gap junctions
3. Individuals have unique flagellated cells—choanocytes—that drive water through canals and chambers constituting the aquiferous system
4. Adults are sessile and typically suspension feeders; larval stages are motile and usually lecithotrophic
5. Type IV collagen basement membranes occur in most Homoscleromorpha and also (to a lesser extent) in the other classes
6. Middle layer—the mesohyl—is variable but always includes motile cells and usually some skeletal material
7. Skeletal elements, when present, composed of calcium carbonate or silicon dioxide (typically in the form of spicules) and/or collagen fibers
8. Neurons do not occur; the only true sense organ is the osculum, which utilizes primary cilia to detect water flow rates
9. Ciliated cells of adult sponges bear only a single cilium (largely lacking the rootlet system seen in other metazoans); some larvae have cilia that have rootlet systems; some larvae have bi-ciliated cells on the surface (postulated by some workers to be products of defective cell division)

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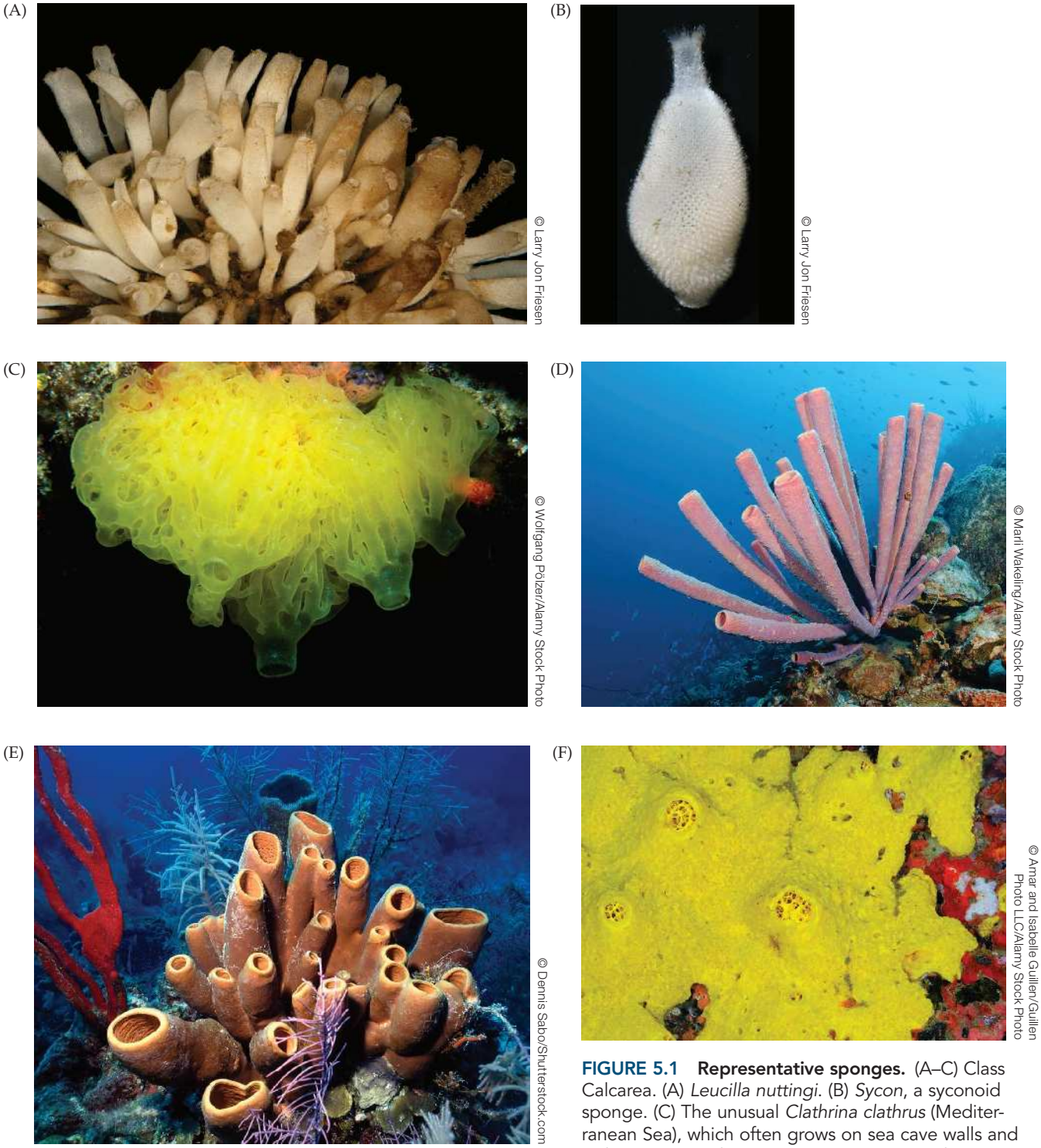

FIGURE 5.1 Representative sponges. (A–C) Class Calcarea. (A) *Leucilla nuttingi*. (B) *Sycon*, a syconoid sponge. (C) The unusual *Clathrina clathrus* (Mediterranean Sea), which often grows on sea cave walls and ceilings. (D–M) Class Demospongiae. (D) *Aplysina archeri* (Caribbean). (E) *Agelas* sp. (Belize). (F) A yellow encrusting *Haliclona* sp. (Gulf of Aden, Djibouti).

(*Continued on next page*)

all very protistlike. So, superficially, sponges might be viewed as tight consortiums of semiautonomous cells, and thus quite simple animals. But, appearances can be deceiving. Read on.

Despite their seeming simplicity, sponges have experimented with various aspects of higher metazoan body organization, and they have developed relatively simple tissues, a sparse basement membrane, in some species even predatory behaviors, and other features typical of the higher Metazoa. Some might argue that poriferans are "caught between two worlds"—the world of protists and the world of higher metazoans—while others would argue they are metazoans in every sense of the word.

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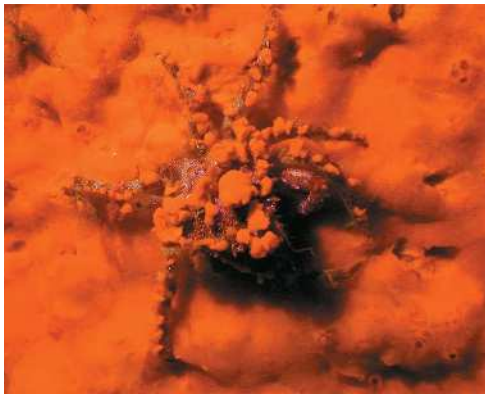

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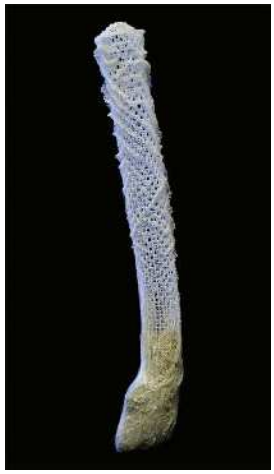

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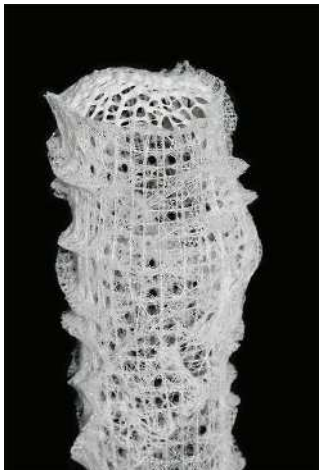

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◀ **FIGURE 5.1 (*continued*) Representative sponges.** (G) *Spheciospongia confoederata* (close-up of pinacoderm showing dermal pores and oscula). (H) *Tethya aurantium*, close-up showing oscula protected by long spicules. (I,J) Tree sponges! Freshwater sponges from all three New World families occur in the rivers of the Amazon Basin—shown here is *Drulia* (?) that lives 5–10 m above the dry-season low-water line (when these photos were taken). (K) The freshwater *Spongilla* (Minnesota, USA). (L) The massive calcareous base of a coralline sponge. (M) A red poecilosclerid sponge growing on the back of a decorator crab makes it nearly invisible (Bounty Islands, New Zealand). (N–P) Hexactinellida. (N) Three specimens of deep-sea glass sponges (from the eastern Pacific) with silica rope stalks. (O) *Euplectella aspergillum* (Venus's flower basket). (P) Close-up of *Euplectella* skeleton showing arrangement of spicule bundles.

One of the most remarkable attributes of sponges is their tendency to maintain symbiotic relationships with a variety of heterotrophic and autotrophic Bacteria, Archaea, Protista, and even some other Metazoa. Some of these intimate relationships have developed to the point that, in some sponges, more biomass is actually contributed by the symbiont than by the sponge, and in these species microscopic examination of the sponge reveals mostly cells of microbes! We are just beginning to explore this community hidden within sponges, but already hundreds of symbiotic species, in over a dozen bacterial and archaean phyla (and several protistan groups), have been documented. As the role of microorganisms in sponges begins to be better understood, the emerging evidence suggests strong mutualism in many cases. Sponges of different types, in different ocean basins, seem to host strikingly similar microbial communities, suggesting the symbiotic relationships are very old. And some of these microbes appear to be transported in the eggs, nurse cells, and even sperm of sponges.

Sponges produce the largest and most diverse storehouse of secondary metabolites of any animal phylum—compounds that function to deter predators, prevent fouling of the sponge's surface, screen ultraviolet radiation, and nurture their symbiotic partnerships. Some sponges even "walk" over rocks, using lobelike extensions of the body that grow and elongate and then disappear, sometimes leaving separate living pieces—progeny—in their wake. At least one lineage of sponges, possibly more, has taken a dramatic evolutionary turn and become predatory carnivores; instead of filter feeding, these magnificent creatures capture and engulf small prey that are caught on highly specialized Velcro-like surfaces formed by spicules. Well over 150 species of carnivorous sponges have been described, mainly in the deep-sea family Cladorhizidae (Poecilosclerida) and two other small families.

Nearly 9,300 living species of sponges have been described, all but about 220 (the freshwater species) being restricted to benthic marine environments. Freshwater species occur at all latitudes, from deserts to equatorial rainforests, and from sea level to alpine lakes and even subterranean habitats. About 60 new sponge species are described each year, and it has been estimated that less than half of the living species have so far been described. Sponges occur at all depths but are most abundant in unpolluted littoral and tropical reef habitats, cold temperate continental shelf regions, and Antarctic seas. However, deep-water "sponge grounds" are also important components of deep-sea ecosystems. Most littoral sponges grow as thick or thin layers, or as erect structures, on hard surfaces. Sponges that live on soft substrata typically are upright and tall or possess funnel-like structures on top of a buried basal body, thus avoiding burial by the shifting sediments of their environment.

Some sponges reach considerable size (up to 2 m in height on Caribbean reefs, and even larger in Antarctica and the deep sea) and may constitute a significant portion of the benthic structure and biomass. In Antarctic seas, sponges can make up almost 75% of the total benthic biomass at depths of 100–200 m. Areas of the deep Antarctic shelf have been called "sponge kingdoms," and here over 300 species have been recorded with high biomass and density. Subtidal and deeper water species that do not confront strong tidal currents or surge are often large and exhibit a stable, even symmetrical (radial), external form. The deeper water hexactinellid sponges often assume unusual shapes, many being delicate glasslike structures, others round and massive, and still others growing in a ropelike fashion. Siliceous sponge reefs have been documented from several periods in Earth history, and they culminated in the Late Jurassic when they formed a discontinuous deep-water reef belt extending more than 7,000 km. This reef system was the largest biotic structure ever built on Earth (at 2,000 km, the Great Barrier Reef of Australia is relatively small compared with the Jurassic sponge reef belt).

Sponges display nearly every color imaginable, including bright lavenders, blues, yellows, crimsons, and pure white, and some are even iridescent. In many species it is the symbiotic bacteria or algae that give color to their host's body, especially in the tropics. And sponges are the only phylum of animals that predominantly utilize silica, rather than calcium carbonate, in their mineral skeleton (in Demospongiae, Homoscleromorpha, and Hexactinellida). In one of the four classes of sponges, Calcarea, the skeleton is composed not of siliceous spicules, but of calcium carbonate spicules (although a few species in other sponge classes are known to secrete a firm calcium carbonate base, upon which the siliceous skeleton rests).

Taxonomic History and Classification

The sessile nature of sponges, and their often amorphous or asymmetrical growth form convinced early naturalists that they were plants. It was not until 1765,

when the nature of their internal water currents was described, that sponges were recognized as animals. The great naturalists of the late eighteenth and early nineteenth centuries (e.g., Jean-Baptiste Lamarck, Carolus Linnaeus, Georges Cuvier) classified sponges under Zoophytes or Polypes, regarding them as allied to anthozoan cnidarians. Throughout much of the nineteenth century they were placed with cnidarians under the name Coelenterata or Radiata. The morphology and physiology of sponges were first adequately understood by Robert E. Grant. Grant created for them the name Porifera, although other names were frequently used (e.g., Spongida, Spongiae, Spongiaria).

Historically, the classes of Porifera have been defined by the nature of their internal skeletons. Until recently, three classes of sponges had long been recognized: Calcarea, Hexactinellida, Demospongiae. For a couple of decades (1970–1990) some workers proposed another class, Sclerospongiae, which included those species that produce a solid, calcareous, rocklike matrix (in addition to the spicular skeleton) on which the living animal grows. Over a dozen species of living sclerosponges, also known as coralline sponges, have been described. Late in the twentieth century, ultrastructural work and DNA analyses showed that the class Sclerospongiae was actually a polyphyletic grouping, and it was thus abandoned, its members relegated to the Calcarea and Demospongiae. Today, the "coralline sponges" are known to be the last survivors of otherwise extinct stromatoporids, sphinctozoans, and chaetetids—ancient reef-building sponges that were highly diversified in Paleozoic and Mesozoic seas. These ancient coralline sponges were probably among the first metazoans to produce a carbonate skeleton. In 2010, the distinctive nature of the Homoscleromorpha (formerly included within the Demospongiae) was seen to merit elevating this group to class status, thus establishing a fourth class of living Porifera.

Demospongiae is the largest sponge class, comprising 81% of the living species. Because of its size and morphological variability, the class Demospongiae presents the greatest number of problems for taxonomists. The only synapomorphy that distinguishes the class Demospongiae is the presence of a spongin-based skeleton, and yet not all species of demosponges possess this feature. For many years, spongiologists followed the classification of C. Lévi, who created two subclasses of demosponges based upon reproductive modes, Tetractinomorpha and Ceractinomorpha. However, by the turn of the century these were widely recognized as polyphyletic, and reproductive modes were recognized as highly labile. In the early twenty-first century, molecular phylogenetics showed both that the class is monophyletic (exclusive of Homoscleromorpha) and that it can be divided into three distinct subclasses, as noted in the following classification.

Although the mainstay of sponge taxonomy has traditionally been the chemical composition, shape, ornamentation, dimensions, and localization of the spicules, additional kinds of information, including secondary metabolite chemistry, and more notably molecular systematics are now being used to develop phylogenetic hypotheses and higher classifications. Indeed, some sponge species lack spicules altogether (e.g., *Oscarella, Hexadella, Halisarca*), whereas many spicule types appear to be homoplastic among sponges (e.g., asters, acanthostyles, sigmata). Sponge specialists also are now using embryological, biochemical, histological, and cytological methods to diagnose and analyze the Porifera. In the past, the considerable difficulty in precisely setting the limits of some sponge species made poriferan taxonomy challenging. Sponges are famous for their paucity of reliable taxonomic characters, and even the great sponge taxonomist Arthur Dendy was known to frequently end a species diagnosis with a question mark.[1]

Since the advent of molecular phylogenetics, the fascinating world of poriferology has grown more tractable, and modern systematics is beginning to build a robust framework for the phylum. In addition to resolving long-standing phylogenetic questions, molecular work has led to the discovery that many "cosmopolitan species" are, in fact, clusters of closely related but distinct species. In addition, since the 1970s important bioactive compounds have been discovered in sponges, many having potential pharmacological significance (e.g., antibacterial, antiviral, anti-inflammatory, antitumor, and cytotoxic compounds, as well as channel blockers and antifouling chemicals). The discovery of these natural products in sponges also has led to a renewed interest in the group.

CLASSIFICATION OF PHYLUM PORIFERA

CLASS CALCAREA Calcareous sponges (Figure 5.1A–C). Spicules of mineral skeleton composed entirely of calcium carbonate laid down as calcite, secreted extracellularly within a collagenous sheath (but with no axial filament); skeletal elements often not differentiated into megascleres and microscleres; spicules usually 1-, 3-, or 4-rayed; body with asconoid, syconoid, leuconoid, or the newly discovered sylleibid and solenoid constructions; many species exhibit superficial radial symmetry around a long axis, but in most there is no visible axial symmetry; early cleavage total and equal; embryonic cleavage patterns probably fundamentally radial; all studied species are viviparous. All marine; occurring at all latitudes; 793 described species. Their microbiome is only starting to be unveiled, with predominance of Proteobacteria and the archaeal

[1]The term a "sleeze" of sponges was coined by Ristau (1978) to describe an aggregation of sponges; the usage is comparable to other such collective nouns that define animal groups (e.g., flock, herd, gaggle).

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group Thaumarcheota. Although embryogenesis and larval morphology of the two subclasses differ profoundly, molecular phylogenetics provides evidence that the class and both subclasses are monophyletic.

SUBCLASS CALCINEA Free-living larva is hollow, flagellated "coeloblastula" (calciblastula); choanocyte nuclei located basally, and flagellum arises independent of nucleus (a presumptive synapomorphy of this subclass); with free, regular, triradiate spicules (e.g., *Clathrina*, *Dendya*, *Leucascus*, *Leucetta*, *Soleneiscus*, the coralline genus *Murrayona*).

SUBCLASS CALCARONEA Free-living larva is a unique, partly flagellated amphiblastula, typically forming by way of eversion of earlier stomoblastula "prelarva" (which is held internally)—a presumptive synapomorphy of this subclass; choanocyte nuclei apical, and flagellum arises directly from nucleus; spicules free or fused (e.g., *Amphoriscus*, *Grantia*, *Leucilla*, *Leucosolenia*, *Sycon*, the coralline genus *Petrobiona*).

CLASS HEXACTINELLIDA Glass sponges (Figure 5.1N–P). Skeleton composed of a large array of siliceous spicules of various shapes and sizes, secreted intracellularly around a square proteinaceous axial filament; spicules with fundamental 3-axon or 6-rayed symmetry (triaxonic); both megascleres and microscleres always present. Entire sponge formed by a single continuous syncytial tissue, the trabecular reticulum, which stretches from the outside or dermal membrane to the inside or atrial membrane, enclosing the cellular components of the animal. Body wall cavernous, filled primarily with a trabecular syncytium, connected via open and plugged cytoplasmic bridges to choanosome, with its flagellated chambers; external pinacoderm absent and replaced by a noncellular dermal membrane; choanosome with anucleate choanocytes embedded in a trabecular syncytium. All studied species are viviparous; some produce a unique hexactinellid larva, the trichimella. Long-lived, exclusively marine, usually vase- or tube-shaped (never encrusting), primarily deep-water sponges (maximum diversity is at 300 to 600 m depth); 682 described species. Many species harbor Archaea-dominated microbial communities within their bodies. The hexactinellid body plan is perhaps the most unusual in the entire animal kingdom because nearly all the tissues in adults consist of a giant multinucleated syncytium that forms the inner and outer layers of the sponge, joined by cytoplasmic bridges to limited uninucleate cellular regions. Two subclasses that are both monophyletic.

SUBCLASS AMPHIDISCOPHORA Body anchored in soft sediments by a basal tuft or tufts of spicules; megascleres are discrete spicules, never fused into a rigid network; with birotulate microscleres, never hexasters (e.g., *Hyalonema*, *Monorhaphis*, *Pheronema*).

SUBCLASS HEXASTEROPHORA Usually attached to hard substrata, but sometimes attached to sediments by a basal spicule tuft or mat; microscleres are hexasters; megascleres free, or can be fused into a rigid skeletal framework, in which case sponge may assume large and elaborate morphology (e.g., *Aphrocallistes*, *Caulophacus*, *Euplectella*, *Hexactinella*, *Leptophragmella*, *Lophocalyx*, *Rosella*, *Sympagella*).

CLASS DEMOSPONGIAE Demosponges (Figure 5.1D–M). With siliceous spicules and/or an organic skeleton (or, occasionally, with neither) or, in some groups, a solid calcitic skeleton; spicules secreted intra- or extracellularly around a triangular or hexagonal axial filament; spicules never 6-rayed (i.e., not triaxons); organic skeleton a collagenous network ("spongin"); most produce parenchymella larvae (see Figure 5.18); ancestrally viviparous, ovipary developed in several taxa of the subclasses Verongimorpha and Heteroscleromorpha; marine, brackish, or freshwater sponges occurring at all depths. Many species exhibit a mesohyl community of Eubacteria, mainly Proteobacteria and gram-positive bacteria, as well as species of Archaea. About 7,400 described species. The two subclasses Tetractinomorpha and Ceractinomorpha, long recognized as polyphyletic, have recently been abandoned, and three subclasses are now recognized. Molecular analyses to date support the monophyly of these new subclasses, although not all have been uniquely defined morphologically.

SUBCLASS KERATOSA Skeleton of spongin fibers only, or with a hypercalcified skeleton (*Vaceletia*). Spongin fibers either homogenous or pithed, and strongly laminated with pith grading into bark. Reproduction typically viviparous, larvae are parenchymella. All commercial sponges belong to this subclass (e.g., *Spongia*, *Hippospongia*, *Coscinoderma*, *Rhopaleoides*). Includes two orders: Dendroceratida (Darwinellidae: e.g., *Aplysilla*, *Darwinella*, *Dendrilla*; Dictyodendrillidae: e.g., *Dictyodendrilla*, *Spongionella*) and Dictyoceratida (Spongiidae: e.g., *Spongia*, *Hippospongia*, *Rhopaleoides*; Thorectidae: *Cacospongia*; *Thorecta*, *Phyllospongia*, *Carteriospongia*; Irciniidae: e.g., *Ircinia*, *Sarcotragus*; Dysideidae: e.g., *Dysidea*, *Pleraplysilla*; Verticillitidae: *Vaceletia*).

SUBCLASS VERONGIMORPHA Without a skeleton or with skeleton of spongin fibers only (with a laminated bark and finely fibrillar or granular pith); one genus with skeleton of siliceous asters (*Chondrilla*). All demosponges lacking a skeleton belong to this subclass (e.g., *Chondrosia, Halisarca, Hexadella, Thymosiopsis*). Reproduction oviparous. Two or three orders are now recognized (e.g., *Aplysina, Aplysinella, Chondrosia, Chondrilla, Halisarca, Hexadella, Ianthella, Suberea, Thymosia, Thymosiopsis, Verongula*).

SUBCLASS HETEROSCLEROMORPHA Skeleton composed of siliceous spicules that can be monaxons and/or tetraxons and, when present, highly diversified microscleres. Reproduction mostly viviparous, but oviparous species occur in some genera (e.g., *Agelas, Axinella, Raspailia, Suberites*). This subclass contains most of the Demospongiae (over 5,000 species), usually organized into 14 orders. Most of the sponges

once assigned to Sclerospongiae are in this subclass, including stromatoporoids (e.g., *Astrosclera*), tabulates (*Acanthochaetetes*, *Merlia*), and ceratoporellids (e.g., *Ceratoporella*, *Goreauiella*, *Hispidopetra*, and *Stromatospongia*). The order Tetractinellida includes all sponges with tetractine spicules (e.g., *Astrophorina*, *Cinachyra, Geodia, Penares, Spirophorina, Stelletta, Tetilla*, and most of those formerly known as lithistids: *Discodermia, Neoschrammeniella, Corallistes*). The freshwater sponge order Spongillida is here, which includes 220 species in 6 families (e.g., *Ephydatia, Lubomirskia, Metania, Potamolepis, Spongilla*). Other orders include Haplosclerida (e.g., *Amphimedon, Callyspongia, Haliclona, Niphates, Petrosia, Xestospongia*), Scopalinida (e.g., *Scopalina, Svenzea*), Sphaerocladina (*Vetulina*), Poecilosclerida (including the family Cladorhizidae) (e.g., *Antho, Asbestopluma, Clathria, Crambe, Desmacella, Hymedesmia, Lycopodina, Mycale, Myxilla*), Agelasida (e.g., *Acanthostylotella, Agelas, Astrosclera, Hymerhabdia*), Axinellida (e.g., *Axinella, Eurypon, Higginsia, Myrmekioderma, Raspailia, Stelligera*), Bubarida (e.g., *Bubaris, Phakellia, Dictyonella*), Desmacellida (e.g., *Desmacella*), Merliida (e.g., *Hamacantha*, *Merlia*), Biemnida (e.g., *Biemna, Neofibularia, Sigmaxinella*), Suberitida (e.g., *Halichondria, Hymeniacidon, Terpios*), Clionaida (e.g., *Cliona, Spirastrella, Placospongia*), Polymastiida (e.g., *Polymastia, Sphaerotylus, Spinularia*), and Tethyida (e.g., *Tectitethya*, *Tethya*).

CLASS HOMOSCLEROMORPHA This most recently proposed class of sponges has been shown to be distinct (and monophyletic) on the basis of molecular phylogenetics, anatomy, and embryology (see Figure 5.19B). Spongin skeleton always absent; rigid skeleton almost always absent, but when present, composed of small (mostly <100 μm) tetraxon (4 often unequal rays) siliceous spicules called calthrops,[2] similar but distinct from certain tetraxon spicules seen in demosponges, or peculiar irregular kinked oxeas (2 uneven rays); all spicules are of a similar size, with no differentiation into megascleres and microscleres (hence the class name); with ciliated exopinacocytes and endopinacocytes; a type IV collagen basement membrane underlies both choanoderm and pinacoderm (this type of collagen has also been found in several species of demosponges and calcareans); zonula adherens cell junctions in adult and larval epithelia; spermatozoids with an acrosome (not exclusive to homoscleromorphs); choanocyte chambers oval to spherical, with large choanocytes. To date, septate junctions have not been found in this class. Homoscleromorphs are viviparous (incubate their embryos), form a hollow blastula by multipolar egression, and develop a unique cinctoblastula larva. Although earlier phylogenetic work had suggested this group might be more closely allied with other metazoans than with other sponges, recent data strongly support its inclusion within a monophyletic Porifera, probably as sister group to Calcarea. Homoscleromorpha are exclusively marine sponges, divided into two families: Plakinidae (spiculate species) and Oscarellidae (aspiculate species). Most species inhabit hard bottoms of the continental shelf, but some are known from more than 1,000 m depth. The fossil record, poor as it is, dates from the early Carboniferous. About 126 species (e.g., *Corticium, Oscarella, Placinolopha, Plakina, Plakinastrella, Plakortis, Pseudocorticium*).

[2]A "caltrop" or "calthrop" was an evil-looking medieval landmine, consisting mainly of four short, sharpened spikes radiating from a common center at equal angles. These were scattered in front of defensive positions and covered under a thin layer of dirt, where they tended to inconvenience charging knights. Homoscleromorph tetractine spicules often have the same general shape.

The Poriferan Body Plan

A mind-boggling diversity exists in the shape, color, and size of sponges. Increases in size and surface area are accomplished by folding of the body wall into a variety of patterns, and also from different growth patterns that appear in response to environmental conditions. This plasticity plus the fact that sponges maintain many of their cells in a pluripotent state compensate in part for the absence of true organs. Two unique organizational attributes define sponges and have played major roles in poriferan success: first is the water current channel system, or **aquiferous system**, and its unique all-purpose cells (for pumping, feeding, gas exchange, and waste expulsion) known as **choanocytes**. Second is the highly pluripotent nature of sponge cells in general. The aquiferous system brings water through the sponge and close to the cells responsible for food gathering and gas exchange. At the same time, excretory and digestive wastes are expelled by way of the water currents. The volume of water moving through a sponge's aquiferous system is remarkable. A single 1 × 10 cm individual of the complex sponge *Leuconia* (Calcaronea) pumps about 23 liters of water through its body daily. Researchers have recorded sponge pumping rates that range from 0.002 to 0.84 ml of water per second per cubic centimeter of sponge body. Large sponges filter their own volume of water every 10 to 20 sec.

The Hexactinellida ("glass sponges") might be the most unusual creatures in the entire animal kingdom. Their triaxonal spicules, with a square proteinaceous internal filament, distinguish them from other siliceous sponges. These siliceous spicules are formed using an enzymatic process driven by the protein glassin, which is completely different from the silicification method used by demosponges driven by the enzyme silicatein. Their syncytial body, which arises by fusion of early embryonic cells, is unique among Metazoa. Both the larvae and adults have elegant combinations of multinucleate and cellular cytoplasmic regions unlike anything seen in any other animal. The continuity of this tissue allows food to be transported symplastically

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(analogous to plants), and it also allows electrical signals to travel throughout the sponge body (analogous to the nervous system of higher Metazoa).

Sponges are not colonial animals. Any and all sponge material bounded by a continuous outer covering (the pinacoderm) constitutes a single individual. The growth of each individual is dictated by a combination of genetics (e.g., most larvae have anterior–posterior symmetry, many adults have a radial–axial growth form) and environmental factors (e.g., water flow dynamics, contours of the substratum). For most sponges, changes in body form can arise anywhere in or on the organism in response to external factors.

Body Structure and the Aquiferous System

The outer surface cells of a sponge make up the **pinacoderm** and are called **pinacocytes**, typically unciliated flattened cells that are also known as "pavement cells." The pinacoderm is now considered a true epithelium thanks to studies of transepithelial resistance in freshwater sponges. Most of the inner surfaces comprise the **choanoderm** and are composed of flagellated cells called **choanocytes**. Both of these layers are a single cell thick. Between these two thin cellular sheets is the **mesohyl**, which may be very thin in some encrusting sponges, or massive and thick in larger species (Figures 5.2 and 5.3). The pinacoderm is

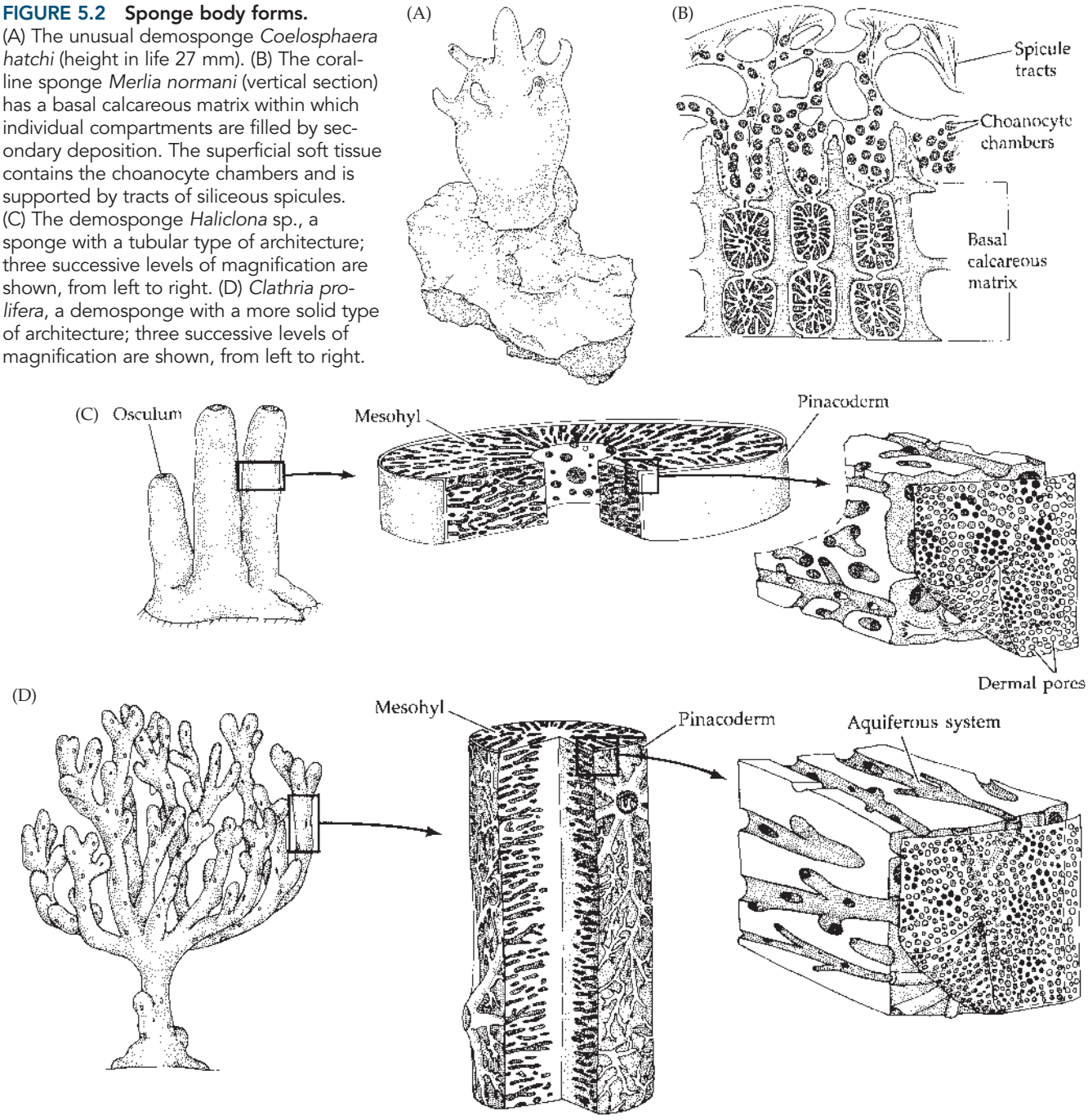

FIGURE 5.2 Sponge body forms. (A) The unusual demosponge *Coelosphaera hatchi* (height in life 27 mm). (B) The coralline sponge *Merlia normani* (vertical section) has a basal calcareous matrix within which individual compartments are filled by secondary deposition. The superficial soft tissue contains the choanocyte chambers and is supported by tracts of siliceous spicules. (C) The demosponge *Haliclona* sp., a sponge with a tubular type of architecture; three successive levels of magnification are shown, from left to right. (D) *Clathria prolifera*, a demosponge with a more solid type of architecture; three successive levels of magnification are shown, from left to right.

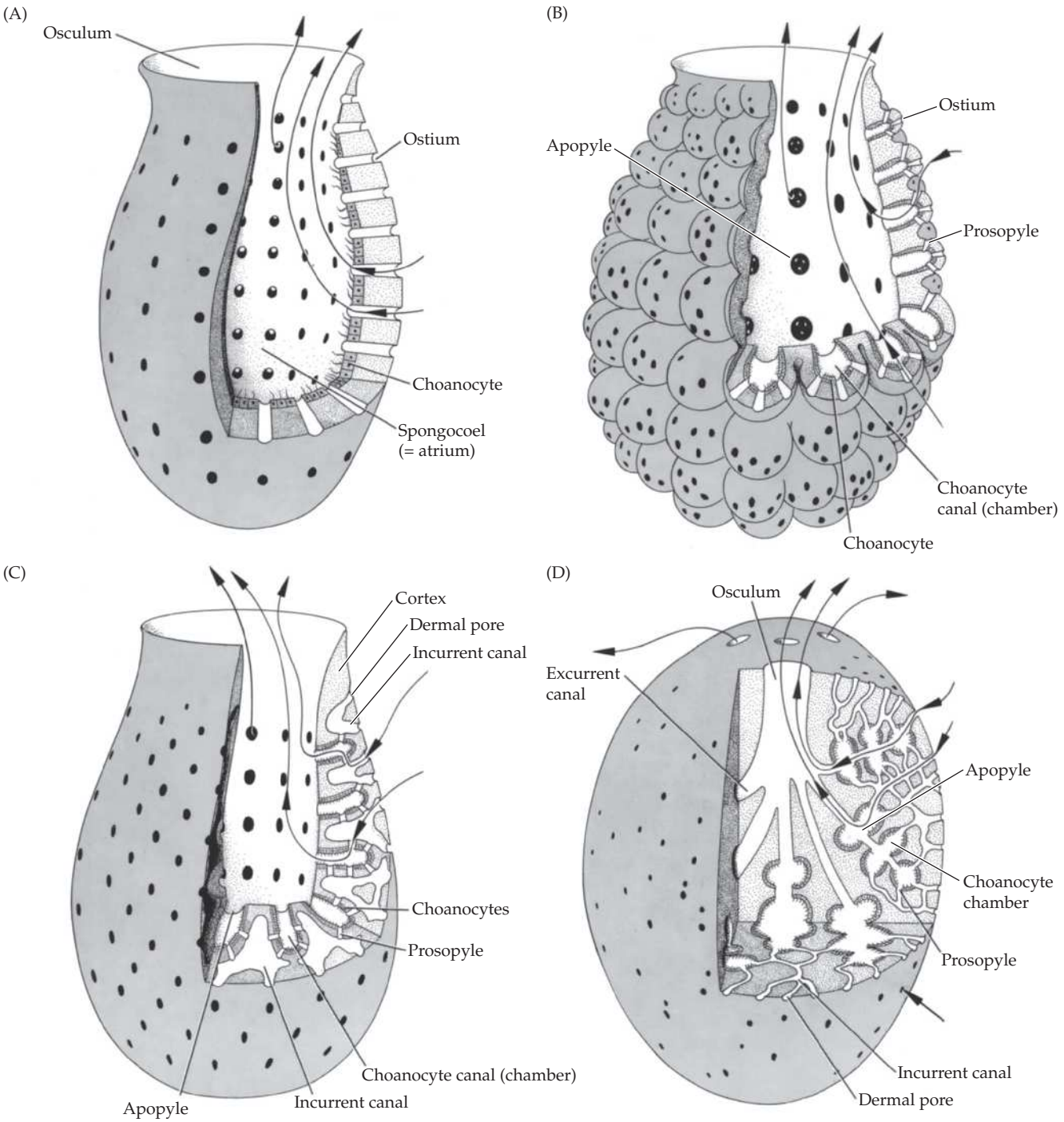

FIGURE 5.3 Body complexity in sponges (arrows indicate flow of water). (A) The asconoid condition. (B) A simple syconoid condition. (C) A complex syconoid condition with ectosomal growth. (D) A leuconoid condition. Asconoid and syconoid anatomies occur only in the class Calcarea.

perforated by small holes called **dermal pores** or **ostia** (sing. ostium), depending on whether the opening is surrounded by several cells or one cell, respectively. Water is pulled through these openings and is driven across the choanoderm by the beating of the choanocyte flagella. The choanocytes pump large volumes of water through the sponge body, thus enabling the aquiferous system. The cost of sponges pushing so much water through the body has been estimated to be about one-third of its overall metabolism. But sponges differ greatly in their pumping capacities, mostly because of their size, effective choanoderm area, and presence/amount of symbiotic microbes.

Sponge choanocytes are thought to be homologous with cells of choanoflagellate protists, although recent studies reveal some differences in organelle ultrastructure (lack of filopodia, cytoplasmic bridges,

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or glycogen in choanocytes), transcriptional profiles, and flagellum beating dynamics. Choanocytes originate during metamorphosis from the ciliated epithelial cells of larvae, and they can also derive from archaeocytes found in gemmules—in both cases, these precursor cells differentiate into choanoblasts that, in turn, grow collars to become choanocytes. Their long flagellum has a basal, bilaterally arranged pair of wing-shaped projections called **vanes**. The flagellar vanes probably lend support to the flagellum. The flagellum is surrounded by a **collar** of microvilli containing actin filaments, the microvilli being connected to one another via a thin membrane composed of a meshwork of extracellular glycoprotein (the **glycocalyx mesh**) (see Figure 5.7 F–H).[3]

A cuticle, or layer of coherent collagen, may cover the pinacoderm in some species. The pinacoderm itself is a simple external sheet (**exopinacoderm**) of cells (**exopinacocytes**), and it also lines some of the internal cavities of the aquiferous system where choanocytes do not occur (e.g., **the canals**). Pinacocytes that line internal canals form the **endopinacoderm** and are called **endopinacocytes**. The choanoderm can be simple and continuous, or folded and subdivided in various ways. The mesohyl varies in thickness and plays vital roles in digestion, gamete production, secretion of the skeleton, and transport of nutrients and waste products by special ameboid cells. The mesohyl includes a noncellular colloidal mesoglea in which are embedded collagen fibers, spicules, and various cells, including symbiotic microbes; it is therefore really a type of mesenchyme. A great number of cell types may be found in the mesohyl. Most of these cells are able to change from one type to another as required, but some differentiate irreversibly, such as those that commit themselves to reproduction or to skeleton formation.

Some sponges actually move from one place to another—ameboid cells along the base of the sponge "crawl," as others carry forward spicules to support the leading edge of the sponge. Studies suggest that some amebocytes can actually break free from a sponge and move about on their own for a time, eventually returning to the parent sponge body. This "locomotion" in sponges obviously is not sufficient to provide them with a quick escape mechanism from predators; we're talking about millimeters a day here!

As a sponge grows, the pinacoderm and choanoderm remain only a single layer of cells. But by increasing folding as the mesohyl volume increases, these layers maintain a surface-area-to-volume ratio sufficient to sustain adequate nutrient and waste exchange throughout the whole individual. Unique to the class Calcarea, some species go through an ontogenetic sequence in which an increasingly complex body architecture develops; adults may express the most complex structure, or they can retain one of the simpler architectures. Thus, some adult Calcarea may retain a largely unfolded, simple, and continuous choanoderm (the **asconoid condition**; Figure 5.3A), or the choanoderm may become folded (the **syconoid condition**; Figure 5.3B,C), or it may become both folded and subdivided into separate flagellated chambers (the **leuconoid**, **sylleibid**, and **solenoid conditions**; Figure 5.3D). Asconoid, solenoid, and syconoid anatomies occur only in the class Calcarea.

The asconoid condition is found in the early growth stage (olynthus) of newly settled calcareous sponges and in some adult, radially symmetrical calcareous sponges (e.g., *Clathrina*, *Leucosolenia*) (Figure 5.4). Asconoid and syconoid sponges rarely exceed a few centimeters in height and remain as simple, vase-shaped (apical–basal radial symmetry) tubular units, or meandering networks of these vase-shaped units, or occasionally even stalked sponges (e.g., some *Clathrina*). The thin walls enclose a central cavity called the **atrium** (= **spongocoel**), which opens to the outside via a single **osculum** (pl. oscula). The pinacoderm of asconoid and very simple syconoid sponges relies on **ostia** as their incurrent pores. Ostia develop during embryogeny as specialized cells (**porocytes**) that elongate and roll to form cylindrical tubes. Each porocyte extends all the way through the pinacoderm, the thin mesohyl, and the choanoderm and thus into the atrium, where it emerges between adjacent choanocytes like a porthole. Porocytes also occur in a few demosponge groups, particularly the freshwater species. The choanoderm is a simple, unfolded layer of choanocytes lining the entire atrium. Water moving through an asconoid sponge thus flows through the following structures: ostium → atrium/spongocoel (over the choanoderm) → osculum (Figure 5.3A).

As stated above, in calcareous sponges, simple folding of the pinacoderm and choanoderm produces the syconoid condition, within which several levels of complexity are possible (Figure 5.3B,C). As complexity increases, the mesohyl may thicken and appear to have two layers. The outer layer (formerly referred to as the cortical region or cortex) is called the **ectosome**. The ectosome contains an accumulation of spicules that are different from those found in the interior portion of the mesohyl. In calcareous sponges with an ectosome, the incurrent openings are lined by several cells (not formed by a single porocyte) and are referred to as **dermal pores**. In the syconoid condition, choanocytes are restricted to specific chambers or diverticula of the atrium called **choanocyte chambers** (also known as flagellated chambers, or radial canals). Each choanocyte chamber opens to the atrium by a wide aperture called an **apopyle**.

[3]Monociliated cells bearing a collar of microvilli surrounding the cilium have been found in almost all metazoan phyla. However, in other metazoans the cilium is usually immobile, lacks vanes, has a striated rootlet, and is frequently involved in sensory processes. It is therefore thought that such cells are not homologues with sponge choanocytes and choanoflagellate protists.

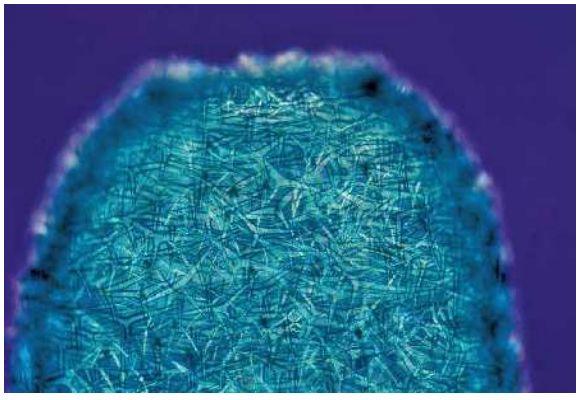

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FIGURE 5.4 The asconoid condition (class Calcarea). (A) An olynthus, the asconoid form that follows larval settlement in calcareous sponges. (B) Major cell types in an asconoid sponge. (C) The simple calcareous sponge *Leucosolenia* shows the asconoid body form and skeleton of $CaCO_3$ spicules.

Syconoid sponges with a thick ectosome possess a system of channels or incurrent canals that lead from the dermal pores through the mesohyl to the choanocyte chambers. The openings from these channels to the choanocyte chambers are called **prosopyles**. In such a complex syconoid sponge, water moving from the surface into the body flows along the following route: dermal (incurrent) pore → incurrent canal → prosopyle → choanocyte chamber → apopyle → atrium → osculum (Figure 5.3B). Syconoid construction is found in many calcareous sponges, including the well-known genera *Grantia* and *Sycon* (formerly known as *Scypha*), and such construction often yields vase-shaped adults, as in many asconoid Calcarea. Some syconoid sponges express a radial symmetry externally, but their complex internal organization is largely asymmetrical.

The leuconoid condition is found in all four sponge classes. Here, the choanoderm is much more highly folded and there is a thickening of the mesohyl by growth of the ectosome. Associated with this is a subdivision of the flagellated surfaces into discrete oval choanocyte chambers (Figure 5.3D). In the leuconoid condition, one finds an increase in number and a decrease in size of the choanocyte chambers, which typically cluster in groups in the thickened mesohyl. The atrium is often reduced to a series of **excurrent canals** that carry water from the choanocyte chambers to the oscula (Figure 5.5). The flow of water through a leuconoid sponge is

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FIGURE 5.5 The surface of a living demosponge (*Clathria*). The complex system of ostia opens into underlying incurrent canals, and large oscula receive several excurrent canals, all visible through the thin pinacoderm.

as follows: dermal pore → incurrent canal → prosopyle → choanocyte chamber → apopyle → excurrent canal → (atrium) → osculum (Figure 5.3D). Leuconoid organization is typical of all noncalcareous sponges and many calcareous sponges (e.g., *Leucilla*).

In Calcarea, solenoid systems are uniquely found in the genus *Leucascus*. They differ from the asconoid architecture in that not all internal cavities are lined by choanocytes. And they differ from leuconoid systems in that they possess anastomosed tubes, making the aquiferous system even more complex. Finally, sylleibid organizations are found both in calcareans and homoscleromorphs, and they are characterized by a radial organization of choanocyte chambers around invaginations of the atrial cavity.

It is important to realize that flow rate is not uniform through the various parts of the aquiferous system. Functionally, it is critical that water be moved very slowly over the choanoderm, allowing time for exchanges of nutrients, gases, and wastes between the water and the choanocytes. The changes in water flow velocity through this plumbing system are a function of the effective accumulated cross-sectional diameters of the channels through which the water moves (see Chapter 3, or your old physics notes). Water flow velocity decreases as the cross-sectional diameter increases—liquids move more slowly in larger pipes—or when a single pipe divides into numerous smaller pipes. Thus, in a sponge, velocities are lowest over the choanoderm, which has the largest cross-sectional area. However, water leaving the osculum must be carried far enough away to prevent it from fouling or being immediately recycled by the sponge, so smaller accumulated cross-sectional diameters (and greater water velocity) are found in excurrent canal–oscula systems.

The recognition of the various levels of organization and complexity among calcareous sponges used to be thought to provide important evolutionary clues. However, there is no evidence that the asconoid plan originated first phylogenetically or that all sponge lineages have moved through these three levels of complexity during their evolution. Nor do most sponges pass through these three stages during development. Calcareous sponges of the leuconoid condition usually do pass through asconoid and syconoid (or even sylleibid or solenoid) stages as they grow, but it is only in this class that all five organizational body plans clearly occur.

The hexactinellid sponges differ strikingly from other sponge classes (Figure 5.6). The bodies of hexactinellid sponges often display a considerable degree of superficial radial symmetry. There is not a typical pinacoderm in hexactinellids. Instead, a **dermal membrane** is present, but it is extremely thin and is continuous with all the other parts of the sponge; no discrete or continuous cellular structure supports it. Incurrent pores are simple holes in this dermal membrane. The main tissue of the hexactinellid is called the **trabecular syncytium**—it forms a syncytial, trabecular network stretching across interconnecting internal cavities (the subdermal lacunae) near the surface of the sponge and penetrating into and forming the supporting framework for the **choanosome** (Figure 5.6A). The trabecular network resembles a three-dimensional cobweb. The thimble-shaped flagellated chambers of the choanosome are arranged in a single layer and are supported within the trabecular network. Both the trabecular network and the walls of the flagellated chambers are syncytial. In these sponges, the choanoblasts produce new collars but do not produce new nuclei, thus creating a single-nucleate syncytium with many collar bodies. As new collars "bud off," the expanding, single-cell body of the choanoblast cell recesses itself beneath the trabecular syncytium, leaving just the collars exposed to do the work. Water enters incurrent pores in the dermal membrane, passes into the subdermal lacunae, and from there enters the syncytial choanosome chambers via the prosopyles. The soft tissue of the syncytium serves to deliver food and other metabolites to all parts of a hexactinellid sponge by cytoplasmic streaming.

The unique structure of hexactinellids is so striking that some workers have even suggested the hexactinellids might be regarded as a separate subphylum or phylum (the "Symplasma"), distinct from the other sponge classes (the "Cellularia"). However, as explained in Chapter 2, phylogenetic relationships are best sought in similarities among groups (i.e., shared derived features), not in differences. By this reasoning, and through molecular phylogenetics, we know without doubt that hexactinellids are poriferans (and probably closely related to

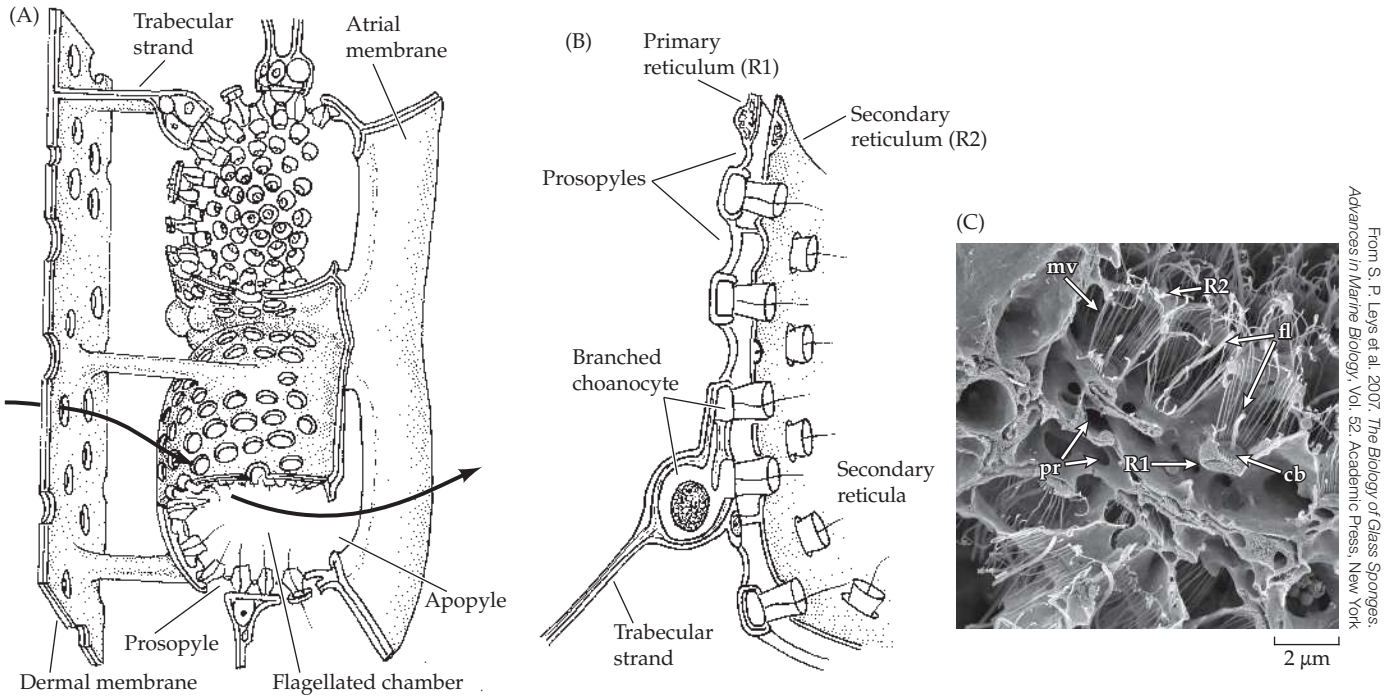

FIGURE 5.6 Internal anatomy of Hexactinellida showing the trabecular network. (A) Two flagellated chambers connected to the dermal membrane by trabecular strands; arrow shows water flow (*Farrea occa*). (B) Section through wall of a flagellated chamber, based on *Rhabdocalyptus dawsoni*. Water is drawn through prosopyles in the primary reticulum and through choanocyte collars by the beating of the flagella. The secondary reticulum surrounds the collars, forcing water through the collar microvilli. (C) Canal system and tissue structure in *Aphrocallistes vastus* (scanning electron micrograph); primary (R1) and secondary (R2) reticula, extensions of the trabecular reticulum, incurrent pores, prosopyles (pr), collar bodies (cb) branching from choanocytes, with collar microvilli (mv) and flagellum (fl). (A after H. Reiswig and D. Mehl. 1991. *Zoomorphology* 110: 301–311, https://link.springer.com/article/10.1007/BF01668020)

demosponges). Nevertheless, hexactinellids are striking and bizarre in that no other metazoan group possesses such extensive syncytial tissues.[4]

More on Sponge Cell Types

Prior to the 1970s, texts generally recognized only a few basic kinds of poriferan cells. However, subsequent detailed histochemical and ultrastructural studies have revealed a broad variety of cell types. These discoveries make succinct "textbook classification" of their cells difficult. We present below a highly abridged version of sponge cell classification.

Cells that line surfaces As noted above, the pinacoderm forms a continuous layer on the external surface of sponges and also lines all incurrent and excurrent canals. The pinacocytes that make up this layer are usually flattened and usually overlapping (Figure 5.7A,B). The external surface, or exopinacoderm, of demosponges has an extracellular matrix beneath it, and in the Calcarea a loose collagenous mesohyl underlies the pinacoderm. In homoscleromorph sponges, and some species in other classes, a true basement membrane underlies the pinacoderm and the choanoderm. In all cases, this layer of secreted material helps maintain the positional integrity of pinacocytes. Basal membranes are sheetlike complexes of extracellular matrix proteins that are secreted by an epithelial layer; they are highly structured and contain type IV collagen. Such membranes

FIGURE 5.7 Cells that line sponge surfaces. ▶ (A) A pinacocyte from the surface of the demosponge *Halisarca* (drawn from an electron micrograph). The outer surface is covered with a polysaccharide-rich glycocalyx coat. The cell is fusiform and overlaps adjacent pinacocytes. (B) Pinacoderm from a calcareous sponge (section). T-shaped pinacocytes alternate with fusiform pinacocytes. (C,D) A porocyte from the calcareous asconoid sponge *Leucosolenia*. (C) Cross section. (D) Side view. (E) Myocytes surrounding a prosopyle. (F) A section of choanoderm, showing three choanocytes; arrows indicate direction of water current. (G) A choanocyte. (H) Ultrastructure of a choanocyte (longitudinal section, drawn from an electron micrograph). (I) A choanocyte chamber opening into an excurrent canal in a demosponge. (H after B. Brill. 1973. *Z Zellforsch Mikrosk Anat* 144: 231–245.)

[4]Syncytial tissues are seen in some other metazoans. For example, the epithelia of some cnidarians and the skeletogenic tissues of echinoids are syncytial, by way of incomplete cytokinesis. The giant neurons in squid, and vertebrate striated muscle cells (your biceps, for example) are multinucleate by fusion of separate cells.

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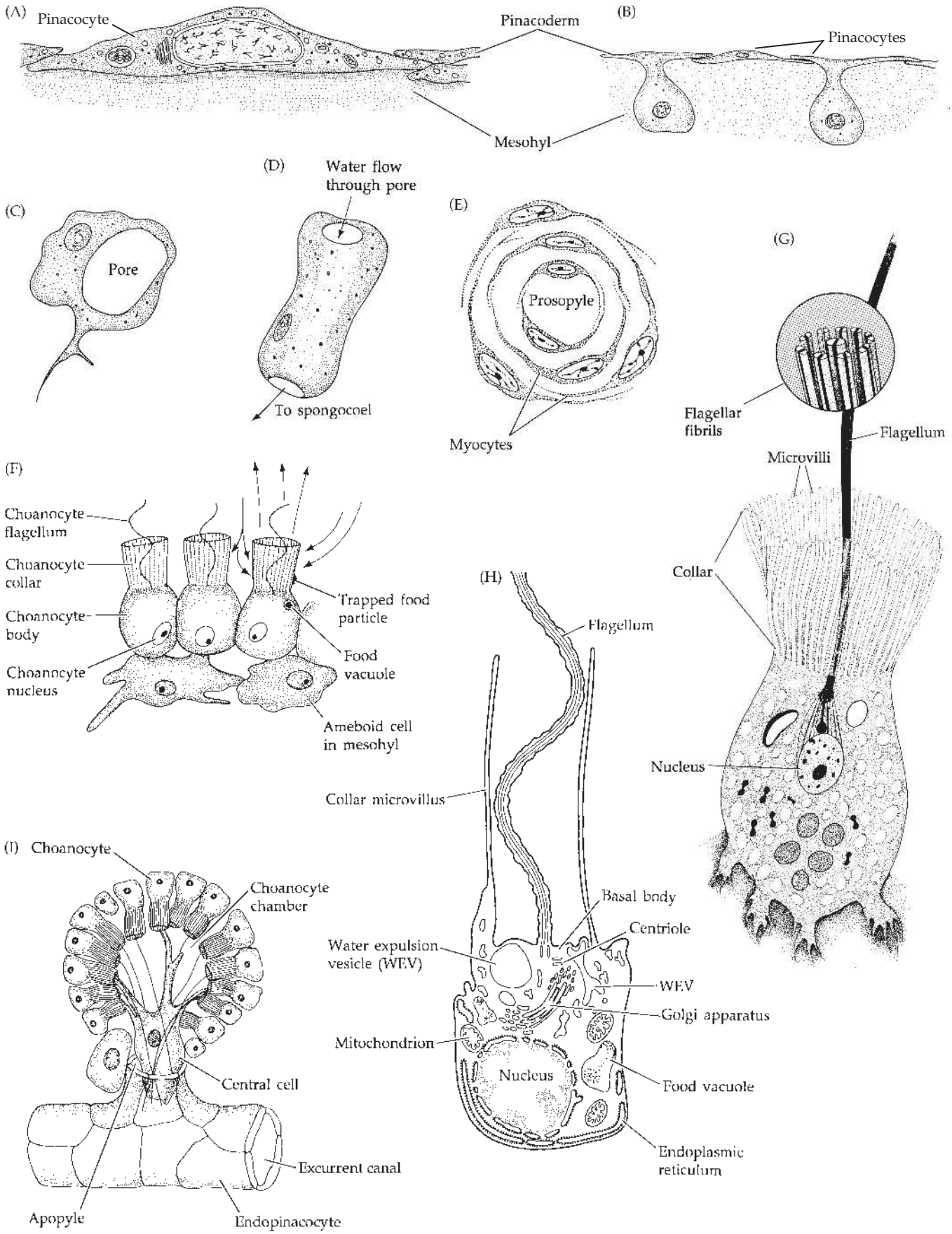

typically underlie epithelial (and endothelial) tissues in the Metazoa, but not in fungi or plants. They provide an added mechanical function as supporting structures and also play a biological role as molecular sieves. The pinacoderm of Homoscleromorpha is especially well organized, forming a well-developed epithelium (with an underlying basal membrane). In demosponges and calcareous sponges, type IV collagen is also found, but its spatial arrangement (whether loosely distributed across the mesohyl or forming a thick layer underlying epithelial layers) is still unknown. In this sense, the apparent absence of a basal membrane in most Porifera distinguishes sponge pinacoderm from the well-developed tissue epithelia of the higher Metazoa.[5]

Internal, canal-lining pinacocytes (**endopinacocytes**) are usually more fusiform in shape and have less overlap than **exopinacocytes**. Although the endopinacoderm is epithelial in function, it is probably phagocytic as well. External cells of the basal or attaching region of a sponge surface are called **basopinacocytes**. These flattened cells are responsible for secreting a fibrillar collagen–polysaccharide complex by which sponges attach to the substratum. In freshwater sponges, the basopinacocytes are active in feeding and extend ameba-like "filopodia" to engulf bacteria. Freshwater sponge basopinacocytes also play an active role in osmoregulation and contain large numbers of water expulsion vesicles, or contractile vacuoles.

As noted earlier, porocytes are cylindrical or flat, tubelike cells of the pinacoderm that form ostia in some sponge species (Figure 5.7C,D). They are contractile and can open and close the pore and regulate the ostial diameter; however, no microfilaments have been observed in them, and their precise method of contraction and expansion is unknown. Some species are capable of producing a diaphragm-like cytoplasmic membrane across the ostial opening that also regulates pore size.

Choanocytes are the flagellated collar cells that make up the choanoderm and create the currents that drive water through the aquiferous system (Figure 5.7F–H). Choanocytes are not coordinated in their beating, not even within a given chamber. However, they are aligned such that the flagella, which beat from base to tip, are directed toward the apopyle. The long flagellum is always surrounded by the choanocyte collar, which is made up of 20 to 55 cytoplasmic microvilli (= villi). The villi have microfilament cores and are connected to one another by anastomosing mucous strands (a mucous reticulum) that form a glycocalyx band around the collar. Choanocytes rest on the mesohyl, held in place by interdigitation of adjacent basal surfaces. In keeping with their central role in phagocytosis and pinocytosis, choanocytes are highly vacuolated.

[5] Type IV collagen, diagnostic of Metazoa, is a long triple helix molecule; it is one of several collagen types found in sponges and other metazoans, and it occurs in all four sponge classes.

Cells that secrete the skeleton There are several types of ameboid cells in the mesohyl that secrete elements of sponge skeletons. In almost all sponges, the entire supportive matrix is built on a framework of fibrillar collagen. The cells that secrete this material are called collencytes, lophocytes, and spongocytes. **Collencytes** are morphologically nearly indistinguishable from pinacocytes, whereas **lophocytes** are large, highly motile cells that can be recognized by a collagen tail they typically trail behind them (Figure 5.8C). The primary function of both cell types is to secrete the dispersed fibrillar collagen found intercellularly in virtually all sponges. **Spongocytes** produce the fibrous supportive collagen referred to as **spongin** (see Figure 5.11A). Spongocytes operate in groups and are always found wrapped around a spicule or spongin fiber (Figure 5.8D).

Sclerocytes are responsible for the production of calcareous and siliceous sponge spicules (Figure 5.8A,B). They are active cells that possess abundant mitochondria, cytoplasmic microfilaments, and small vacuoles, although the inherently distinct formation of siliceous and calcareous spicules indicates their convergent morphology. Numerous types of sclerocytes have been described; these cells always disintegrate after spicule secretion is complete.

Contractile cells Contractile cells in sponges, called **myocytes**, are found in the mesohyl (Figure 5.7E). They are usually fusiform and grouped concentrically around oscula and major canals. Myocytes are distinguished by the great numbers of microtubules and microfilaments contained in their cytoplasm, and they rely on the classic actin-myosin structure seen in all animals. Because of the nature of their filament arrangement, it has been suggested that myocytes are homologous with the smooth muscle cells of higher invertebrates. However, myocytes are independent effectors with a slow response time, and unlike neurons and true muscle fibers, they are insensitive to electrical stimuli.

Stem cells Both archaeocytes and choanocytes are part of the stem cell lineage in sponges, although with different transdifferentiation properties. **Archaeocytes** are highly versatile, largely totipotent ameboid cells that are capable of quickly differentiating to give rise to virtually any other cell type. These large, highly motile cells also play a major role in digestion and food transport (Figure 5.9). They possess a variety of digestive enzymes (e.g., acid phosphatase, protease, amylase, lipase) and can accept phagocytized material from the choanocytes. They also phagocytize material directly through the pinacoderm of water canals. Archaeocytes carry out much of the digestive, transport, and excretory activities in sponges. And, as cells of maximum totipotency, archaeocytes are essential to the developmental program of sponges and to various asexual processes (e.g., gemmule formation). However, there is not a single type

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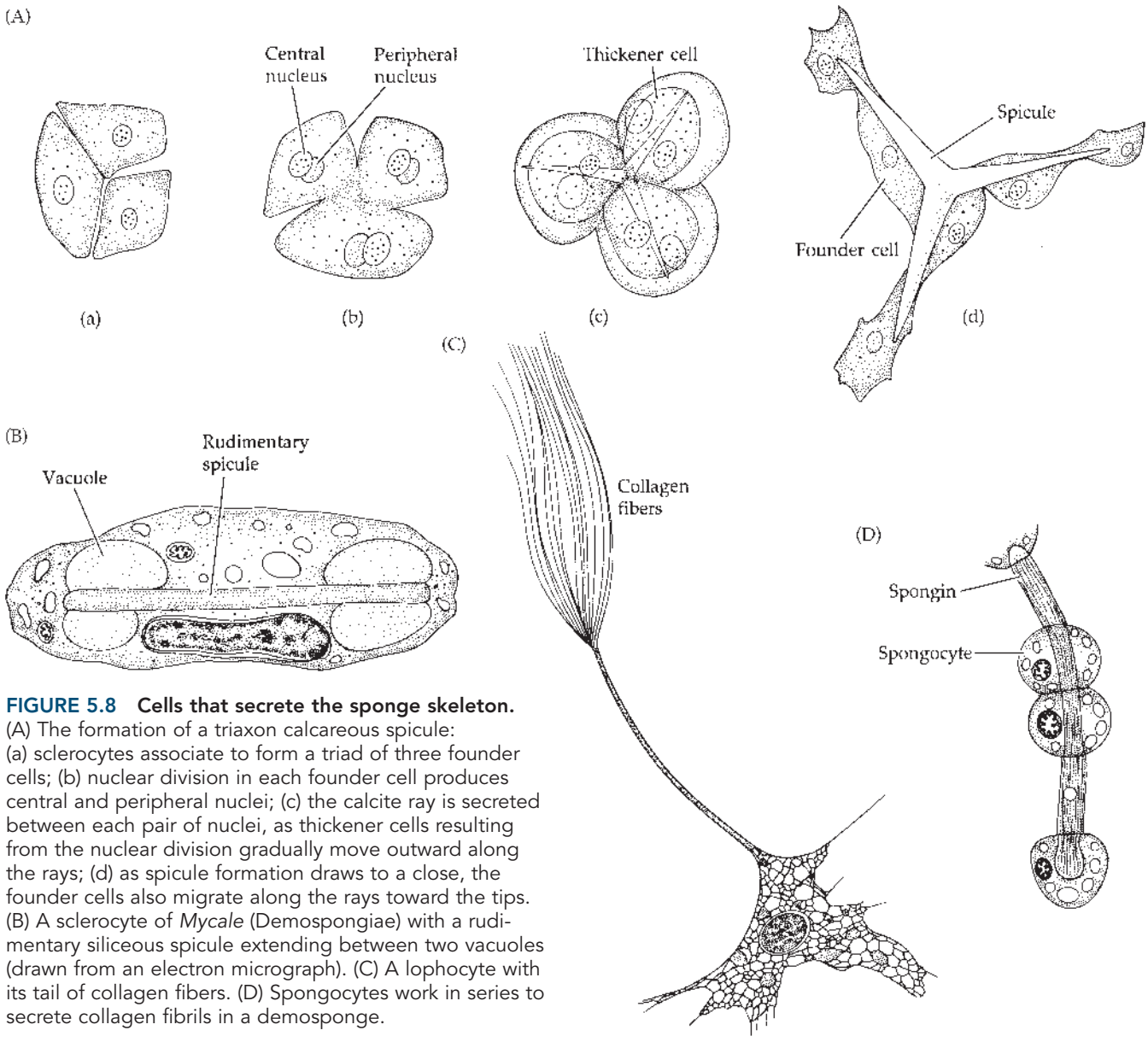
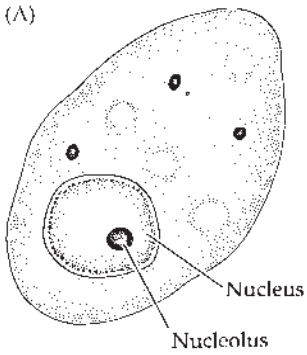


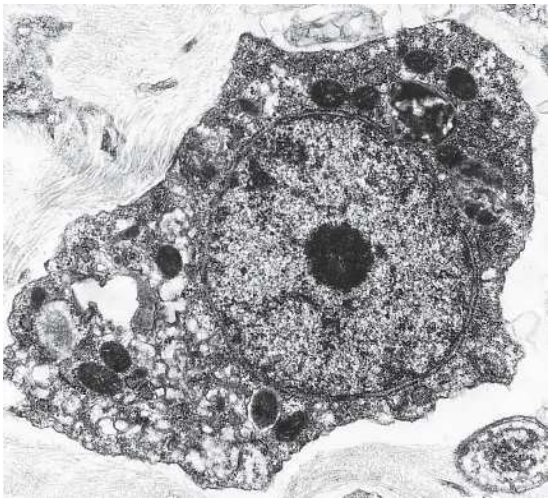
FIGURE 5.8 Cells that secrete the sponge skeleton. (A) The formation of a triaxon calcareous spicule: (a) sclerocytes associate to form a triad of three founder cells; (b) nuclear division in each founder cell produces central and peripheral nuclei; (c) the calcite ray is secreted between each pair of nuclei, as thickener cells resulting from the nuclear division gradually move outward along the rays; (d) as spicule formation draws to a close, the founder cells also migrate along the rays toward the tips. (B) A sclerocyte of *Mycale* (Demospongiae) with a rudimentary siliceous spicule extending between two vacuoles (drawn from an electron micrograph). (C) A lophocyte with its tail of collagen fibers. (D) Spongocytes work in series to secrete collagen fibrils in a demosponge.

of archaeocyte, as they differ in their organelle complements, nucleus-to-cytoplasm ratio, and transcriptional profiles. But, since we lack a proper system to differentiate them, this pool of cells is still referred to collectively as archaeocytes (as long as they have a nucleolated nucleus, ameboid shape, and phagocytic capacities).

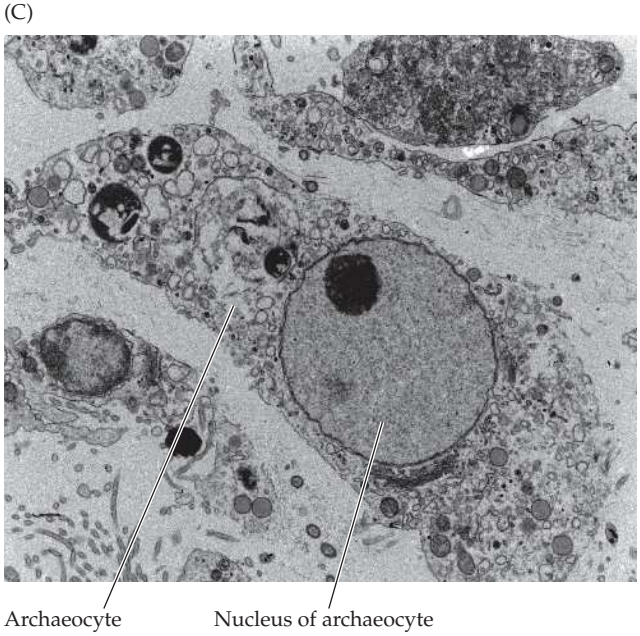
Other cell types Several sponge cell types are known to produce and secrete different molecules. Among them, **spherulous cells** are very common. They are large mesohyl cells containing various chemical inclusions.

Cell reaggregation Around the beginning of the twentieth century, Henry V. Wilson first demonstrated the remarkable ability of sponge cells to reaggregate after being mechanically dissociated. Although this discovery was interesting in itself, lending insight into the plasticity of cellular organization in sponges, it also foreshadowed more far-reaching cytological research that has since shed light on basic questions about how cells self-recognize, adhere, segregate, and specialize. Many sponges that are dissociated and maintained under proper conditions will form aggregates, and some will eventually reconstitute their aquiferous system. For example, when pieces of the Atlantic "red beard sponge" (*Clathria prolifera*: Poecilosclerida) are pressed through fine cloth, the separated cells immediately begin to reorganize themselves by active cell migration. Within 2 to 3 weeks, a functional sponge reforms and the original cells return to their respective functions. Furthermore, if cell suspensions of two different sponge species are mixed, the cells sort themselves out and reconstitute individuals of each separate species—a remarkable display of cellular self-recognition. The controversial sponge biologist M. W. de Laubenfels described the situation in 1949 in





From P. R. Bergquist. 1978. *Sponges*. Hutchinson & Co. Ltd., London



Courtesy of A. Riesgo

FIGURE 5.9 Archaeocytes. (A) A typical archaeocyte with a large nucleus and a prominent nucleolus. (B) Photo of a typical archaeocyte. (C) An archaeocyte engages in phagocytosis (*Crambe crambe*).

slightly different terms: "Sponges endure mutilation better than any other known animal." The discovery that dissociated sponge cells will reaggregate to form a functional organism was the basis for the establishment of sponge cell cultures that have been used as a model for the study of fundamental processes in developmental biology and immunology. We now know that sponge cells (like other animal cells) have surface markers that allow for self- versus non-self-recognition.

Support

The skeletal elements of sponges are of two types, organic and inorganic. The former is always collagenous, and the latter either siliceous (hydrated silicon dioxide) or calcareous—calcium carbonate in the form of calcite or aragonite. Sponges are the only animals that use hydrated silica as a skeletal material. Calcite is a common crystalline form of natural calcium carbonate, $CaCO_3$, that is the basic constituent of many protist and animal skeletons, as well as the fossiliferous sedimentary rocks known as limestone, marble, and chalk.[6]

Collagen is the major structural protein in invertebrates; it is found in virtually all metazoan connective tissues. In vertebrates, about 20 different kinds of collagen have been identified, but in Porifera only 3 are known so far: type I–like collagen (fibrillar collagens),

[6]Calcite and aragonite are closely related calcium carbonate ($CaCO_3$) minerals representing the two most common, naturally occurring, crystalline forms. Both are formed by biological and physical processes—primarily precipitation in marine and freshwater environments—and both are used by animals in the construction of their skeletons. Calcite is the more stable of the polymorphs of calcium carbonate. Calcite crystals are trigonal-rhombohedral, though actual calcite rhombohedra are rare as natural crystals. In animal skeletons, calcite occurs as lamellar or compact deposits, or occasionally in a fibrous form. Calcite is transparent to opaque. Single calcite crystals display an optical property called birefringence (double refraction) that causes objects viewed through a clear piece of calcite to appear doubled. Although calcite is fairly insoluble in cold water, acidity can cause its dissolution (a big problem for animals and protists living in an acidifying global ocean). Calcite exhibits an unusual characteristic called retrograde (or inverse) solubility in which it becomes less soluble in water as the temperature increases. Aragonite's crystal lattice differs from that of calcite, resulting in a different crystal shape, an orthorhombic system with needlelike crystals. Aragonite may be columnar or fibrous. Aragonite is thermodynamically unstable at standard temperature and pressure and tends to alter to calcite on scales of 107 to 108 years. Because calcite is more stable than aragonite and dissolves more slowly than aragonite in water, it is more likely to fossilize. Thus, the fossil record for Paleozoic corals is better than the fossil record for Cenozoic corals, the former being made of calcite, the latter of aragonite.

Calcite skeletons occur in most invertebrates that have hard skeletons, including sponges, brachiopods, echinoderms, most bryozoans, and most bivalves. Coccoliths and planktonic foraminiferans also have calcitic skeletons, and certain red algae (coralline red algae) also produce it. Because calcite is so stable, larger calcite shells in the fossil record (e.g., bivalves) thus tend to the "real thing," not mineral replacements. Purely aragonite-based shells do exist, such as in the molluscan class Polyplacophora (the chitons), but they are rare.

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type IV, and short-chain collagens (non-fibrillar collagens). Collagen type IV is a key component of basal membranes, and it has to date been found primarily in the Homoscleromorpha but also in a number of species of demosponges and calcareans.

In sponges, fibrillar collagen is either dispersed as thin fibrils in the intercellular matrix or organized as a fibrous framework called spongin in the mesohyl. Although the dispersed collagen fibers seen in many sponges are sometimes referred to as "spongin," true spongin (fibrillar collagen forming a skeletal framework in the mesohyl) is found only in members of the class Demospongiae (Figure 5.11A). The amount of this fibrillar collagen varies greatly from species to species—in hexactinellids it is quite sparse, whereas in demosponges it is abundant and may form dense bands in the ectosome. Unlike the ectosome of calcareous sponges, which is fundamentally a layer of concentrated spicules with very little collagen, the ectosome of demosponges is a feature of the outer mesohyl and is basically a well-developed collagen layer lacking choanocyte chambers. The network often contains very thick fibers, and it may incorporate siliceous spicules into its structure. Interestingly, the symbiotic bacteria preferentially locate among the collagenous deposits of the mesohyl. Spongin often cements siliceous spicules together at their points of intersection. The encysting coat of the asexual gemmules of freshwater (and some marine) sponges is also composed largely of spongin.

Mineral skeletons of either silica or calcium are found in almost all sponges, except a few species of demosponges and homoscleromorphs. Sponges lacking mineral skeletons possess only fibrous collagen networks, and these are still used as bath sponges despite the prevalence nowadays of synthetic "sponges." Several demosponge and homoscleromorph genera lack both spongin and a spicule skeleton (e.g., *Chondrosia*, *Halisarca*, *Hexadella*, *Oscarella*).

Sponges have been harvested for millennia. There is evidence of an active Mediterranean sponge trade by Egyptians at least as early as 3000 BCE, and later in the ancient Phoenician, Greek, and Roman civilizations (Figure 5.10). Homer and other ancient Greek writers mention a thriving Mediterranean sponge trade. Prior to the 1950s, active natural sponge fisheries existed in southern Florida, the Bahamas, and the Mediterranean. The industry peaked in 1938, when the world's annual sponge catch (including cultivated sponges) exceeded 2.6 million pounds, 700,000 pounds of which came from the United States and the Bahamas. Almost all commercial sponges belong to the genera *Hippospongia* and *Spongia* (subclass Keratosa), but these sponges have now been largely "fished out" in the traditional sponge hunting grounds of the Mediterranean and Florida. In addition, they are prone to current-transmitted epidemic

Courtesy of R. Brusca

FIGURE 5.10 **Mediterranean bath sponges (*Spongia officinalis*) for sale in an open-air market in the Provence region, France.**

diseases (three such events wiped out bath sponge populations in both the Old World and the New World in 1938, 1947, and the late 1980s).

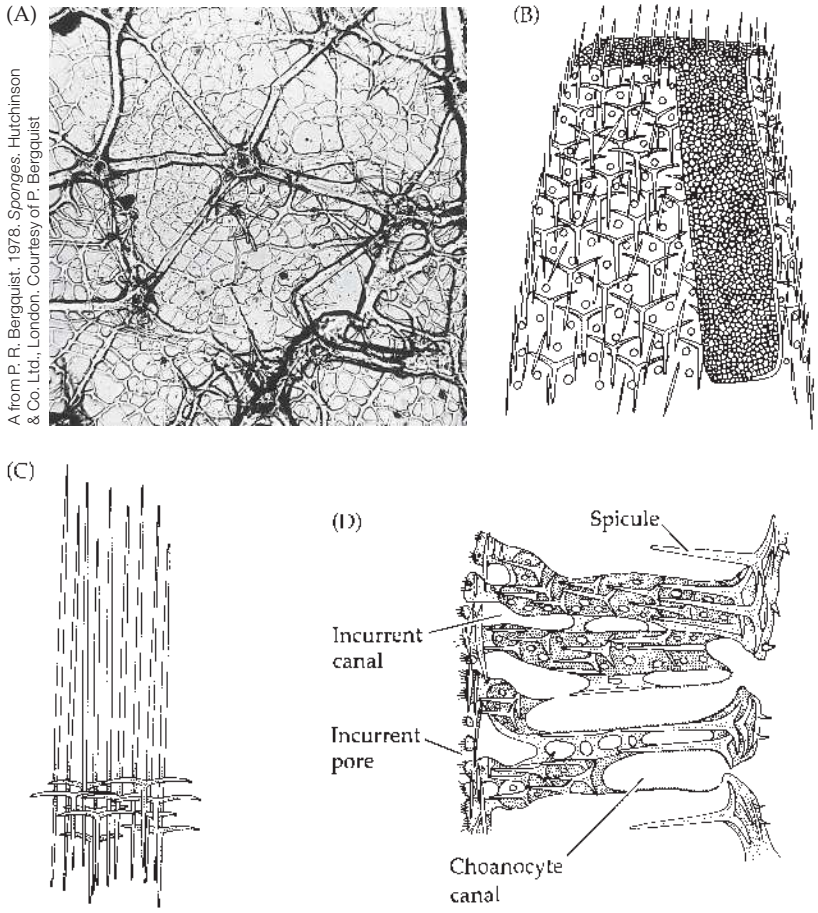
Mineralized sponge spicules (Figure 5.11) are produced by special mesohyl cells called sclerocytes, which are capable of accumulating calcium or silicate and depositing it in an organized way. In some cases, one sclerocyte produces one spicule; in others, several sclerocytes work together cooperatively to produce a single spicule, often two cells per spicule ray (Figure 5.8A–D).

The construction of a siliceous spicule begins with the secretion of an organic axial filament within a vacuole in a sclerocyte. This axial filament is composed of the enzyme silicatein in demosponges and glassin in hexactinellids, but its enzymatic origin in homoscleromorphs is yet unknown. As the axial filament elongates at both ends, hydrated silica is secreted into the vacuole and deposited around the filament core. Recent work suggests that, at least in some homoscleromorph species (e.g., *Corticium candelabrum*), pinacocytes might also be capable of siliceous spicule production. About 92% of all living sponge species are siliceous. One might wonder how a skeleton made of glass (as in the Hexactinellida) could be strong enough to provide support while not being fragile as a windowpane. The trick is that glass sponges have evolved a highly sophisticated, multilayered biomechanical structure to their skeleton. They construct their glass skeleton by first consolidating nanometer-scale silica spheres, arranged in microscopic concentric rings separated from one another by alternating layers of an organic matrix-glue to form laminated spicules. The spicules are then bundled together by an organic, silica-based cement, resulting in the formation of micron-scale, multilayered "beams." The beams are then assembled into the recognizable square-lattice cagelike structure we see in glass sponges, such as *Euplectella*. The lattice itself is further reinforced by diagonal ridges, giving the whole skeleton remarkable strength plus a resilient

flexibility. In species of *Euplectella*, seven hierarchical structural levels have been identified in the skeleton—a textbook example in biomechanical engineering, and perhaps one day an inspiration for glass fiber manufacturers. Even in Demospongiae and Homoscleromorpha, the siliceous spicules exhibit exceptional flexibility and toughness due to their composite, layered construction.

Unlike siliceous spicules, calcium carbonate spicules do not have an organic axial core. Calcareous spicules are produced extracellularly, in intercellular spaces bounded by a number of sclerocytes. Each spicule is essentially a single crystal of calcite or aragonite. The enzymes responsible for its polymerization, carbonic anhydrases, are commonly found in almost all metazoans. In calcareous sponges, there are several carbonic anhydrases that act in coordination, and even more importantly, some of them are spicule-type specific.

Considerable taxonomic weight has been given to spicule morphology, and an elaborate nomenclature exists to classify these skeletal structures. Spicules are termed either **microscleres** or **megascleres**. The former are small to minute reinforcing (or packing) spicules; the latter are large structural spicules. The demosponges and hexactinellids have both types; calcareous sponges often have only megascleres (although the spicules can differ considerably in size). Descriptive terms that designate the number of *axes* in a spicule end in the suffix *-axon* (e.g., monaxon, triaxon). Terms that designate the number of *rays* end in the suffixes *-actine* or *-actinal* (e.g., monactinal, hexactinal, tetractinal). In addition, there is a detailed nomenclature specifying shape and ornamentation of various spicules (Figure 5.11).



A from P. R. Bergquist. 1978. *Sponges*. Hutchinson & Co. Ltd., London. Courtesy of P. Bergquist

A spicular skeleton may be viewed as a supplemental supporting structure. If the amount of inorganic material is increased in relation to organic material, the sponge becomes increasingly solid until the texture approaches that of a rock, as it may in some members of the demosponge order Tetractinellida and a few others (e.g., the formerly named "lithistid" sponges, a polyphyletic group). In contrast to discrete spicules, the massive calcareous skeletons of some species (the coralline sponges, or sclerosponges) have a polycrystalline microstructure; they are composed of needles ("fibers") of either calcite or aragonite embedded in an organic fibrillar matrix. The advantage of incorporating organic matter into the calcareous framework has been compared to that of using lath and plaster, or reinforced concrete. The mix of organic and inorganic materials probably yields fibrous calcite and aragonite that are less prone to fracture while also producing substances that are more easily molded by the organism. In some demosponges (e.g., the "lithistids") and many Hexactinellida, the spicules may be linked or fused into such a rigid framework that it is capable of fossilizing.[7]

Nutrition, Excretion, and Gas Exchange

Although sponges lack the complex organs and organ systems seen in most other Metazoa, they are nevertheless a hugely successful group of animals. As noted above, their success seems partly due to their "ancientness"—the flexibility inherent in their developmental programming, cellular pluripotency, highly versatile aquiferous system, and the general plasticity of their body form.

Unlike most Metazoa, nearly all sponges rely on intracellular digestion, and thus on phagocytosis and pinocytosis as means of food capture. The aquiferous system has already been described; with it, sponges more or less continuously circulate water through their

[7]The order Lithistida has long been recognized as polyphyletic but kept mainly as a matter of convenience, essentially because it is used by paleontologists. However, as with the former taxon Sclerospongiae, it is clearly time to abandon the name "Lithistida" and begin reassigning its component species.

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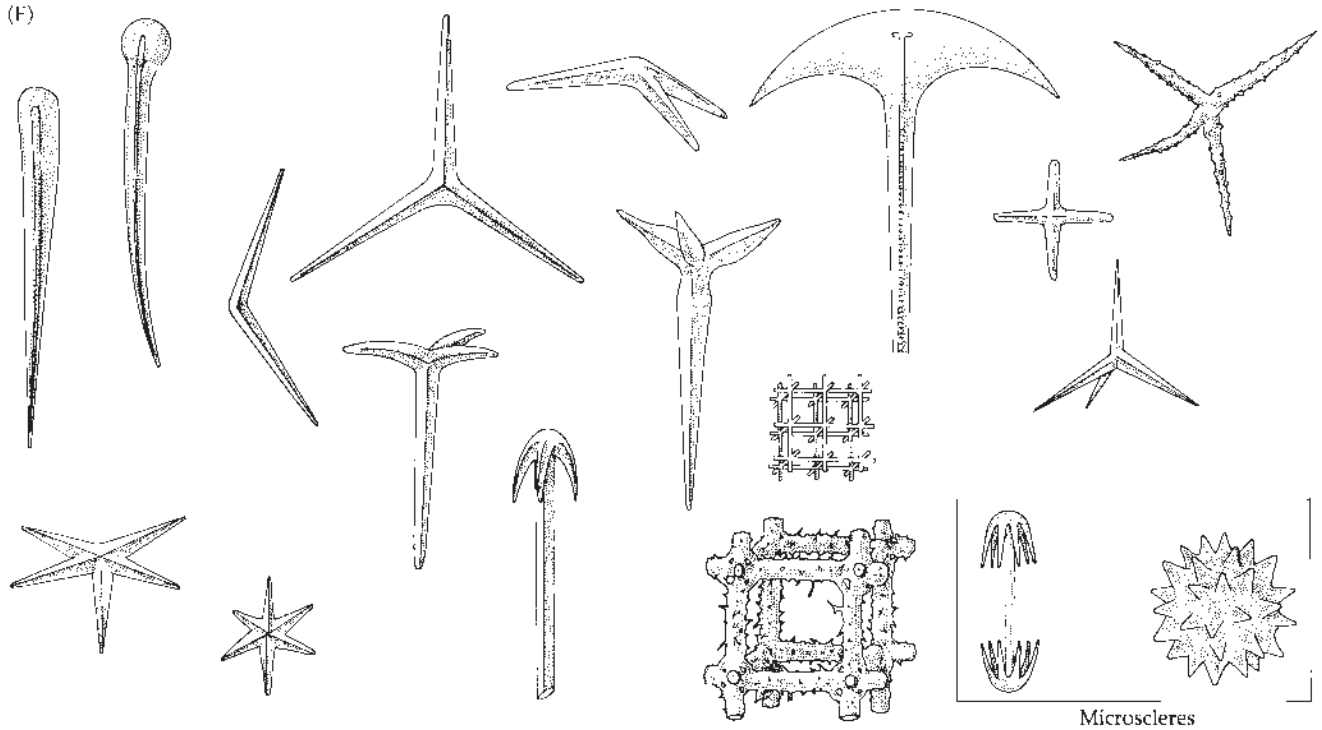


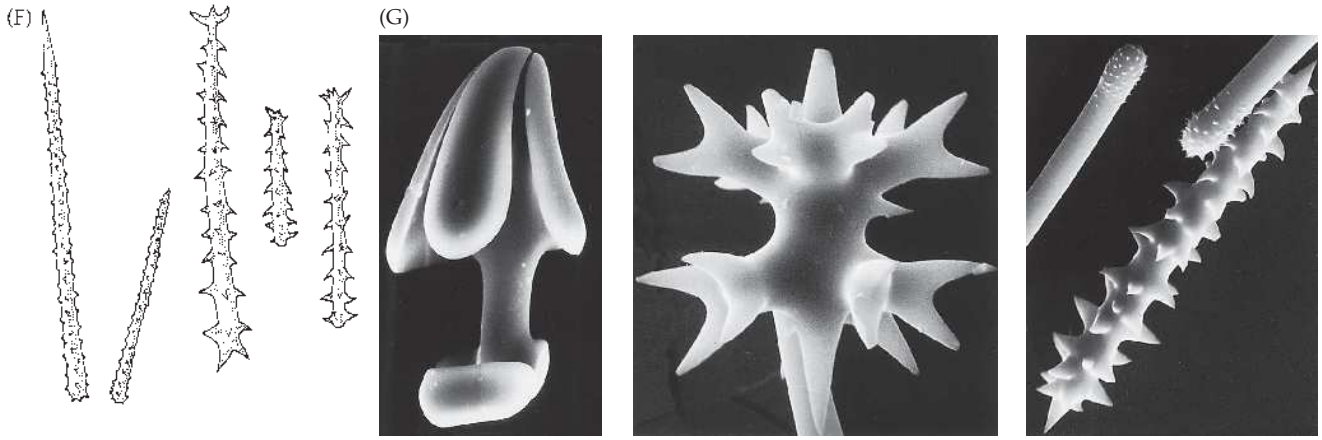
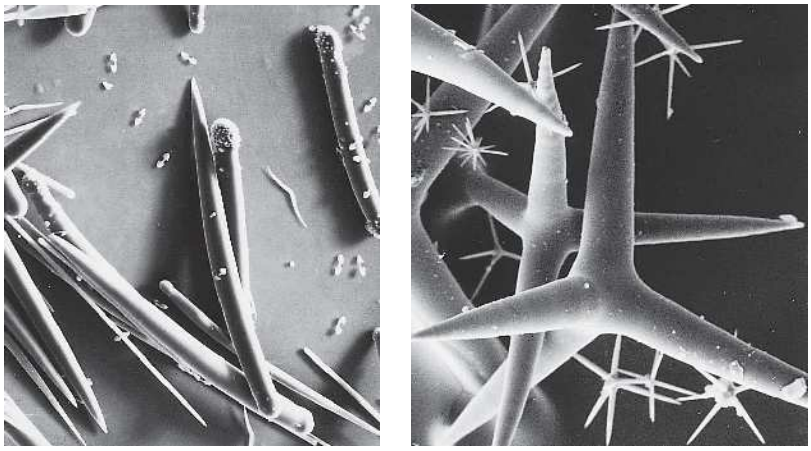


FIGURE 5.11 Sponge skeletal systems. (A) Photomicrograph of the superficial dermal spongin-fiber skeleton typical of the demosponge family Callyspongiidae. (B) Arrangement of calcareous triaxon spicules near the oscular opening in *Leucosolenia*. (C) Arrangement of monaxon and triaxon calcareous spicules near the oscular opening of *Sycon*. (D) Cross section of a simple syconoid calcareous sponge (atrium on right) illustrating placement of triaxon spicules. (E) Some common types of siliceous spicules from demosponges. (F) Some siliceous spicules from sclerosponges. (G) Various spicule types (SEMs).



From P. R. Bergquist. 1978. *Sponges*. Hutchinson & Co. Ltd., London. Photo of asterose microscleres courtesy of B. Beaumont

bodies, bringing with it the microscopic food particles upon which they feed. They are size-selective particle feeders, and the arrangement of the aquiferous system creates a series of "sieves" of decreasing mesh size (e.g., dermal pores or ostia → canals → prosopyles → choanocyte villi → intertentacular mucous reticulum). The upper limit of the diameter of incurrent openings is usually around 50 μm, so larger particles do not enter

the aquiferous system. A few species have larger incurrent pores, reaching diameters of 150 to 175 μm, but in most species the incurrent openings range from 5 to 50 μm in diameter. Internal particle capture in the 2 to 10 μm range (e.g., bacteria, small protists, unicellular algae, organic detritus) is by choanocytes and by phagocytic motile archaeocytes that move to the lining of the incurrent canals. As in the choanoflagellate protists, the propagation of the flagellar wave in sponge choanocytes is thought to draw water in through the microvilli of the collar, which then slows or blocks food particles, allowing them to be phagocytized. The smallest particles, large organic molecules and small bacteria in the 0.1–0.2 μm range (the distance between adjacent villi is ~1.5 μm or less), may be trapped on the collar itself. Larger particles, up to ~3 μm, adhere to the body of the choanocyte only to be engulfed by "pseudopodial" extensions (phagocytosis) that may be longer than the collar villi themselves. Undulations of the collar might move some trapped food particles down to the choanocyte cell body, or stalled food might be captured by long phagocytizing pseudopods that form from the collar microvilli and migrate from the base of the collar (as in choanoflagellates) or by pseudopods from the choanocyte cell body itself.

Interestingly, it would seem that food particle capture can take place almost anywhere on the surface of a sponge. Even pinacocytes are known to be capable of phagocytizing particles as large as 6 μm on the surface of a sponge. It has been estimated that the pinacocytes lining canals can take particles as large as 50 μm.

In the case of archaeocyte phagocytosis, digestion takes place in the food vacuole formed at the time of capture. In the case of choanocyte capture, food particles are partly digested in the choanocytes and then quickly passed on to a mesohyl archaeocyte (or other wandering amebocyte) for final digestion. In both cases, the mobility of the mesohyl cells assures transport of nutrients throughout the sponge body.

The efficiency of food capture and digestion was dramatically shown in an elegant study long ago, by Schmidt (1970), using fluorescence-tagged bacteria fed to the freshwater sponge *Ephydatia fluviatilis* (Heteroscleromorpha). By monitoring the movement of the fluorescent material, Schmidt determined that 30 minutes elapsed from the onset of feeding until the bacteria had been captured by choanocytes and moved to the base of the cells. Transfer of the fluorescent material to the mesohyl commenced 30 minutes later. Twenty-four hours later, fluorescent wastes began to be discharged into the water, and no fluorescent material remained in the sponges after 48 hours. Additional studies on this same species led to an estimate of 7,600 choanocyte chambers per cubic centimeter of sponge body, each chamber pumping a phenomenal 1,200 times its own volume of water daily. More complex leuconoid sponges have as many as 18,000 choanocyte chambers per cubic millimeter. In some thin-walled asconoid and simple syconoid sponges, a distinctive mesohyl is hardly present. In these sponges the choanocytes assume both capture and digestive/assimilative functions. More recent studies have shown that sponges are capable of removing up to 95% of the bacteria and heterotrophic protists from the water they filter.

Such a frantic flagellar activity of choanocytes can translate into a relatively short life of these cells, and indeed, substantial expulsion of filtering cells has been observed in the water. Recently, this newly discovered form of discharged organic matter in reef ecosystems has been proposed to fuel the productivity of these otherwise oligotrophic systems (i.e., the "sponge loop").

Many sponges appear to also take up significant amounts of dissolved organic matter (DOM) by pinocytosis from the water within the aquiferous system, and there is some evidence that this is needed by the microbial symbionts within the sponge. Studies have shown that 80% of the organic matter taken in by some shallow-water marine sponges can be of a size below that resolvable by light microscopy. The other 20% comprises primarily bacteria and dinoflagellates. On the other hand, some sponges appear to rely very little on DOM for nutrition (e.g., some hexactinellids that have been studied). Recent studies show that at least some sponges form simple fecal pellets. Experiments on the widespread North Atlantic species *Halichondria panicea* (Heteroscleromorpha) have revealed that undigested material is expelled as discrete pellets coated with a thin layer of mucus. Exactly how these pellets are formed is unclear.

Although the phylum Porifera is characterized by filter feeding, members of the deep-sea demosponge family Cladorhizidae display an entirely different and unique mode of feeding. Species in this group have lost most or all of the characteristic choanocyte-lined aquiferous system and instead feed as macrophagous carnivores; in fact, they are passive suspension-feeding predators, spending a minimal amount of energy during long periods between rare feeding opportunities! They feed by trapping small prey on hook-shaped spicules that protrude from the surfaces of tentacle-like structures (Figures 5.12 and 5.13). Trapped prey are gradually enveloped by migrating feeding cells that undertake digestion and absorption. Most cladorhizids live at great ocean depths, and *Lycopodina occidentalis* is the deepest known sponge, although it can also be found at diving depths on the west coast of Canada. Most cladorhizids probably remain undescribed and, unfortunately, are common on the tops of seamounts—a habitat threatened by fishing and mineral extraction interests. Luckily, one species of *Lycopodina* (*L. hypogea*) lives in shallow caves in the Mediterranean, where it has been the subject of considerable study, shedding light on the biology of this enigmatic sponge. One of the more bizarre cladorhizids is *Chondrocladia lyra*

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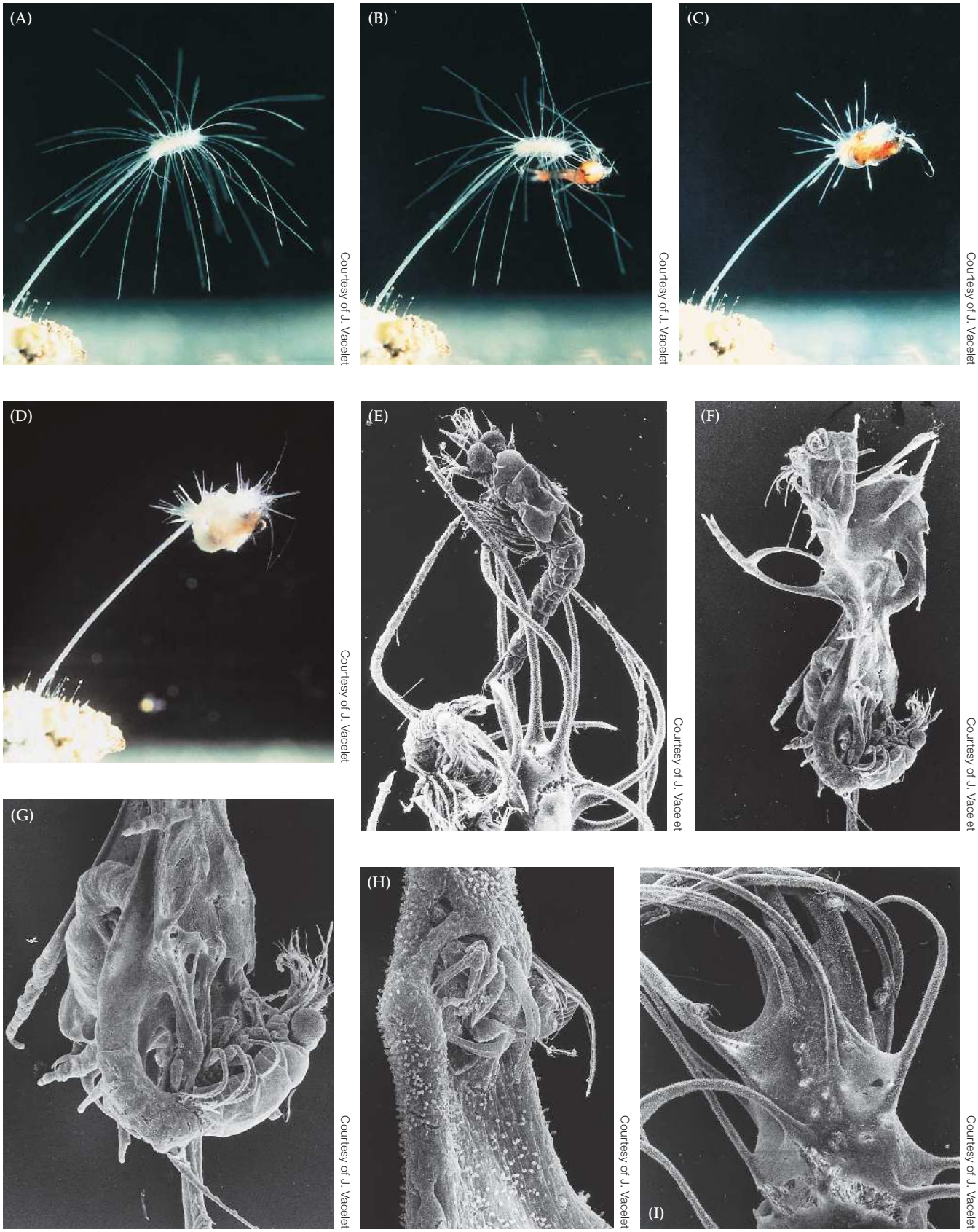
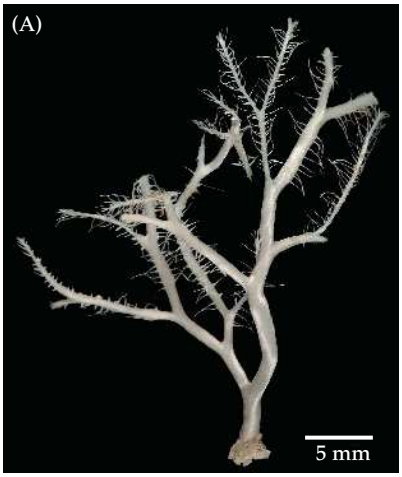


FIGURE 5.12 These remarkable color photos and SEMs show predation in the carnivorous sponge *Lycopodina hypogea* (family Cladorhizidae). (A–D) Sponge in ambush posture (A), followed by capture of a mysid. (E) Fifteen minutes after capture of a mysid on its tentacle-like feeding filaments. (F–H) The mysid prey has been partly engulfed by the sponge. (I) The prey is entirely engulfed.



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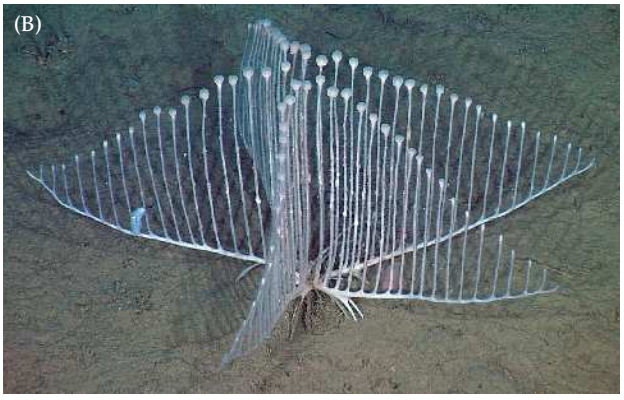

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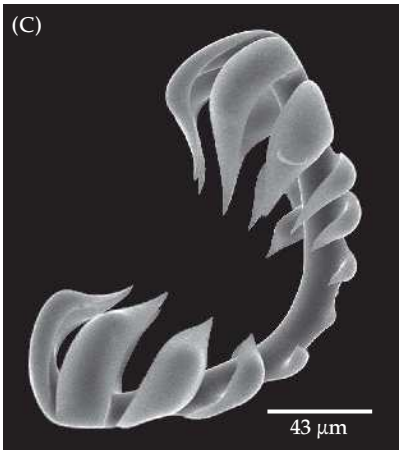

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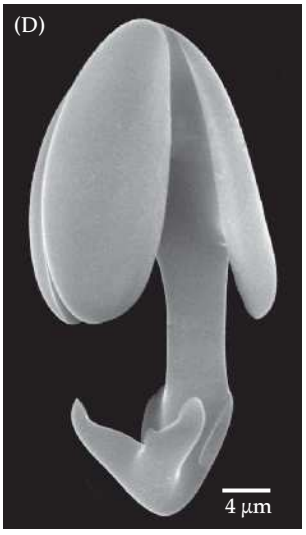

From J. Vacelet. 2006. *Zool J Linn Soc* 148: 553–584

FIGURE 5.13 More carnivorous sponges (family Cladorhizidae). (A) *Asbestopluma desmophora*, a treelike carnivorous sponge from New Zealand. Large, clear megascleres are aligned vertically along the main "trunk," twisting around it to give a silky sheen to the creature. The small, thin, side branches are covered in microscleres that snare passing prey. (B) The remarkable lyre sponge, *Chondrocladia lyra*, from a depth of 3.5 km off the coast of Monterey, California, reaches 36 cm in height and has up to six long vanes that grow from the main body, each vane with a series of parallel side branches that are used for passive suspension feeding of small invertebrates, particularly crustaceans, using Velcro-like barbed hooks (microscleres). (C) A microsclere from *Abyssocladia carcharias*, named for the remarkable shape of the "abyssochelae" microscleres, which resemble the jaws of the great white shark *Carcharodon carcharias*. (D) Microsclere ("anisochelae") of *Asbestopluma agglutinans*. In carnivorous sponges, microscleres are involved in snaring prey and typically line the sponge's surface.

(the lyre sponge; Figure 5.13B), which has a series of vanes extending from the central body, each vane in turn with a series of upright side branches, creating a lyrelike or harplike structure that works for passive suspension capture of small zooplankters, especially crustaceans. Cladorhizids apparently lack oscula, ostia, and a canal system, and some may even lack choanocytes! Another of the remarkable cladorhizid sponges, *Cladorhiza methanophila*, has been discovered to harbor methanotrophic bacterial symbionts in its cells, such as seen in many animals inhabiting hydrothermal vents and cold seeps. The sponge thus feeds both by predation and by direct consumption of its microbial symbionts. Recently, species in several other deep-sea families have shown evidence of carnivory, suggesting that this habit has perhaps evolved several times among the Demospongiae.

Sponges continuously excrete waste from their body via the osculum. Occasionally, they also undergo a stereotypic series of whole-body contractions, sometimes called a "sneeze." It appears that these contractions are stimulated by a reduction in water flow through the oscula, which would typically be caused by obstruction from an excessive accumulation of particulates that can clog the aquiferous system. The decrease in oscular flow is registered by special short cilia that line the inner osculum epithelium. Unlike most cilia, which possess the classic 9+2 anatomy, these oscular cilia lack the central pair of microtubules and are nonmotile. Their sole function seems to be the detection of flow rates through the oscula. Such cilia, called "primary cilia," are known from other metazoans, where they typically sense changes in fluid movement. Thus, the sponge osculum can be viewed as a true sense organ—the only one known in this phylum! Experimentally de-osculated sponges cannot be triggered to sneeze.

Excretion (primarily ammonia) and gas exchange are by simple diffusion, much of which occurs across the choanoderm. We have already seen how folding of the body, combined with the presence of an aquiferous system, overcomes the surface-to-volume dilemma posed by an increase in size. The efficiency of the poriferan body plan is such that diffusion distances never exceed about 1.0 mm, the distance at which gas exchange by diffusion becomes notably inefficient. In addition, water expulsion vesicles (contractile vacuoles) occur in freshwater sponges and presumably aid in osmoregulation.

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Activity and Sensitivity

Sponges do not possess neurons, a nervous system, or discrete adult sense organs (except for the oscula, see above), and nothing resembling the synaptic connections (or gap junctions) of most other Metazoa is known in these animals. Neuronal synapses, which provide for chemically mediated and directional nerve impulse transmission, do not occur in sponges (these occur in every metazoan phylum except Porifera and Placozoa).

Despite the absence of a nervous system, sponges are capable of responding to a variety of environmental stimuli by closure of the ostia or oscula, canal constriction, backflow, body contractions that flush the aquiferous system ("sneezing"), and reorganization of flagellated chambers. Acetylcholinesterase, catecholamines, and serotonin have all been shown to be present in sponges, and these probably play roles in coordinating "tissue" contractions, although electrophysiological evidence of a conducting mechanism is still lacking. Sponge larvae show both positive and negative phototaxis, depending on whether they are in their planktonic or settling phase. In larvae of the demosponge *Reniera*, there is a posterior ring of columnar monociliated epithelial cells with pigment-filled protrusions thought to be photoreceptors. In addition, the ability to conduct electrical impulses (when stimulated by an electrical probe) has been shown to exist in some Hexactinellida, where the absence of cellular membranes within the syncytium presumably allows action currents to spread in any direction from sites of depolarization. When the action currents reach choanocytes within the trabecular network, choanocyte activity is suppressed. In all sponges, the "default" behavior seems to be active pumping by the choanocytes to keep the aquiferous system functioning; and the usual effect of environmental stimuli is to reduce or stop the flow of water through the aquiferous system. For example, when suspended particulates become too large or too concentrated, sponges will respond by closing the incurrent openings and immobilizing the choanocyte flagella. Indeed, sponges have long been known to contract their ostia and oscula, and portions of their canal system, although the rates of propagation are very slow for most but not all. Lack of flow detected by sensory ciliated cells in the osculum can trigger a sneeze response, forcing water and particles to be expelled out of the sponge body. Direct physical stimulation will also elicit pumping pauses, which is easily observed by simply running one's finger across a sponge surface and observing the dermal pore or oscular contractions with a hand lens or low-power microscope. In addition, the mesohyl of some species has been shown to react to mechanical stimulation by stiffening.

Choanocyte pumping activity also varies with certain endogenous factors. For example, during a major growth phase, such as canal or chamber reorganization, choanocyte-pumping activity typically decreases. Periods of reproductive activity also cause a substantial decrease in water pumping, in part because many choanocytes are expended in the reproduction process (see the Reproduction and Development section). Even under normal conditions, variations in pumping rates occur. Some sponges cease pumping activity periodically, for a few minutes or for hours at a time; others cease activity for several days at a time—reasons for these changes in activity are not always apparent.

The switch from full pumping activity to complete cessation requires at least several minutes; considering the organism, however, this is a fairly fast response time. The spread of stimulation and consequent response in most sponges appears to be by simple mechanical action (stimulation from one cell to the adjacent cells) and perhaps also by diffusion of certain chemical messengers (hormones, or other kinds of signaling molecules) released by cells. The process by which cells communicate with other cells by secreting specific chemicals released into the surrounding extracellular matrix is called **paracrine signaling**, or a **paracrine system**, and some workers consider sponges to use this kind of cell–cell signaling.

The contractile myocytes of sponges act as independent effectors; they are organized into a network formed by contacts between filopodial extensions of adjacent myocytes and pinacocytes. Response time of myocytes is relatively slow. Latency periods average 0.01 to 0.04 sec, and conduction velocities are typically less than 0.04 cm/sec (except in the hexactinellids, where velocities of 0.30 cm/sec have been recorded).[8] Conduction is unpolarized and diffuse, and it may rely on both hormones (or other signaling molecules) and direct mechanical action of one cell on the next. Considerable research once focused on the myocytes in attempts to shed light on the possible presence of a sponge nervous system analogous to or homologous with that in other Metazoa. But, in spite of these efforts, there has been no verification of such a system.

Reproduction and Development

All sponges are capable of sexual reproduction, which is generally their primary reproductive strategy, but several types of asexual processes are also common. Many of the details of these processes are unknown, however, largely because sponges lack distinct or localized gonads (gametes and embryos can generally occur throughout the mesohyl). All hexactinellids, homoscleromorphs, and calcareous sponges are probably viviparous, as are most demosponges.

[8]It has been suggested that, in hexactinellids, the syncytium serves as an electrical conduction pathway, propagating impulses along its membranes that trigger flagellar arrests in the flagellated chambers.

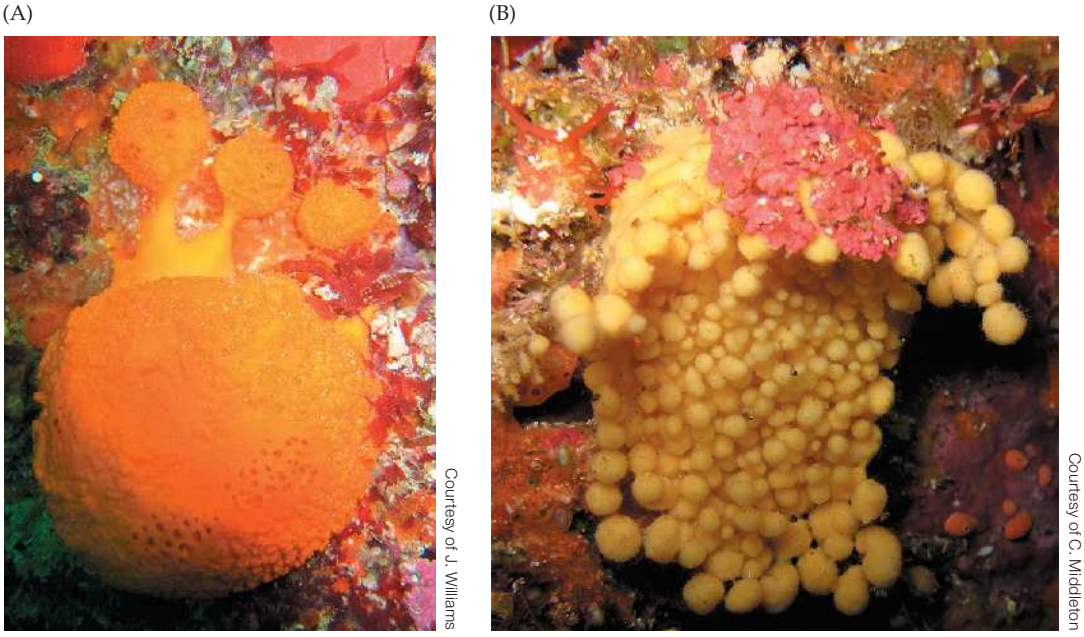

FIGURE 5.14 Budding in three demosponge species from New Zealand. (A) *Tethya burtoni*. (B) *Stelletta* sp. (C) *Tethya bergquistae*.

Asexual reproduction Probably all sponges are capable of regenerating viable adults from fragments. Many species "pinch off" buds of various types (Figure 5.14) by a process of cellular reorganization, whereas in others (especially branching species) pieces of the sponge body are simply broken off by storm surges. Either way, the dislodged pieces fall off and regenerate into new individuals. This regenerative ability was once commonly used by commercial sponge farmers, who propagated their sponges by attaching "cuttings" to submerged rocks or cement blocks. Even today, in Pohnpei (Federated States of Micronesia) sponge farmers string cuttings of *Coscinoderma mathewsi* (Keratosa) on lines in lagoons, growing them into large bath sponges. Additional asexual processes of poriferans include formation of gemmules and reduction bodies, budding, and possibly formation of asexual larvae.

In freshwater sponges, small spherical structures called **gemmules** are produced at the onset of winter (Figure 5.15). These dormant, overwintering bodies are invested with a thick collagenous coating in which supportive siliceous microscleres (**gemmoscleres**) are embedded. Gemmules are highly resistant to both freezing and drying. The gemmules of some species can withstand exposure to –70°C for up to an hour, whereas others experience mortality at –10°C. Experiments suggest that gemmules of at least some species can also withstand seasonal anoxic conditions. Fossil gemmules have been found as far back as the Cretaceous, and these ancient forms are very similar to modern ones. Gemmule morphology is highly specific and is used diagnostically at the family, genus, and even species levels. Three of the six freshwater sponge families do not produce gemmules: Lubomirskiidae and Metschinkowiidae (both known only from the Caspian Sea and Lake Baikal) and Malawispongiidae (from the ancient lakes of Africa's Great Rift Valley, through the Middle East, and to Sulawesi Island in the Indian Ocean).

The formation and eventual growth of gemmules are remarkable examples of poriferan cell totipotency. As winter approaches, archaeocytes aggregate in the mesohyl and undergo rapid mitosis. "Nurse cells," called trophocytes, stream to the archaeocyte mass and are engulfed by phagocytosis. The result is a mass of archaeocytes containing food reserves stored in elaborate vitelline platelets. This entire mass eventually becomes surrounded by a three-layered spongin

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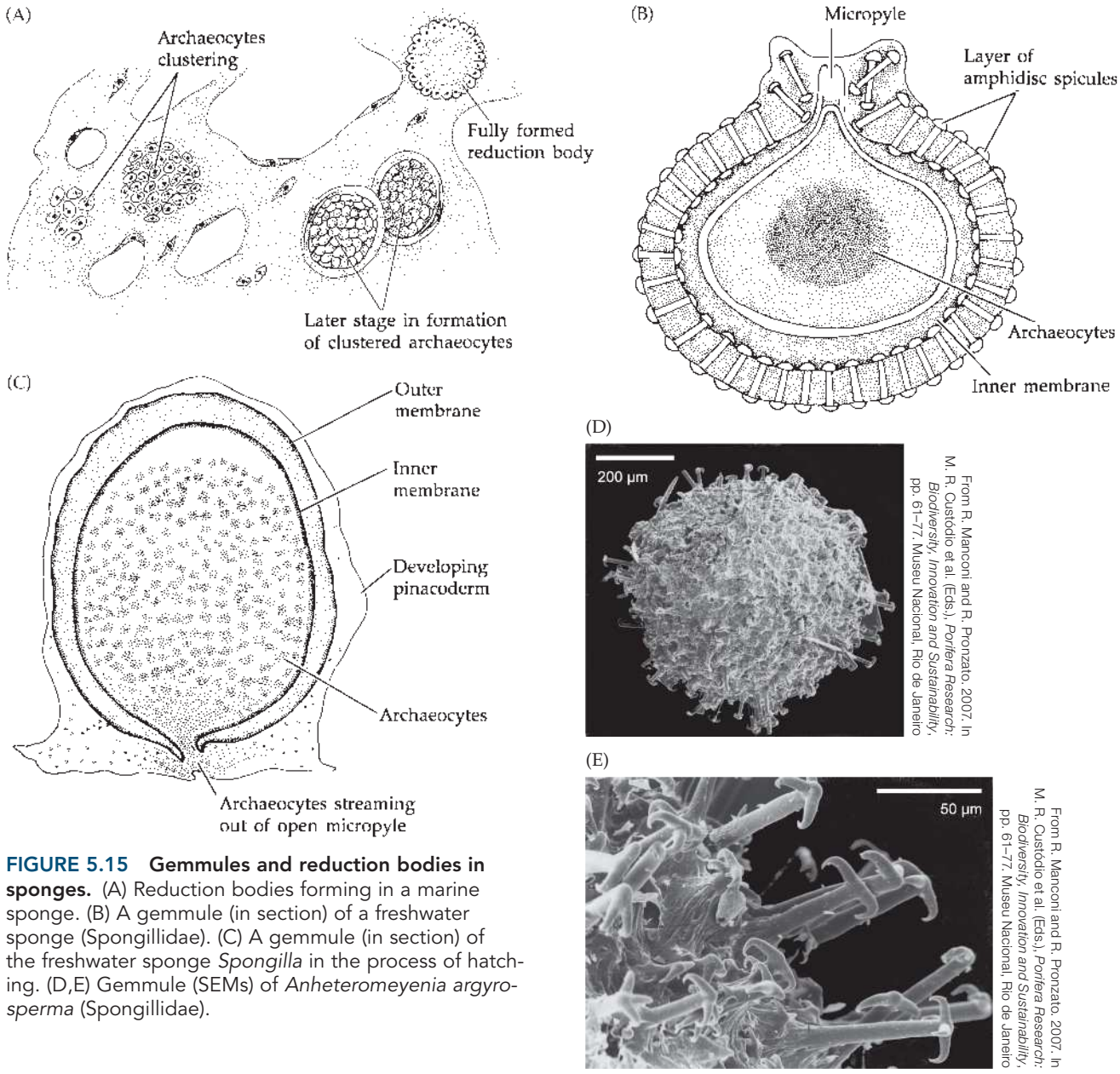

FIGURE 5.15 Gemmules and reduction bodies in sponges. (A) Reduction bodies forming in a marine sponge. (B) A gemmule (in section) of a freshwater sponge (Spongillidae). (C) A gemmule (in section) of the freshwater sponge *Spongilla* in the process of hatching. (D,E) Gemmule (SEMs) of *Anheteromeyenia argyrosperma* (Spongillidae).

covering. Developing gemmoscleres, **amphidisc spicules** (spicules having a stellate disk at each end) in most species, are transported by their parent cells to the growing gemmule and incorporated into the spongin envelope. The final bit of the gemmule to be enclosed by the spongin case is covered only by a single layer of spongin that is devoid of spicules; this single-layered patch is the micropyle. Thus formed, hibernation of the gemmule commences, while the parent sponge usually dies and disintegrates—such species can be thought of as "annuals."

When environmental conditions are again favorable, the micropyle opens and the first archaeocytes begin to flow out (Figure 5.15C). They immediately flow onto the substratum, whereupon they begin to construct a framework of new pinacoderm and choanoderm. The second wave of archaeocytes to leave the gemmule colonizes this framework. In the course of gemmule "hatching," and in an impressive example of cellular totipotency, archaeocytes quickly give rise to every cell type of the adult sponge. Gemmule dormancy appears to be of two types, a quiescence and a true diapause. Quiescence is imposed by generally unfavorable conditions, including low temperatures, and it ends when suitable conditions return. Diapause, on the other hand, typical of annual species, is imposed by a combination of endogenous mechanisms and adverse environmental conditions. The breaking of a diapause state typically requires exposure to very low temperatures for a prescribed number of days. This phenomenal ability of freshwater sponges to develop from quiescent gemmules that

are easy to store in the laboratory has been and continues to be exploited by researchers to understand many biological processes that might otherwise be very difficult to reproduce in the lab.

Many marine species produce asexual reproductive bodies (called **reduction bodies**) that are roughly similar to freshwater gemmules, though much simpler in design and cell wall structure, and these incorporate a variety of amebocytes. And in several genera of marine sponges (e.g., *Haliclona, Chalinula*), asexual reproductive bodies very similar to gemmules are formed, with a spongin coat containing spicules (oxeas).

Sexual processes Sponges express an extreme variability of reproductive and developmental strategies. Many are hermaphroditic; some typically produce eggs and sperm at different times, but others do both simultaneously. Sequential hermaphroditism may take the form of protogyny or protandry, and the sex change may occur only once, or an individual may repeatedly alternate between male and female. In some species, individuals appear to be permanently male or female. In still other species, some individuals are permanently gonochoristic, whereas other individuals in the same population are hermaphroditic. In all cases, cross-fertilization is probably the rule.

Embryogenesis in sponges shares many cardinal features with other Metazoa, including the uniquely metazoan process of programmed cleavage and tissue layering through the process of embryonic morphogenesis that we regard as true gastrulation. However, sponge embryogenesis also expresses great variability. In fact, the range of ontogenetic adaptation among sponges is so broad that it is difficult to generalize about their development. The same cleavage pattern and blastula type may lead to several different larval types, and the same larval types may develop from different cleavage patterns.

Sperm appear to arise primarily from choanocytes or archaeocytes in hexactinellids; eggs from choanocytes or archaeocytes. Spermatogenesis usually occurs in distinct **spermatic cysts** (= **sperm follicles**), which form either when all the cells of a choanocyte chamber are transformed into spermatogonia, or when transformed choanocytes migrate into the mesohyl and aggregate there (Figure 5.16A). During oogenesis, solitary oocytes typically develop in the mesohyl or within cysts surrounded by a layer of follicle cells and, sometimes, nurse cells (**trophocytes**) (Figure 5.16B).

In Demospongiae and Calcarea, mature sperm and (in the case of demosponge oviparity) oocytes are released into the environment through the aquiferous system. The rapid release of sperm from sponge oscula can be highly visible and quite dramatic in large specimens, and such individuals are often referred to as "smoking sponges" (Figure 5.16D). Sperm release may be synchronized in a local population or restricted to certain individuals. Fertilization takes place in the water (oviparity) leading to planktonic larvae, or within the female sponge itself (viviparity). In the viviparous coral-boring sponge *Cliona vermifera*, each zygote inside the sponge body becomes encapsulated; these are eventually released into the water in a series of rapid pulsations of the aquiferous system. In viviparous species, sperm (probably from a different individual) are taken into the aquiferous system and then must cross the cellular barrier of the choanoderm, enter the mesohyl, locate the oocytes, penetrate the follicular barrier, and finally fertilize the egg. In all studied species of the subclass Calcaronea, and some homocleromorphs, this impressive feat involves sperm capture by choanocytes and enclosure in an intracellular vesicle (somewhat like the formation of a "benign food vacuole"). The choanocyte then loses its collar and flagellum and migrates through the mesohyl as an ameboid cell, transporting the sperm to the oocyte (Figure 5.17A). The migratory choanocyte is called a **carrier cell**, or **transfer choanocyte** (Figure 5.17B). Choanocytes no doubt regularly consume and digest the unlucky sperm of different species of sponges and other benthic invertebrates, but by some as yet undescribed recognition mechanism, they respond with a remarkably different behavior to sperm of their own kind. Presumably this process is directed by cell surface proteins/glycoproteins. In the demosponge group Poecilosclerida, another remarkable fertilization mechanism has been proposed for *Crambe crambe*, in which a highly modified sperm cell with an elongate and highly bent body is thought to pierce the female epithelium and swim through the collagenous mesohyl hunting the oocytes. Also in Poecilosclerida, the carnivorous cladorhizids had to adapt their reproduction to the absence of an active aquiferous system. Sperm is therefore encysted in complex structures resembling floating planktonic larvae that are later captured by the mother sponge, whereupon the sperm are released and also swim through the mesohyl looking for the oocytes.

In viviparous species, embryos are typically released as mature swimming larvae, either via the excurrent plumbing of the aquiferous system or

FIGURE 5.16 Sexual reproduction in Demospongiae. ▶ (A) Sperm follicle (in section) containing mature spermatozoa. (B) An oocyte (in section) of *Ephydatia fluviatilis* is phagocytizing a trophocyte. Inside the oocyte is a trophocyte that was recently ingested. (C) The unusual armored "hoplitomella larva" typical of boring sponges in the genus *Thoosa*. The armoring consists of flat plates that are actually highly modified spicules (called "discotrienaenes"). The long fibers emerging from the larva are also modified spicules that presumably aid in flotation. (D) Sperm release from *Xestospongia muta*, Florida. (E) Oocyte release in *Xestospongia muta*, Florida.

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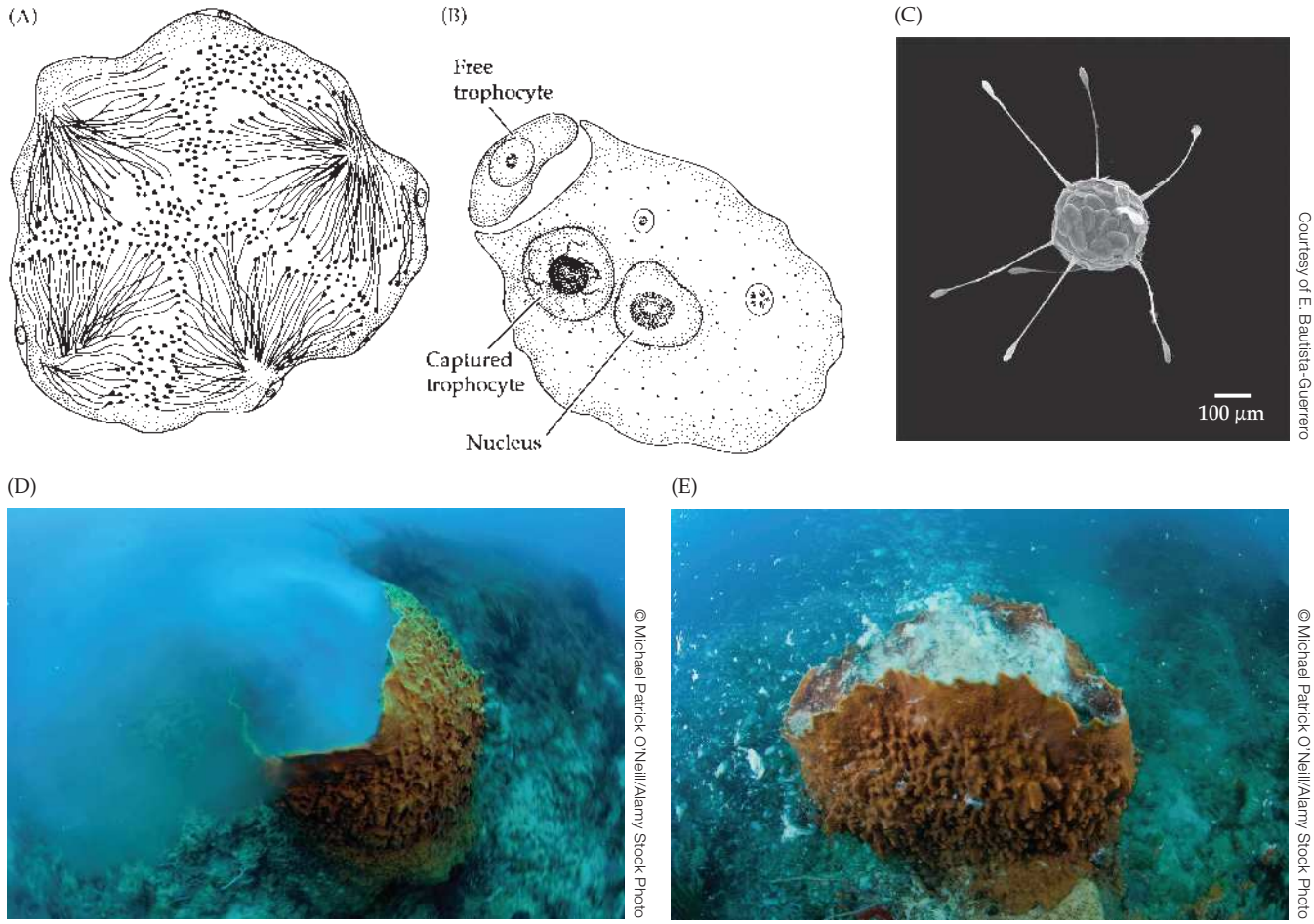

through a rupture in the parent's body wall. Larvae may settle directly, they may swim about for several hours or a few days before settling, or they may simply move about the substratum until ready to attach. In all sponge species that have been studied, the larvae are lecithotrophic. In general, littoral sponges tend to produce planktonic larvae, whereas the larvae of subtidal species tend to settle directly or move about on the ocean floor for a few days before beginning to grow into a new adult individual.

Until very recently, cases of hybridization across different sponge species were unknown, although long suspected. Even though gamete recognition proteins are surely part of the barriers that sponges have in order to prevent cross-fertilization by different species, in very closely related species such

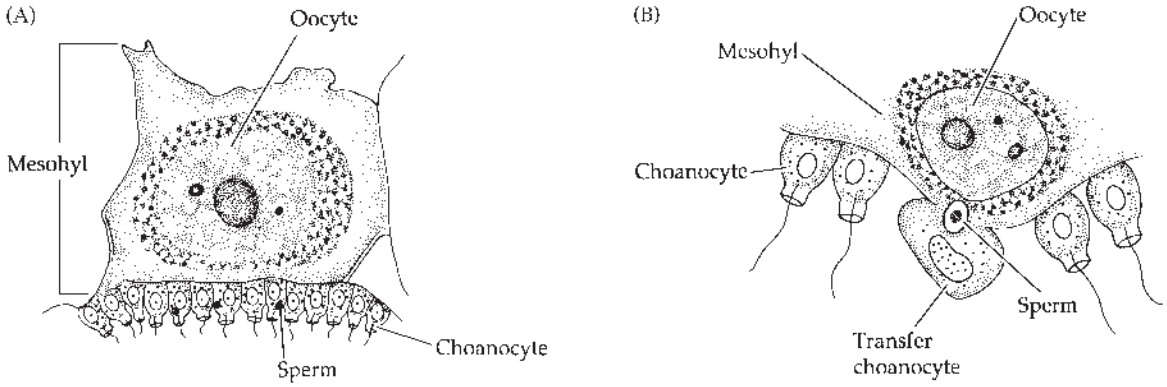

FIGURE 5.17 Fertilization in the calcareous sponge. (A) Sperm are trapped by choanocytes; an egg is lying in the mesohyl adjacent to the choanoderm. (B) A transfer choanocyte gives up its sperm to the egg; note that the egg lies next to the choanoderm and that the choanocyte has lost its flagellum.

barriers perhaps are not powerful enough to avert fusion of gametes. Such was the case of the sister species *Ircinia variabilis* and *I. fasciculata*, where asymmetric gene flow during hybridization was detected predominantly from *I. fasciculata* to *I. variabilis* using several microsatellite markers. Such a phenomenon is unlikely to be an isolated case, and with the advent of high-throughput sequencing, the coming years will probably see a massive flow of evidence proving hybridization across many groups of Porifera.

Embryogenesis and larvae Until fairly recently, larval development in sponges was surrounded by a great deal of mystery, partly because it had not been well studied and partly because huge variation exists. The broad array of blastulation/gastrulation processes and larval types seen in sponges is mind boggling, and many different, but distinct, larval types have been described. In fact, a number of embryogenic pathways occur in sponges that have not been observed in any other Metazoa (e.g., multipolar egression in Homoscleromorpha, polarized delamination in some demosponges). Since the 1990s, significant new work has altered our view of development in this phylum, although many questions still remain. The diversity of sponge developmental pathways is remarkable, and in some instances the same cleavage pattern and blastula type may be characteristic of several different larval types. On the other hand, the same larval type may arise from very different cleavage patterns. For example, the parenchymella larva of *Reniera* (Demospongiae: Haplosclerida) develops as a result of chaotic (seemingly unpatterned) cleavage and multipolar delamination, whereas the parenchymella larva of *Halisarca* (Demospongiae: Halisarcida) arises by polyaxial cleavage and multipolar ingression.

Much of the confusion surrounding sponge embryogenesis has centered on the question of when gastrulation occurs. Many older studies had reported that, during larval development, the external ciliated cells lost their cilia and migrated internally, whereupon they differentiated into adult choanocytes. These studies suggested that larvae formed in this way represented the blastula stage, with later gastrulation coinciding with larval metamorphosis. Such embryonic processes, producing blastular larvae, would make sponges unique among metazoans. However, recent work suggests that this report of migration/inversion of cell layers during larval development was probably a misinterpretation in most if not all cases, and in fact sponge larvae probably represent post-gastrulation-stage individuals (as with most other metazoan larvae). Cell migrations such as these do occur in some poriferans, but only *after* embryogenesis has formed a fully differentiated bilayered or trilayered larva, and such cell movements are thus not related to gastrulation. It now seems that most, if not all, sponge larvae derive from cellular reorganization that can be equated (though not necessarily with step-by-step homologies) with gastrulation processes seen in other metazoans. Thus, gastrulation precedes the larval stage, and probably no sponge larvae represent a blastula stage.[9]

Specialists have long wondered what the original, or ancestral, cleavage pattern in sponges (and

[9]The question of whether or not, and when, gastrulation occurs in sponges has long been debated. In fact, it depends on how one defines "gastrulation." Some workers define gastrulation simply as the epithelialization of embryos, thus clearly indicating sponges undergo gastrulation. Other workers define it as the embryogenic process through which metazoan ectoderm and endoderm, and a gut, are derived; but, of course, sponges have no guts and their inner and outer cell layers appear not to be homologous with the epithelia of higher metazoans, and on this basis one could argue that gastrulation does not occur in Porifera. Spongologists following this line of logic refer to "embryonic morphogenesis" rather than "gastrulation." Still others have defined poriferan gastrulation as the process of metamorphosis from larva to adult, when the choanocyte chambers are formed. In this book, we define gastrulation (in the general sense) as the reorganization of cells of the blastula to form multiple embryonic germ layers—the tissues upon which all subsequent development depends. Gastrulation, in most cases, creates the separation of those cells that must interact directly with the environment, and those cells that process materials taken in from the environment. Thus, gastrulation is a keystone, defining feature of the Metazoa. By our definition then, gastrulation in sponges takes place during formation of the larva, when the first germ layers are laid down, regardless of the process. It is worth noting, however, that the absence of solid cell–cell adhesion, and the ability of sponge cells to become mobile, might argue against true gastrulation in sponges because there is not necessarily conservation of cells in specific germ layers.

Interestingly, the term "gastrulation" derives from the name given by Ernst Haeckel (in 1872) to a stage in the development of calcareous sponges; in his **gastrula** stage, a ciliated egg-shaped larva settled to the benthos and, according to Haeckel, formed a "mouth and a gut." Haeckel claimed that the gastrula stage could be found in the development of all animals and thus represents the recapitulation of the ancestral metazoan, a hypothetical ancestor he called the **gastraea**—a diploblastic animal with a ciliated gut. This recapitulation, he argued, was proof that the Metazoa are monophyletic. Until recently, only one other observation of Haeckel's "gastrula" stage in calcareous sponges had been made, by the German philosopher and biologist Ernst Hammer, in 1908. And yet, "gastrulation by invagination" has been widely conceived, for over 100 years, to be the ancestral mode of germ layer formation in animals. The conundrum, of course, is that we now know sponges don't form a typical metazoan gut, so the transient cavity formed by invagination during settlement cannot represent a future gut. The outstanding sponge biologist Sally Leys has recently shown that what Haeckel (and later Hammer) witnessed was a very brief transitory stage in which the anterior cells of a settled calcareous sponge larva invaginate into the posterior half of the larva. However, the "invagination hole" closes completely and it is not until some days later that the sponge forms an osculum (not a gut!) at its apical pole. Hence, there is no reason to assume that this transitory "gastrula" stage is a precursor for formation of a gut via invagination in higher animals. Further, it is the earlier formation of the two cellular regions of the larva that comprises the actual gastrulation event (whereas metamorphosis upon settlement involves the reorganization of these already differentiated regions).

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Metazoa) might be—most researchers would probably vote for radial cleavage, and indeed this form of cleavage is seen in many demosponges, although it is not known from any other sponge class. At least three other forms of holoblastic cleavage have been described: chaotic (also known as "anarchic") cleavage, table palintomy, and polyaxial cleavage. **Chaotic cleavage** (seemingly random, or unpatterned) is characteristic of many demosponges. In **table palintomy**, the cleavage furrows pass obliquely relative to the egg's animal–vegetal axis; this form of cleavage occurs in some calcareous sponges (Calcaronea). It is also reminiscent of the green algal genus *Volvox* and several other colonial protists. However, the Calcaronea also undergo an utterly unique process of inversion of the blastula, and this has led some workers to suggest that palintomy is an aberrant cleavage process. **Polyaxial cleavage** is characteristic of the genus *Halisarca* and possibly also the Calcinea (Calcarea). It is characterized by cleavage furrows that form perpendicular to the surface of the embryo during the transition from the 8- to the 16-cell stage, with axes of symmetry that radiate at certain angles from the center of the embryo; however, after the 16-cell stage, division becomes chaotic.

Although sponge embryogenesis is highly variable, all species go through an ordered sequence of blastomere divisions and movements leading to morphogenesis of larval tissue structures (which we consider to be gastrulation) and formation of a larval axis that is often referred to as an anterior–posterior axis. Spongiologists have so far recognized at least seven types of sexual development in sponges, though continued research may reveal even more. These seven types are recognized by their resultant larval forms: (1) trichimella (Hexactinellida), (2) calciblastula (Calcarea: Calcinea), (3) amphiblastula (Calcarea: Calcaronea), (4) cinctoblastula (Homoscleromorpha), (5) disphaerula (Demospongiae: Halisarcidae), (6) direct development (Demospongiae, Tetractinellida, *Tetilla*), and (7) parenchymella (most Demospongiae). These seven developmental pathways are depicted in Figure 5.18 and described below. The anterior flagellated end of swimming sponge larvae (e.g., amphiblastula, cinctoblastula, parenchymella; Figure 5.19) putatively corresponds to the animal pole of other metazoan larvae, and it is this larval region that gives rise to the internal choanoderm, while ameboid cells at the posterior end generate the outer layer (pinacoderm) of the adult sponge.

Homologues of metazoan developmental genes are just beginning to be described from Porifera, but many more should be revealed soon with the recent sequencing of "complete genomes" for two heteroscleromorph demosponges, *Amphimedon queenslandica* and *Ephydatia muelleri*. Already, a diversity of metazoan homeobox genes have been identified in sponges, and in *A. queenslandica* a broad range of transcription factor gene classes, many of which appear to be metazoan specific, are expressed during development. However, the possible homologies of adult sponge tissues with metazoan endoderm and ectoderm remain quite uncertain, and for this reason the terms "gastrodermis" and "epidermis" are used for sponges to avoid implications of embryological homology (and the inner mesohyl layer certainly does not appear to be homologous with the mesoderm of triploblastic Metazoa). This inability to directly homologize sponge tissues with those of other Metazoa is one of the reasons some workers reject use of the term "gastrulation" for Porifera. With the exception of the homoscleromorphs, typical epithelial anatomy (with underlying basal lamina) appears to be lacking in sponges. The ability of pinacocytes to migrate into the mesohyl and convert to other cell types has also argued against considering this layer to be true ectodermally derived epithelium (the motility of pinacocytes has been ascribed to the general absence of specialized desmosomal junctions among these cells).

Because there is so much variation in sponge developmental processes, each class is reviewed separately here.

Calcarea So far as is known, all calcareous sponges are viviparous. In the subclass Calcinea, oocytes develop within the mesohyl and grow in size (by phagocytizing neighboring amebocytes). Embryos also develop in the mesohyl, and cleavage is total and equal to produce a hollow blastula larva (coeloblastula). The coeloblastula of some species has two types of cells: ciliated outer cells, and one or two posterior granular cells. After larval release, and just prior to larval attachment to the substrate, in some species, some cells lose their cilia and ingress into the blastocoel via ingression.

In the subclass Calcaronea, oocytes differentiate from choanocytes and move into the mesohyl. After a period of growth, they migrate to the periphery of the sponge. Cleavage is total and equal, and the first three divisions are meridional. The fourth division (at least in *Leucosolenia*) is oblique, almost exactly like the cleavage in the colonial green alga *Volvox*—a type of cleavage referred to as table palintomy (see above). The resulting embryo is a cup-shaped blastula, with a small opening at the side closest to the choanoderm. While most of the cells continue to cleave in the same manner, forming a single-layered epithelium, a few that lie directly under the choanoderm do not; these remain much larger than the other cells, with their cytoplasm filled with large yolk granules. The most unusual feature of the calcaronean embryo is that cilia, which

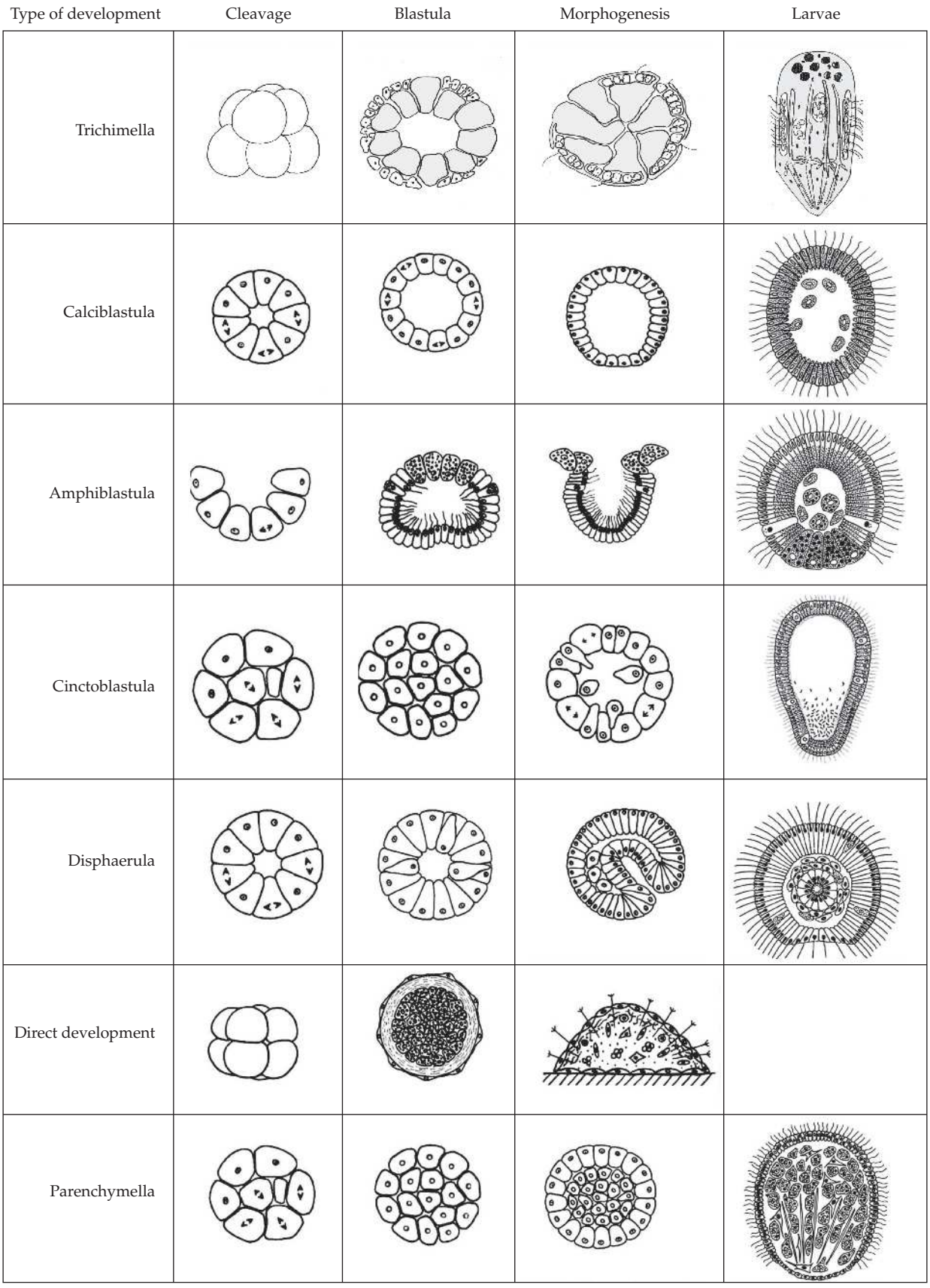

FIGURE 5.18 **Schematic diagram summarizing the various types of development and their resultant larvae in different groups of Porifera; see text for details.**

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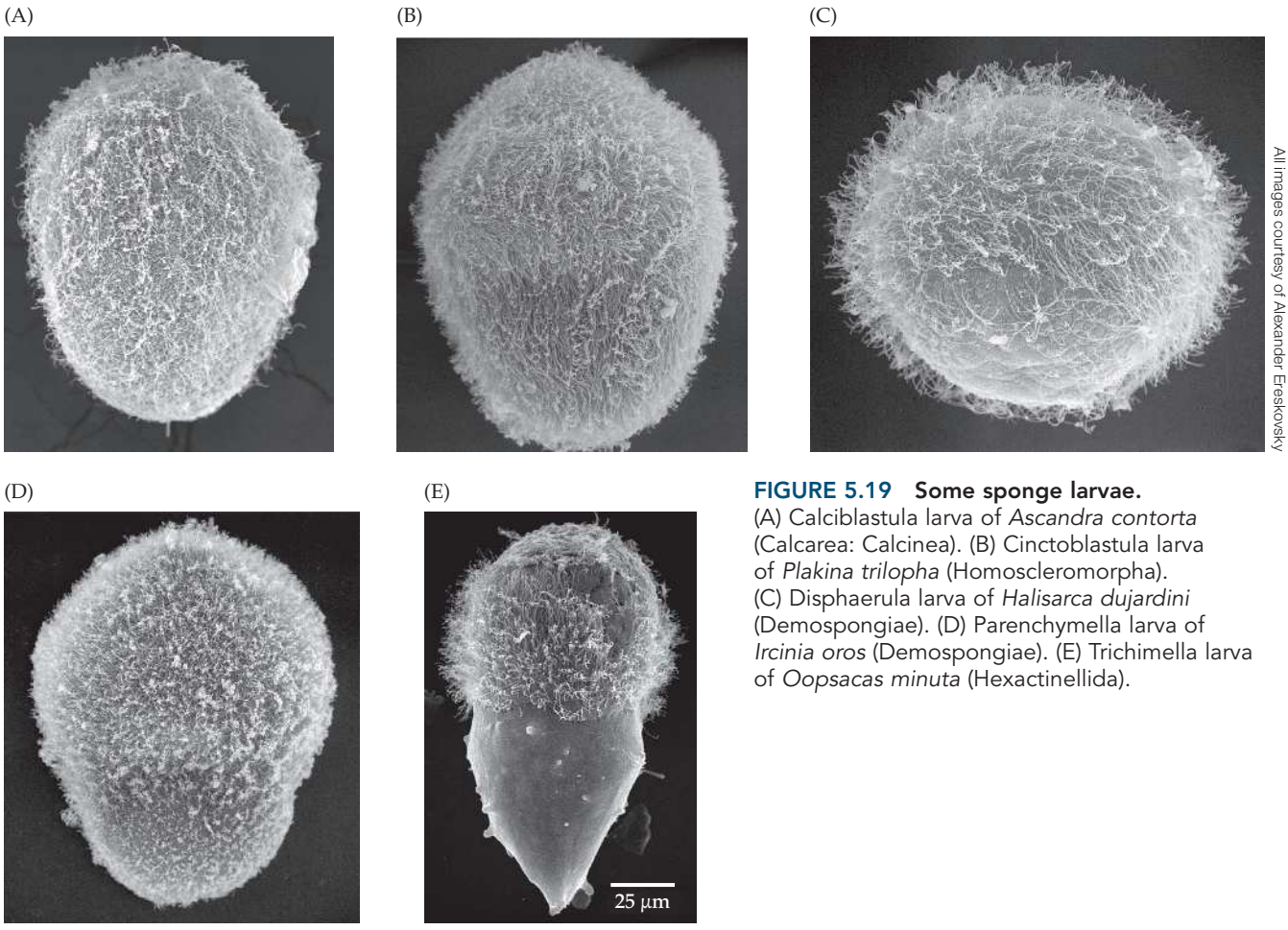

FIGURE 5.19 Some sponge larvae. (A) Calciblastula larva of *Ascandra contorta* (Calcarea: Calcinea). (B) Cinctoblastula larva of *Plakina trilopha* (Homoscleromorpha). (C) Disphaerula larva of *Halisarca dujardini* (Demospongiae). (D) Parenchymella larva of *Ircinia oros* (Demospongiae). (E) Trichimella larva of *Oopsacas minuta* (Hexactinellida).

differentiate on the micromeres, project into the center of the blastocoel (inverted, compared with those in all other sponge embryos); this stage is called a **stomoblastula** (Figure 5.20B–D). To reach the final orientation, the embryo actually turns itself inside out. To do this, the ciliated blastomeres move upwards and through the opening as a "single epithelium," into the choanocyte chamber (much as a bag is turned inside out). The resulting larva is an **amphiblastula** (Figure 5.20E), composed of anterior ciliated cells, posterior granular cells, and inner nutritive amebocytes.

The free-swimming amphiblastula larva of *Sycon* (class Calcaronea) exits the parent sponge via the osculum and settles within 12 hours, attaching by its cilia, which are thought to be adhesive (probably via glycoproteins on the cell surface). In some cases, the larva settles on its anterior end, on the hole left from the earlier invagination event. The hole is thus unrelated to the future osculum (nor is it a primitive "mouth" of any kind); it is, in fact, engulfed by the newly forming epithelium of the metamorphosing larva. Thus, the transient cavity that is formed by invagination is not the future osculum of the sponge, as Ernst Haeckel long ago intimated, and this invagination does not represent gastrulation. Once settled, the larva quickly undergoes metamorphosis into a juvenile (sexually immature) sponge.[10] During metamorphosis, the anterior cells lose their cilia and migrate in to form an inner cell mass; some of these cells differentiate into choanocytes, while others remain ameboid. Metamorphosis of this larva seems to involve a rapid proliferation of the "macromeres" to form pinacoderm that overgrows the flagellated hemisphere. The flagellated cells pocket inward to form a chamber lined with cells destined to become choanocytes (Figure 5.20F). An osculum breaks through, and the tiny asconoid-like sponge becomes capable of circulating water and feeding. This initial functional stage is called an **olynthus** (Figure 5.4A). After further growth, it will become an asconoid, syconoid, or leuconoid adult, depending upon the species.

Hexactinellida Because reproductive individuals in this class are rarely encountered, and most species live in deep water, almost all of our knowledge on

[10]This is the stage that Ernst Haeckel focused upon as the root of gastrulation. Haeckel, however, mistook the amphiblastula for a bilayered planula larva and claimed a number of observations that have never been repeated. It is likely that the microscopical tools that Haeckel had were simply insufficient to resolve the rapidly unfolding changes during embryogenesis and metamorphosis in *Sycon*.

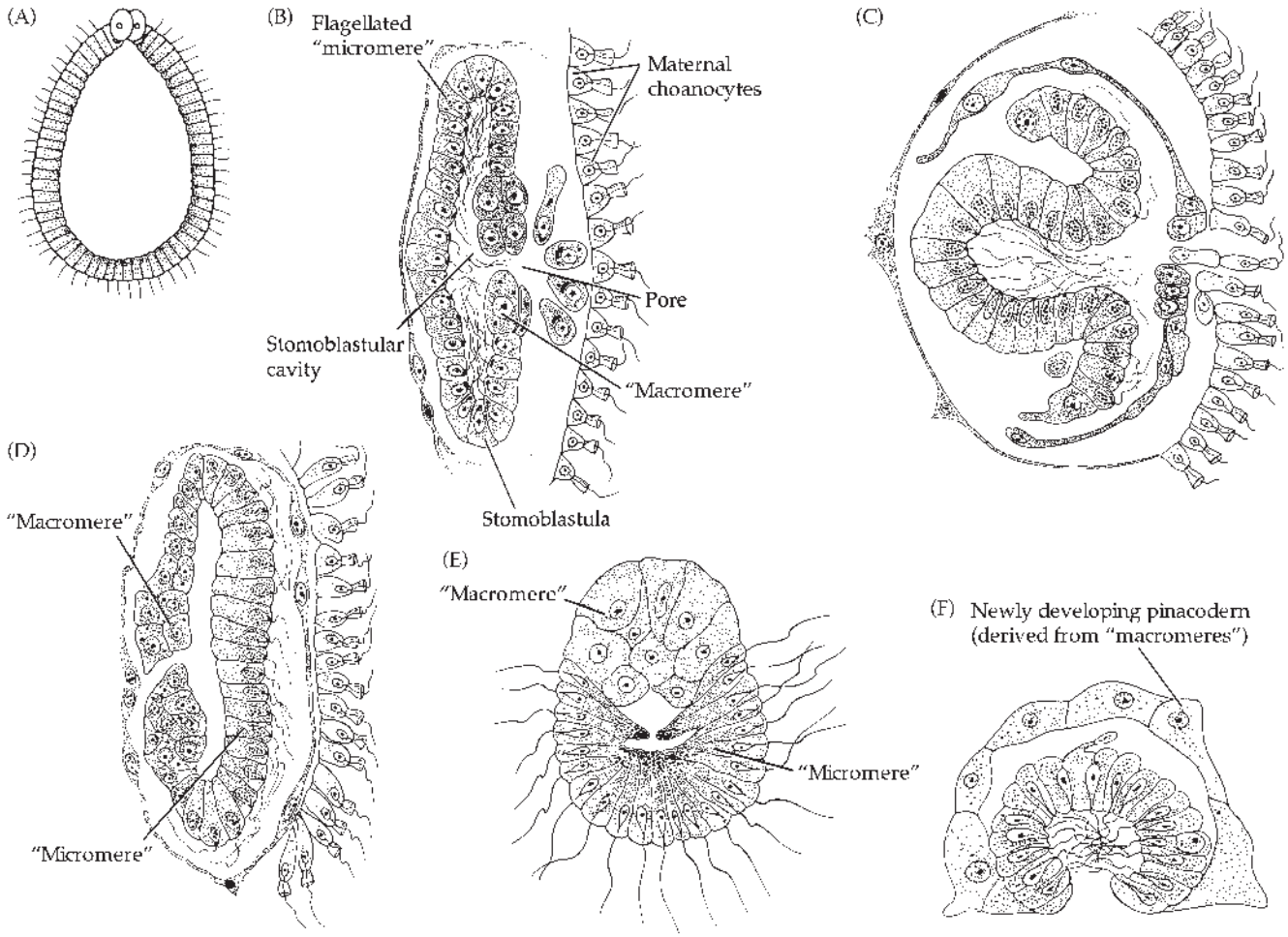

FIGURE 5.20 "Coeloblastula" and amphiblastula larvae (in section). (A) Typical "coeloblastula" larva with its posterior "macromeres." (B–D) During the remarkable process of inversion in *Sycon*, the stomoblastula turns itself inside out to form an amphiblastula larva with externally directed flagella. (E) A typical amphiblastula larva (*Sycon*). (F) Settled young sponge (*Sycon*) after invagination of flagellated cells.

development comes from a few small cave-dwelling species that are accessible by scuba. Although based upon studies of only a few species, a general overview of glass sponge development is as follows. Hexactinellids are probably all viviparous. Gametes arise from groups of archaeocytes that are suspended within the trabecular reticulum (since choanocytes are anucleate). Each archaeocyte cluster is called a **congery**, and all the cells are connected by cytoplasmic bridges (although mature oocytes are independent cells). It is not yet known how sperm find oocytes or how fertilization occurs. Cleavage to the 32-cell stage is total, equal, and asynchronous. The first cleavage is generally meridional, and the second either equatorial or rotational. By the 16- and 32-cell stages, the embryo is a hollow blastula. The following cleavages are unequal, producing smaller micromeres that lie on the outside and larger yolk-rich macromeres on the inside. The macromeres divide unequally, gradually filling the center of the blastocoel, and eventually they envelop the micromeres with massive filopodia. Uniquely, these cells then fuse to form a single multinucleated giant tissue, the new trabecular syncytium, which completely envelops the micromeres. In this way, the embryo gains its outer epithelium. The formation of micromeres was originally considered to represent gastrulation by cellular delamination. However, the epithelialization of the larva—the enveloping of the micromeres by the incipient trabecular reticulum—is probably better viewed as the true gastrulation event. The fully differentiated hexactinellid larva is a **trichimella** (Figure 5.18). The major tissue of the larva is the syncytial trabecular reticulum, continuous throughout the larva, including its surface "epithelium." After swimming for one to several days, the larva settles on its anterior, lipid-filled pole and undergoes metamorphosis. The flagellated cells of the trichimella are multiciliated, a condition unique among sponges.

Demospongiae The class Demospongiae is large and diverse—without an easily characterized or uniform developmental pattern. Detailed recent embryological

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studies have been accomplished for only a dozen or so of the 7,600 described species. Both viviparity and oviparity occur in this class. Development is highly varied among the orders, families, and genera and, in some cases, even within single species. Spermatocytes may develop in special cysts within the mesohyl, and in most demosponges these derive from choanocytes. Oocytes may be isolecithal or telolecithal, and they usually arise from archaeocytes in the mesohyl—although in the family Lubomirskiidae (freshwater sponges in Lake Baikal) they are thought to derive from choanocytes—and they may be accompanied by yolk-rich nurse cells, or follicular cells, that form a thick coating around them, the yolk being incorporated into the cytoplasm of the oocytes. Spawning of eggs and sperm has been linked to lunar cycles in some species, as in many other invertebrates. Fertilization is usually external, either in the water column or in the excurrent canals where eggs are released.

Cleavage appears to be complete, equal or unequal, often chaotic, and (at least in some species) produces micromeres and macromeres. Micromeres develop a cilium, and eventually both macromeres and micromeres segregate out until the ciliated micromeres cover the periphery of the embryo (a process termed multipolar delamination). At this point, the embryo may be a solid blastula (stereoblastula) or a coeloblastula (although the central cavity may be filled with bacteriocytes and small granular cells of the follicle layer). Many species appear to produce parenchymella larvae that are polarized and possess a ciliated outer layer. Settlement seems to occur quickly, and in some species the eggs are released in a mucus mass and a planktonic larval stage is absent (larvae develop upon the substratum near the parent sponge).

Among the Demospongiae, the genus *Halisarca* stands out in several ways. It completely lacks a skeleton and has mixed developmental pathways (that have been studied for over 100 years). Most or all species are gonochoristic and viviparous. Spermatocytes originate from choanocytes. Oocytes also derive from choanocytes, and during vitellogenesis symbiotic microbes characteristic of the mesohyl of adults are incorporated into the oocyte. Cleavage is total and equal, producing a hollow blastula. In many cases, cells invade the blastocoel by both multipolar and unipolar ingression. Cilia appear on the external cells of the 32- to 64-cell-stage blastula, while internal cells differentiate to become archaeocytes. At this point, things get strange, because three very different kinds of larvae can now develop, even within the same individual parent sponge. The first is a coeloblastula, with a single layer of surface cells surrounding a small lumen. The second is a parenchymella that has an outer layer surrounding an inner cell mass of ameboid cells. The third has two layers of epithelial cells, one external and the other internal, that line a small lumen; this type of larva is called a disphaerula. All three types are polarized by external patterns of ciliation, and all swim by rotating in a left-handed direction.

Homoscleromorpha The eggs of homoscleromorphs are isolecithal, rich in yolk inclusions, and completely surrounded by a follicle formed of parental endopinacocytes and, once they are fertilized, symbiotic bacteria. Cleavage is holoblastic and equal. During the first divisions, bacteria colonize the cleavage furrows and are incorporated into the cleaving embryo. At the third division, cleavage becomes irregular and asynchronous, and it proceeds to form a solid morula of undifferentiated yolk-rich blastomeres. At about the 64-cell stage, the outer layer of the morula begins to differentiate. The blastomeres close to the surface divide more actively, while the internal cells migrate to the periphery of the embryo to gradually form a monolayered larva with a central cavity that contains symbiotic bacteria and maternally secreted cells. The resulting embryo is a hollow coeloblastula, and as the outer layer differentiates, the cells grow cilia. So far as is known, the centrifugal migration of cells from the center to the periphery of the morula, to form the coeloblastula, is unique not only within Porifera but for all of Metazoa. This unusual process has been termed **multipolar egression**. The ciliated cells of the outermost layer become elongate (columnar) and are closely linked by desmosome-like junctions.

Loose collagen fibrils fill most of the internal cavity as the coeloblastula matures into a larva. However, immediately below the outermost cell layer there develops a tough extracellular matrix of consolidated collagen fibrils, and beneath that there is a second layer of more loosely consolidated collagen fibrils. These two layers of collagen constitute a basement membrane similar to the one found below the pinacoderm and choanoderm of adult homoscleromorphs. (A similar network of extracellular matrix has been described from beneath the larval epithelium of one demosponge larva.) The outermost cell layer of homoscleromorph larvae is a true epithelium, homologous with that seen in adult sponges and in other Metazoa, its cells being columnar and producing a basement membrane/basal lamina.

As development continues, the central cavity is progressively filled by collagen fibrils (along with the symbiotic bacteria) and the larval epithelium becomes regionally differentiated, giving the larva a polarity that most regard as truly anterior–posterior. The homoscleromorph larva was originally called an "amphiblastula" because it was thought to possess two fairly distinct regions, one ciliated and the other not. However, morphogenesis in sponges of this group is not at all like that of sponges in the Calcaronea (a group for which the amphiblastula larva is characteristic), and the larvae are in fact completely ciliated. Thus it was suggested that the homoscleromorph larva be called a **cinctoblastula**, a

term which more accurately describes its distinctive feature of paracrystalline intranuclear inclusions that form a belt around the posterior end. The free-swimming cinctoblastula larva is ovoid or pear shaped, wider at the anterior end than the posterior pole, and the entire surface is ciliated. All larvae that have been observed swim with a left-handed rotation.

Some Additional Aspects of Sponge Biology

Some basic sponge ecology has been presented in the previous sections of this chapter. However, because sponges play such important roles in so many marine habitats, and because they are intrinsically interesting in their phylogenetic "primitiveness," we add here some additional aspects of their natural history.

Distribution and Ecology

Certain distributional patterns are evident among the four classes of sponges. Calcareous sponges (and coralline demosponges) are far more abundant in shallow waters (less than 200 m), although they are not uncommon at slope depths, and a few species (particularly in the genus *Sycon*; Figure 5.1B) have even been reported from depths to 3,800 m. Hexactinellids, which were common in shallow seas of past eras, are now largely restricted to depths below 200 m, except in extremely cold environments (such as western Canada and Alaska, New Zealand, and Antarctica), where some species occur in shallow waters. Demosponges live at all depths, whereas homoscleromorphs occur from the continental shelf to around 1,000 m depth. Calcareous and homoscleromorph sponges may be restricted largely to shallow waters because they require a firm substratum for attachment. On the other hand, many demosponges and hexactinellids grow on soft sediments, attaching by means of rootlike spicule tufts or mats. The coralline sponges, once a predominant group on shallow tropical reefs, are now largely restricted to shaded crevices and caves, to subreef depths, or to warm-temperate waters where their potential competitors (the hermatypic corals) cannot grow (Figure 5.1L). They are thought to be relicts of major reef-constructing sponge clades of Mesozoic and Paleozoic seas.

Although sponges are very sensitive to suspended sediment in their environment, they seem to be quite resistant to hydrocarbon and heavy metal contamination. Many species can actually accumulate these contaminants without apparent harm, and these may be seen, for example, in the ferric granules on the spongin skeleton of fibrous bath sponges from intertidal regions. The capacity of certain species to accumulate metals at far higher levels than that of the ambient environment has been suggested as a possible defense mechanism (antipredation, antifouling). Detergents also do not appear to affect many sponges and, in fact, may even serve as a source of nutrition for these amazingly adaptable animals.

Sponges are the dominant animals in a great many benthic marine habitats. Most rocky littoral regions harbor enormous numbers of sponges, and they often occur in vast numbers (and large sizes) around Antarctica. Although many animals prey on sponges, the amount of serious damage they do is usually slight. Some tropical fishes (e.g., some angelfish) and turtles (e.g., hawksbill turtles) crop certain kinds of sponges, a number of sea stars and shelled gastropods are sponge predators, and smaller predators (mainly heterobranch gastropods that closely match the prey sponge's color) consume limited amounts of living sponge material in both warm and temperate seas. Overall, however, sponges appear to be very stable and long-lived animals, perhaps in part due to their spicules and toxic or distasteful compounds that discourage would-be predators.

Anthropogenic pressures affect sponges in many ways, including by reducing their habitat, warming seawater to temperatures that allow sponge pathogens to thrive, and reducing sponge populations by overfishing (in the North Atlantic, fishing-ground sponge bycatch can sometimes be many tons). Studies of the impact of global warming on temperate and Antarctic sponges have found high thermal tolerances in their transcriptional (molecular) responses and remarkable acclimation patterns after relatively short exposures to high temperatures. Perhaps their relatively high tolerance to global warming, compared with that of corals, is one thing giving tropical sponges an advantage in the reef ecosystems of the Caribbean, where they are now largely dominant. We may be approaching a scenario where we must call them sponge reefs!

Biochemical Agents

Seashore explorers and scuba divers quickly notice that sponges are just about everywhere. Most grow on open rock or occasionally mud surfaces, where they are obviously exposed to potential predation. Clearly, some mechanism(s) must be working to prevent these animals from being cropped excessively by predators. The primary defense mechanisms in sponges are mechanical (skeletal structures) and biochemical. Studies have also shown that sponges manufacture a surprisingly broad spectrum of biotoxins, some of which are quite potent. A few, such as the heteroscleromorphs, *Tedania* and *Neofibularia*, can cause painful skin rashes in humans. Whether these toxins are produced by the sponges or their symbiotic bacteria is still a topic of much research.

Research in sponge biochemistry has also revealed the widespread occurrence of antimicrobial agents in sponges. Sponges appear to use "chemical warfare," not only to reduce predation and prevent infections,

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but also to compete for space with other invertebrates such as bryozoans, ascidians, and even other sponges. Different species have evolved chemicals (allelochemicals) that may be species-specific deterrents or actually lethal weapons for use against competing sessile and encrusting organisms. For example, the coral-inhabiting sponge *Siphonodictyon* releases a toxic chemical into the mucus exuded from its oscula, thus preventing potential crowding by maintaining a zone of dead coral polyps around each osculum (Figure 5.21).

Many of the chemicals produced by sponges and other marine invertebrates are being closely studied by natural product chemists and biologists interested in their potential as pharmaceutical agents. Compounds with respiratory, cardiovascular, gastrointestinal, anti-inflammatory, antitumor, cytotoxic, antiviral, antihelminthic, and antibiotic activities have been identified from many marine sponges. One study found that 87% of the temperate sponges and 58% of the tropical species examined in New Zealand produced extracts with specific antibacterial activity. One New Zealand sponge (*Halichondria moorei*: Heteroscleromorpha) has long been used by native Maoris to promote wound healing and was recently discovered to contain remarkably high concentrations (10% of the sponge dry weight) of the potent anti-inflammatory agent potassium fluorosilicate. In the 1950s, compounds belonging to a class of chemicals called arabinosides, which are active against viruses, were found in the tropical sponge *Tectitethya crypta* (Heteroscleromorpha). This led to the development of a number of important drugs that are in use today, including cytarabine, sold under the trade names Ara-C and Cytosar-U. Cytosar-U was approved for treatment of certain leukemias in 1969, making it the first such approved marine-derived drug for use in cancer chemotherapy. Other drugs derived from natural products in *T. crypta* include AZT (zidovudine), manufactured under the trade name Retrovir by the drug company GlaxoSmithKline, which was the first drug licensed for the treatment of HIV infection, and Ara-A, an antiviral compound often prescribed for treating herpes.

Some sponges, including the western Pacific species *Luffariella variabilis*, produce a remarkable terpenoid compound called manoalide that not only is an extremely powerful antibacterial compound, but also acts as both an analgesic and anti-inflammatory agent. Sponges of the genera *Halichondria* and *Pandaros* are known to produce potent antitumor compounds belonging to a group of chemicals called halichondrins. For example, eribulin mesylate (sold under the trade name Halaven), a powerful treatment for metastatic breast cancer, is a synthetic analogue of halichondrin B, a product isolated from the marine sponge *Halichondria okadai*.

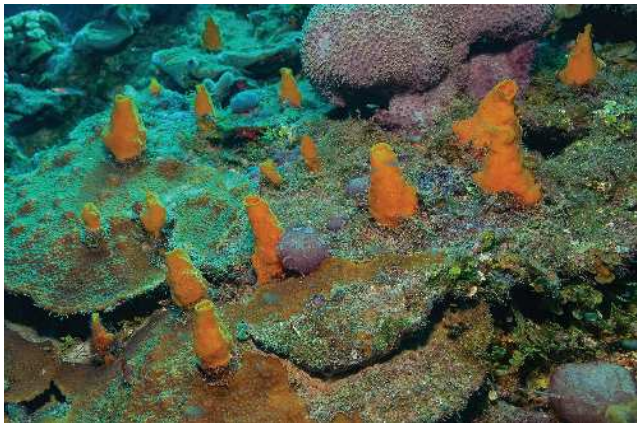

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FIGURE 5.21 ***Siphonodictyon coralliphagum* infests the hermatypic coral *Siderastrea siderea* on a Caribbean reef.** Note the "dead zone" between the oscular chimneys of the sponge and the coral polyps.

Growth Rates

Little is known regarding growth rates in sponges, but rates appear to vary widely among species. Some species are annuals (especially small-bodied calcareous sponges of colder waters); hence, they grow from larvae or reduction bodies to reproductive adulthood in a matter of months. Most, however, appear to be perennials and often grow so slowly that almost no change can be seen from one year to the next; this growth pattern is especially true of tropical and polar demosponges. Until recently, age approximations of perennial species ranged from 20 to 100 years. However, research on the Caribbean giant barrel sponge *Xestospongia muta*, which can exceed 2 m in height, suggests that this species might be capable of living more than 2,000 years. Radiocarbon dating of several hexactinellid *Rossella* species from Antarctica recently revealed growth rates of about 3 mm per year, aging the sponges at about 440 years old. Even more impressive, the western Pacific species *Monorhaphis chuni* has giant SiO_2 spicules that can reach lengths of nearly 3 m, representing the largest biogenic silica structures in the animal kingdom; the life-span of the spicule is estimated to be 11,000 (±3,000) years, making this the longest-lived animal species on Earth!

Some sponges are capable of very rapid growth, and they regularly overgrow neighboring flora and fauna. For example, the tropical encrusting sponge *Terpios* (Heteroscleromorpha) is known to overgrow both living and nonliving substrata. In Guam, this sponge grows at rates averaging 23 mm per month, over almost every live coral species in the area as well as over hydrocorals, mollusc shells, and many algae. Experiments have shown that *Terpios* is toxic to living corals and, presumably, to many other animals. However, in most cases of observed sponge overgrowth of living corals, the corals have been stressed (by temperature, sediment, pollution) or damaged and presumably weakened.

Still another physiological trick of some sponges is the ability to rapidly produce copious amounts of

mucus when disturbed. On the west coast of North America, the beautiful red-orange *Antho* (*Plocamia*) *karykina* (Heteroscleromorpha) covers itself with a thick layer of mucus when injured or disturbed. Yet the little red sea slug *Rostanga pulchra* has evolved the ability to live and feed inconspicuously on this and other red-colored sponges, and it even lays its camouflaged red egg masses on the sponge's exposed surface without eliciting the mucous reaction.

Symbioses

Symbiosis is common among sponges of all kinds. It would be difficult to find a marine sponge that is not utilized by at least some smaller invertebrates and often by fishes (e.g., gobies and blennies) as refuge. The porous nature of sponges makes them ideally suited for habitation by opportunistic crustaceans, ophiuroids, molluscs (e.g., scallops, mussels), and various worms. A single specimen of *Spheciospongia vesparium* from Florida marine waters was found to have over 16,000 alpheid shrimps living in it, a study from the Gulf of California found nearly 100 different species of plants and animals on and in a 15 × 15 cm *Geodia hentscheli*, and an examination of eight sponge species off the coast of South Carolina and Georgia (at depths of 18 to 875 m) recorded 236 symbiotic invertebrate species. The last study concluded that sponge-symbiont assemblages can constitute legitimate ecological communities harboring complete food webs as well as gravid and juvenile individuals. Even freshwater sponges host abundant symbionts, and many freshwater invertebrate taxa have been recorded with sponges (e.g., Hydrozoa, Nematoda, Annelida, Gastropoda, Bivalvia, Isopoda, Amphipoda, Ostracoda, Copepoda, Hydrachnidia, Bryozoa).

Most symbionts of sponges use their hosts only for space and protection, but some rely on the sponge's water current for a supply of suspended food particles. A classic example of this phenomenon is the male-female pair of shrimp (*Spongicola*) that inhabit the globally distributed, deep-water hexactinellid sponges known as Venus's flower baskets (*Euplectella*; Figure 5.1O,P). The two shrimp enter the sponge when they are young, only to become trapped in their host's glasslike case as they grow too large to escape. Here they spend their lives as "prisoners of love." Appropriately, this sponge (with its guests) is a traditional wedding gift in Japan—a symbol of the lifetime bond between two partners. Also in Japan's waters, the sponge *Spongia* sp. uses the powerful water current produced by the filtration system of its endosymbiotic oyster, *Vulsella vulsella*, to enhance the incurrent flow for its own filtration.

Other symbiotic relationships with sponges are also common. Some snails and clams characteristically have specific sponges encrusting their shells, and many species of crabs (hermits and brachyurans) collect certain sponges and cultivate them on their shell or carapace (Figure 5.1M). Demosponges, such as *Suberites*, are commonly involved in these commensalistic relationships. The sponge serves primarily as protective camouflage for its host, and it perhaps benefits by being carried about to new areas. The sponge also no doubt feeds off small bits of organic material dislodged during the feeding activities of its host. Evidence suggests that scallops and oysters with their shells overgrown by sponges (frequently *Halichondria panicea*) experience reduced predation from starfish. Certain dromiid crabs carry sponges on their carapace, probably also as a predator avoidance adaptation, and numerous species of decorator crabs stick pieces of sponge on their carapace as camouflage. A particularly odd symbiosis occurs in the Mediterranean Sea, where most colonies of the bryozoan *Smittina cervicornis* are overgrown by the thinly encrusting sponge *Halisarca harmelini*; somehow, the feeding currents actually appear to be strengthened for both partners by this collaboration. On the other hand, the Indonesian sponge *Mycale vansoesti* seems to rely on a coralline alga (*Amphiroa* sp.) as its skeleton; the alga completely infuses the sponge and holds it erect, the sponge itself having almost no spicular skeleton of its own.

Other spectacular examples of poriferan symbioses are sponge–Bacteria/Archaea and sponge-algae associations, some of which appear to be mutualistic, whereas others are not. For example, a typical member of the demosponge order Verongida contains a mesohyl bacterial population accounting for some 38% of its body's volume, far exceeding the actual sponge-cell volume of only 21%. In other cases, like deep-sea sponges of the genus *Geodia*, the bacterial volume can probably account for more than 70% of the sponge volume (Figure 5.22). Presumably, the sponge matrix provides a rich medium for bacterial growth, and the host benefits by being able to conveniently phagocytize the bacteria or their by-products for food. Similar relationships are common between poriferans and various Cyanobacteria. The Indian Ocean demosponge *Tethya orphei*, and other haplosclerid sponge species, have been shown to harbor an ectosome permeated by filamentous cyanobacteria (probably *Hormoscilla spongeliae*). Vertical transmission of symbiotic bacteria (from the parent sponge to the next generation) is a specific trait of poriferan development. The bacteria are transmitted to the buds or gemmules when the sponge reproduces asexually. During sexual reproduction the bacteria are transmitted through eggs (in oviparous species) or through larvae (in viviparous forms). However, although highly prevalent, vertically transmitted symbionts have now been revealed to be an inconsistent and relatively random proportion of the mother microbiome. In *Tethya seychellensis*, the green alga *Ostreobium* sp. grows exclusively along the siliceous spicule bundles in order to capture sunlight via these natural optical fibers, and other evidence from *T. aurantium* also suggests that siliceous spicules act like fiber

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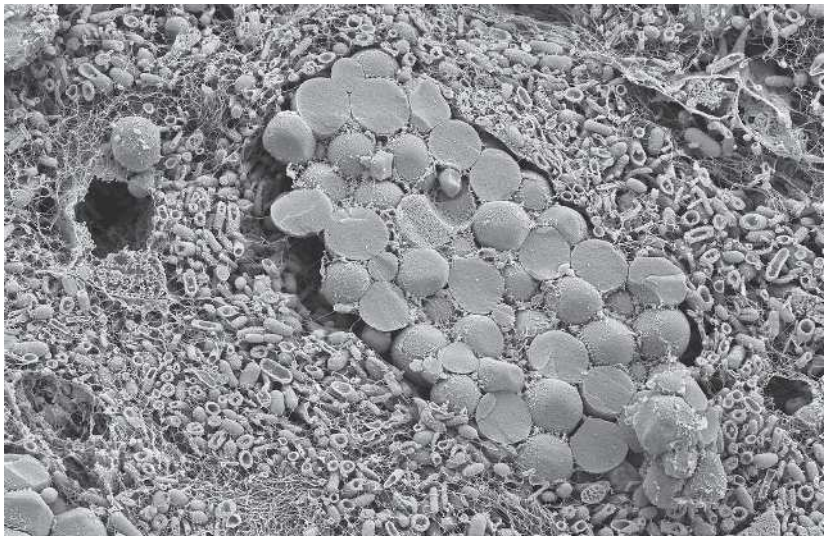

Courtesy of Ana Riesgo and Vasilliki Koutsouveli

FIGURE 5.22 Sponge cell surrounded by symbiotic bacteria in the mesohyl of *Geodia barretti*.

optics, channeling light to photosynthetic microbes living deep inside their bodies. Recent evidence suggests that some products of normal cyanobacterial metabolism (e.g., glycerol and certain organic phosphates) are translocated directly to the sponge for nutrition. In many sponges, both bacteria and Cyanobacteria co-occur, the former in deeper cellular regions, the latter closer to the surface where light is available. On the far-offshore regions of the Great Barrier Reef, 80% of the sponge individuals harbor commensal Cyanobacteria. In one remarkable study, C. R. Wilkinson (1983) showed that six of the ten most common sponge species on the fore-reef slope of Davies Reef (Great Barrier Reef) are actually net primary producers, with three times more oxygen produced by photosynthesis (by their symbionts) than consumed by respiration. Such relationships also exist with certain dinoflagellates, filamentous green algae, and red algae.

Recent studies of the Caribbean giant barrel sponge (*Xestospongia muta*) have provided evidence of two very different cyanobacterial symbionts in the *Synechococcus* group, both of which are implicated in "sponge bleaching" events in this species (similar to coral bleaching). There is no evidence that either species of *Synechococcus* maintains a mutualistic relationship with *Xestospongia muta*. One species seems to be a commensal, benefiting from the relationship but doing nothing positive or negative to the sponge. This species dies back on a cyclical basis (as do about 25% of the sponges off southern Florida), probably in association with abnormally warm seawater temperatures, and the cyanobacterial death causes a temporary bleaching (whitening) of the host sponge, but it does not kill it. The other species of *Synechococcus*, which also dies back with warmer than normal waters (and perhaps under other conditions), may be a pathogen, and it kills its host sponge as it dies. Similar deaths, which are often associated with a distinctive orange "death band" that moves across the sponge body, have been recorded for several species of *Aplysina* in the Caribbean.

In some areas of the Caribbean and Great Barrier Reef, sponges are second only to corals in overall biomass, and they appear to owe their rapid growth to the presence of large populations of symbiotic Cyanobacteria. Most freshwater spongillids maintain similar relationships with zoochlorellae (symbiotic green algae, or Chlorophyta). These sponges grow larger and more rapidly than specimens of the same species that are kept in dark conditions. Some marine sponges (e.g., the boring sponges *Cliona* and *Spheciospongia*) harbor commensal zooxanthellae (e.g., *Symbiodinium*) similar to those of corals that confer on them advantages to enhance their growth.

Many species of sponges prefer to grow on the roots of mangrove trees in littoral habitats, and experiments have shown that sponge-infested roots elongate much faster than those without sponges. Stable isotope studies have suggested transfer of dissolved inorganic nitrogen from sponge to mangrove, and transfer of carbon from mangrove to sponge! However, this unusual sponge-plant symbiosis is not well understood.

One of the most intriguing examples of poriferan symbiosis is the rare case of intimate association between two different sponge species. In North America, for example, *Halichondria poa* is almost always overgrown by *Hymeniacidon perlevis*, while in Europe *Haliclona cratera* almost always overgrows *Ircinia oros*. And in the Gulf of California (Mexico), *Haliclona sonorensis* overgrows *Geodia media*. It is not known how the covered species of sponge obtains sufficient water flow to survive, or what the cost-benefit relationships are of these unusual associations.

The boring demosponges (e.g., *Cliona, Spheciospongia*) excavate complex galleries in calcareous material such as corals and mollusc shells (Figure 5.23). This phenomenon, known as bioerosion, causes significant damage to commercial oysters as well as to natural coral, bivalve, and gastropod populations. In fact, in the Caribbean the boring sponge *Cliona delitrix* has been shown to undercut entire coral heads by their excavations, resulting in a collapse of the head. The active boring process involves chemical and mechanical removal of fragments or chips of the calcareous coral or shell material by specialized archaeocytes called **etching cells**, which release acid phosphatase. The coarse silt-sized excavated chips are expelled in

(A)

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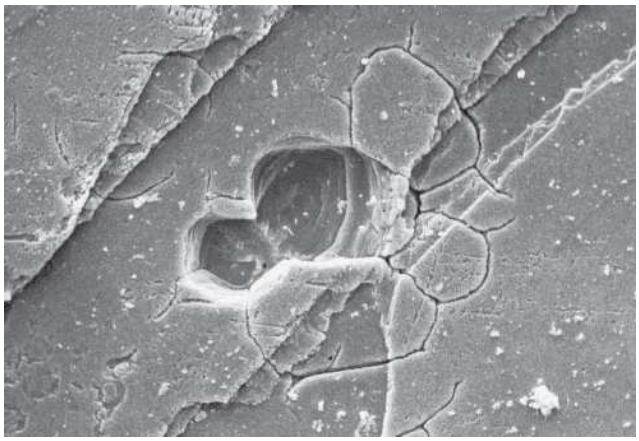
(B)



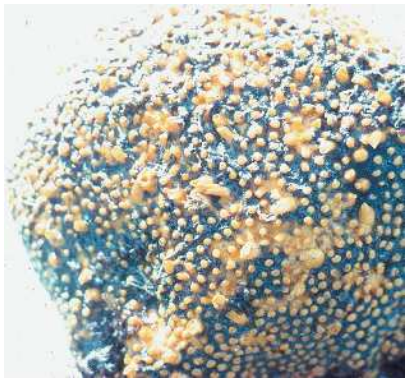
From K. Rützler and G. Reiger. 1973. *Mar Biol* 21: 144–162. https://link.springer.com/article/10.1007/BF00354611

FIGURE 5.23 Boring sponges. (A) Surface of a coral infected by the yellow boring sponge *Cliona*. (B) A close view (SEM) of the surface of a clam shell, showing six eroded "chips," two of which have been entirely removed and four that are only partly etched by *Cliona*.

the excurrent canal system and can actually contribute significantly to local sediments. Many species in the remarkable boring genus *Cliona* (family Clionaidae) have two or three different growth forms (e.g., *C. californiana* of the eastern Pacific region). The alpha stage (Figure 5.24A) is purely boring (living internally within the "host"), the beta stage (Figure 5.24B) is eruptive (having "escaped" to overgrow the surface of the calcareous substratum), and the gamma stage is "free-living" (i.e., has given up the boring stage of its life history) (Figure 5.24C,D).

Sponge bioerosion has a significant impact on coral reefs. Perhaps even more important than actual erosion

(A)



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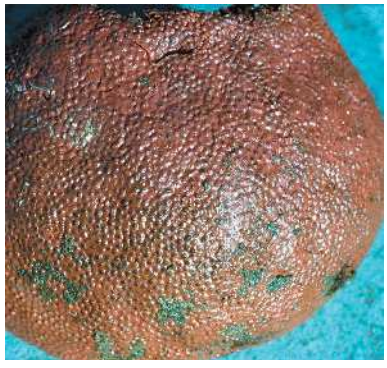

(E)

All images courtesy of R. Brusca

FIGURE 5.24 The three life history stages of the Pacific boring sponge *Cliona californiana*. (A) In the alpha stage, the sponge lives primarily within the shell (or other calcareous structure) in which it bores. (B) In the beta stage, the sponge erupts from its calcareous home and begins to overgrow the substratum. (C,D) In the gamma stage, the sponge is entirely free-living. (E) On most beaches in the world, cast-ashore shells show evidence of boring sponge activity.

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is the weakening of attachment regions of large corals. This action can result in considerable coral loss during heavy tropical storms, and it is increasing as corals are weakened by bleaching events and ocean acidification resulting from increased atmospheric CO_2. Boring sponges do not appear to gain any direct nourishment from their host coral; rather, they use it as a protective space in which to reside. If you carefully examine the shells of dead bivalves along any shoreline, you will discover that most of them are perforated with minute holes and galleries from boring sponges (Figure 5.24E). Bioeroding sponges are responsible for a major portion of the initial breakdown of such calcareous structures, and thus they set the stage for their eventual decomposition and recycling through Earth's biogeochemical cycle.

Poriferan Phylogeny

The Origin of Sponges

Being a very early branch of the tree of life, sponges are a key group in which to look for innovations that form the basis of the metazoan body plan. But sponges are an ancient group, and the important events in their origin and early evolution lie hidden in the Neoproterozic Era of the Precambrian. Both the ancient and the unique nature of the poriferan body plan are strikingly revealed by the aquiferous system, cellular pluripotency, and reproductive flexibility; and by the lack of a gut, fixed reproductive organs, nervous system, muscles, cell gap junctions, or strong adult body polarity. These features, along with the choanoflagellate-like choanocytes of sponges, suggest a poriferan ancestry not far removed from the protistan origin of the Metazoa. Generally speaking, sponges clearly stand apart from all other metazoans in their possession of such features as an aquiferous system and choanocytes with flagella bearing paired vanes (nearly identical to those of the protist phylum Choanoflagellata), although choanocyte-like cells are found, in small numbers, in some other animals (see below). Molecular phylogenetic dating estimates that Metazoa and Choanoflagellata diverged about 600 million years ago, or perhaps earlier. This early origin of Metazoa is also supported by some Poriferan fossil biomarkers. Just as this book was going to press, a paper in the journal *Nature* (Turner 2021) suggested that 890 Ma vermiform fossils from the StoneKnife Formation of northwestern Canada are possibly fossilized tissues of keratose sponges. We look forward to the follow up work on this intriguing hypothesis.

Although subtle ultrastructural differences exist, the collar cells (choanocytes) of sponges are nearly identical to the collar cells of choanoflagellates, including the unique possession of two distinct winglike projections (the vanes), which arise on either side of the flagellum, and a glycocalyx sheath on the collar that joins the microvilli. In choanoflagellates, the collars are funnel shaped, and the sheath forms an uninterrupted fibrous layer on the cell surface. In sponge choanocytes, the collars tend to be tubular, and the glycocalyx forms a mesh that both holds the microvilli together and connects adjacent collar microvilli. The vanes, in both groups, are also formed from horizontal fibers of glycocalyx that extend from the flagellum. The vanes in sponge choanocytes appear to be wider than those described from Choanoflagellata, spanning the full width of the collar with the edges of the two wings lying against the inside of the collar (and perhaps attached to it) in sponges. Differences account for very specific features that are present in choanoflagellates but not choanocytes: filopodia, cytoplasmic bridges, and glycogen reserves.

Somewhat similar collar cells (but without flagellar vanes and generally with a nonmotile cilium) have also been found in some other metazoan phyla (e.g., in the gut of certain echinoderm larvae and adults, in some corals, in the trunk epithelium of the enteropneust *Harrimania kupffferi*). The homology of these other metazoan cells to sponge choanocytes needs further study. However, it is emerging from single-cell molecular analysis that the transcriptional profiles of archaeocytes, rather than choanocytes, may be more similar to those of choanoflagellates.

But in any case, so similar are choanoflagellates and sponges that periodically through the eighteenth and nineteenth centuries the proposal came up that sponges are no more than highly organized colonial choanoflagellates. However, the presence of distinctly animal features in Porifera, including metazoan developmental genes, gastrulation during embryogenesis, spermatogenesis, adherens junctions in some species, and type IV collagen, argues against this idea. And recent molecular developmental work suggests that certain genes found in sponges and other metazoans probably played critical roles in the transition from unicellularity to multicellularity. Homologues of many typical metazoan genes have now been identified in sponges, such as those encoding proteins involved in immune responses, myosin production, developmental patterning, the formation of the extracellular matrix, reproduction, and other vital functions. Even the chitin synthase gene has been found in sponges, especially in Hexactinellida, where it could be responsible for the chitin envelope of the spicules.

The major class of transcription-factor-encoding genes that regulate animal development is called homeobox. The ANTP-class of the homeobox group includes genes in the subclasses Hox, ParaHox, and NKL, all of which are paralogues (i.e., they have arisen from a shared ancestor as a result of ancestral gene-duplication events). These genes, which are involved in multiple developmental processes, are often found in clusters, and in some animals their expression is temporally or spatially correlated to their

position within the cluster (a phenomenon known as colinearity). Until relatively recently, no homeobox genes had been found in the phylum Porifera, leading to the suspicion that this gene family did not evolve until the emergence of a line subsequent to sponges—the name "ParaHoxozoa" was given to that lineage of phyla with ParaHox subclass genes. But when the first sponge genome was sequenced (from a species of Demospongiae), a group of gene clusters was found that are known to be neighbors of Hox and ParaHox genes in higher metazoans, and later several research groups found ANTP-class homeobox genes in many other demosponges. This led to a proposal in 2012 that these developmental genes had been present in the common ancestor of all animals but had been secondarily lost in sponges—an idea called the "ghost locus" hypothesis. A test of this hypothesis came in 2014, when researchers looked closely at sponge genomes in the class Calcarea and proposed that this sponge class contained both NK and ParaHox genes remarkably similar to those of other animals. In fact, they found that the expression of these homeobox genes in the choanoderm cell layer was very similar to that seen in the endoderm of bilaterians. However, in 2019, the putative ParaHox genes of calcareous sponges were finally assigned to the NKL subclass, and therefore sponges remain out of ParaHoxozoa. But in any case, the discovery of non-Hox ANTP-class genes in calcarean sponges adds further data to the recognized molecular complexity of the entire phylum Porifera. The future will see what homoscleromorph and hexactinellid genomes add to this conundrum.

Recently, genes belonging to the cadherin family have been identified in sponges. The cadherin family of genes comprise critical mediators of metazoan cell adhesion and signaling and provide the structural basis for vital developmental processes, including tissue morphogenesis and maintenance, cell sorting, and cell polarization. Plants and fungi lack cadherins, which so far are known only from metazoans and choanoflagellates. Cadherin activity has been identified in choanoflagellates in the actin-filled microvilli that comprise the apical collar, at the basal pole of the cell, and in certain cellular bodies of unknown function. The localization of cadherins on the collar suggests that actin filaments and cadherins have been associated since before the origin of the Metazoa. In metazoan epithelial cells, recruitment of β-catenin facilitates essential interactions between classical cadherins and the actin cytoskeleton to establish and maintain cell shape and polarity.

Evolution within the Porifera

Sponges comprise such an ancient and enigmatic phylum that their phylogeny largely eluded scientists until fairly recently. Although the Porifera have nearly consistently appeared near the basal splits of metazoan molecular and morphological trees, data have been slow to resolve the relationships of sponges to the other metazoan clades (e.g., Cnidaria, Ctenophora, Placozoa, Bilateria), and as this book went to press, those relationships were still unsettled, although overall evidence still supported them as one of the earliest metazoan phyla to split off from the rest. Recent genomic-level studies strongly suggest that Placozoa arose later than sponges, placing them as sister group to Cnidaria or as sister group to Bilateria, but the placement of Ctenophora and Porifera remains contentious.

With respect to the internal relationships of sponges, only since the early twenty-first century have there been robust phylogenetic hypotheses of relationships among the four poriferan classes. Molecular clocks and sterol biomarkers place the origin of sponges sometime during the Precambrian, in the Neoproterozoic era, and imply an early Cambrian origin of the Calcarea (Figure 5.25). Although fossil sponges have been described from the Precambrian, there is no reliable evidence supporting assignment of Ediacaran specimens to sponges, and not even from isolated spicules.

Even considering some preservation biases in the fossil record, well over 1,000 fossil genera have been described, about 20% of which are still extant. The fossil record suggests that sponges might have had their ecological heyday in the Paleozoic and Mesozoic when massive tropical reefs developed, composed largely of four groups: the archaeocyathans, stromatoporids, sphinctozoans, and chaetetids. The oldest of these, the coralline Archaeocyatha (Figure 5.26), had a short life within the Cambrian (550–500 Ma). Sphinctozoans and stromatoporids also appeared in the Cambrian (about 540 Ma), while chaetetids first appeared in the Ordovician (about 480 Ma). The affinities of these four coral-like groups have been debated for 100 years, and various alliances with Cyanobacteria, red algae, bryozoans, cnidarians, and foraminiferans have been proposed. However, the discovery of living coralline sponges has led most workers to believe that the majority of species in these four groups were primitive, but true, sponges. Research suggests that the calcium-carbonate-secreting sponges utilize the same α-carbonic anhydrase genetic pathway as seen in other animals that biomineralize. And it was exploitation of this gene group that led the explosion of mineralized skeletons among the Metazoa during their rapid Cambrian radiation.

Unlike the coralline sponges, which have decreased in abundance and diversity since the Mesozoic, the Calcarea and Demospongiae appear to have increased in diversity throughout their history. The demosponges were well established by the mid-Cambrian. Several recent molecular analyses favor the hypothesis that Hexactinellida and Demospongiae are sister groups, a clade called Silicea, being the first two of the four sponge classes to appear reliably in the fossil record. The Upper Devonian extinction event brought many

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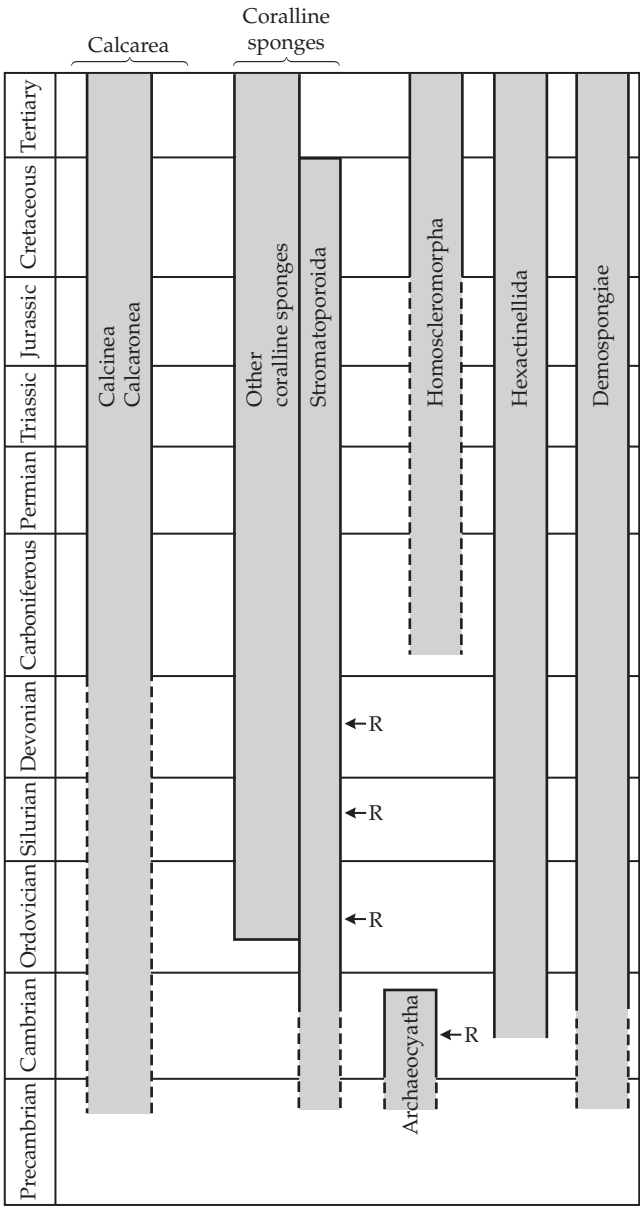

FIGURE 5.25 Fossil record of three of the extant sponge classes, the Archaeocyatha, and the other coralline sponges. Dashed lines indicate suggested occurrence, even though fossils have not yet been found. Dashed line for Homoscleromorpha indicates spicule evidence in the fossil record. "R" indicates the times when the group in question is known to have been an important marine reef builder.

demosponge clades to an end, and the modern demosponge lineages largely appeared subsequent to that event. All known orders of modern demosponges are found in Cretaceous rocks.

Hexactinellids were most diverse and abundant in the Jurassic, when they formed enormous reefs, and their fossilized remains crop up all round the world, but they declined in the Cretaceous and have largely disappeared. The oldest hexactinellid fossils, of the early Cambrian, were all thin-walled, saclike sponges with a dispersed surface spicule layer that probably could not support a thick body wall. During the Paleozoic, hexactinellids were common in shallow-water environments. Since then, however, they have become restricted largely to deeper oceanic regions. In 1987 the Geological Survey of Canada was engaged in routine surveys of the seafloor off British Columbia. Here, at around 200 m depth in ancient glacially scoured seafloor troughs, they discovered massive hexactinellid sponge reefs. Since that discovery, teams of scientists have documented the extent and composition of these living sponge reefs, which appear to be about 9,000 years old. The reefs cover roughly 700 km^2, and they are composed of fewer than a dozen hexactinellid species. They are largely identical to the massive hexactinellid-"lithistid" sponge reefs of Mesozoic times, known to paleontologists as "reef mounds" or "mud mounds," which culminated in the Late Jurassic when a 7,000-kilometer-long reef existed on the northern shelf of the Tethys Sea—the largest bioconstruction ever built on Earth.

The long fossil record of hexactinellids comprises two principal clades, the Amphidiscophora and the Hexasterophora, differing in shape and type of their microscleres. Hexactinellid synapomorphies are many, including their unique cellular and syncytial tissue organization, possession of triaxon spicules, an axial filament with a square section, and use of the enzyme glassin for building their siliceous spicules.

Until recently, two fundamentally opposing views of sponge phylogeny existed. One hypothesis suggested that the living sponge classes that produce

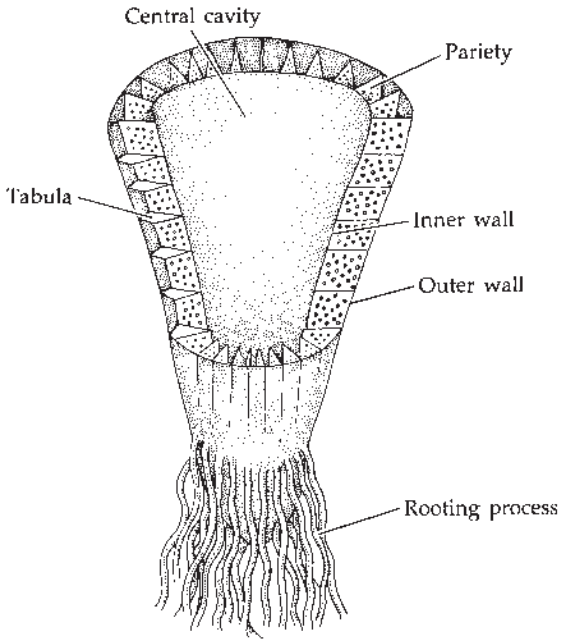

FIGURE 5.26 A typical archaeocyathan. A vertical section has been partly cut away to show the structure between the inner and outer walls (i.e., vertical parieties and horizontal tabula).

siliceous spicules comprise a monophyletic lineage (e.g., Demospongiae, Homoscleromorpha, Hexactinellida), with the Calcarea being phylogenetically more distant. The other view proposed that the classes of cellular sponges (Demospongiae, Homoscleromorpha, Calcarea) comprise a clade, with the syncytial Hexactinellida standing apart from them.

The first hypothesis was proposed in 1955 by de Laubenfels, who reduced the siliceous groups to a single class, Hyalospongiae. Subsequent authors renamed the two groups Silicea (or Silicispongia) and Calcarea (or Calcispongia). An obvious objection to this concept had been the profoundly different anatomies and spicule geometry of Hexactinellida, Demospongiae, and Homoscleromorpha. However, a very similar process of secretion of the siliceous spicules within sclerocytes around an axial filament occurs in all three groups, and that itself might be viewed as a synapomorphy of the Silicea. In addition, these three groups lack cross-striated rootlets, which are present in Calcarea and other metazoans (as well as in choanoflagellates and some other protists). Thus, *loss* of this structure may be another synapomorphy of the Silicea.

The second hypothesis of class-level relationships in Porifera suggests that the Hexactinellida stand apart from the other sponges by their unique syncytial body plan. This view recognized two groups: Symplasma (or Nuda) for hexactinellids, and Cellularia (or Gelatinosa) for demosponges (including homoscleromorphs) and calcareous sponges. One of the arguments against this view has been that hexactinellid sponges begin their lives as cellular embryos and partly cellular larvae, only later transitioning to the syncytial adult body form (by fusion of individual blastomeres), thus suggesting that Hexactinellida may have arisen from a demosponge-like ancestry.

As it turns out, neither of these views of sponge phylogeny is likely fully correct. DNA analyses since 2009 favor a version of the first hypothesis, but with the homoscleromorphs removed from the demosponges (Figure 5.27). It now appears that Demospongiae and Hexactinellida comprise a clade (Silicea), as do Calcarea and Homoscleromorpha.

The key synapomorphy of the Calcarea is their monocrystalline calcareous spicules (unique among sponges). DNA analyses also support the monophyly of the two classes of Calcarea: Calcinea and Calcaronea. An important proposed synapomorphy of the Calcinea is the basal position of nuclei in choanocytes, with no relation to the flagella. A proposed synapomorphy of the Calcaronea is the formation of the amphiblastula larva through the original process of eversion of the stomoblastula.

For many years, Homoscleromorpha was viewed as the earliest group and the most primitive looking of living Porifera (although embedded phylogenetically within the Demospongiae) owing to its seemingly simple anatomic organization. One species, *Oscarella lobularis*, was even suggested as the prototype of all sponges because of its reduced mesohyl (and appearance of having only two layers, choanoderm and pinacoderm) and lack of a mineral skeleton. For a brief period of time, some workers proposed the Homoscleromorpha be removed from the Porifera altogether and allied with the Eumetazoa (a grouping dubbed Epitheliozoa). However, just the opposite view now prevails. Recent discoveries have shown that Homoscleromorpha are not demosponges but should stand alone as a monophyletic fourth class of living sponges (closely allied to Calcarea) on the basis of DNA sequence data (18S and 28S rRNA, complete mitochondrial DNA sequence data, and more recently, a large data set of protein-coding genes) and the unique cross-striated rootlet in larval ciliated cells. In fact, homoscleromorphs have a number of distinctly metazoan-like attributes, some of which have also recently been found to be present in other sponge classes. These attributes include apical cell junctions, flagellated exopinacoderm, a well-developed basement membrane beneath both the pinacoderm and the choanoderm (in larvae and adults), acrosomes in their spermatozoa (also known from a few other sponges), and a basal apparatus of flagellated larval cells with true cross-striated rootlets (as also seen in some Calcarea and some demosponges). The fact that some of these metazoan-like features are not exclusive to Homoscleromorpha suggests that sponges are actually far more "evolved" than conventional wisdom holds and that they have undergone a massive simplification since their origin, traces of which can be seen in the Homoscleromorpha and a few other sponges.

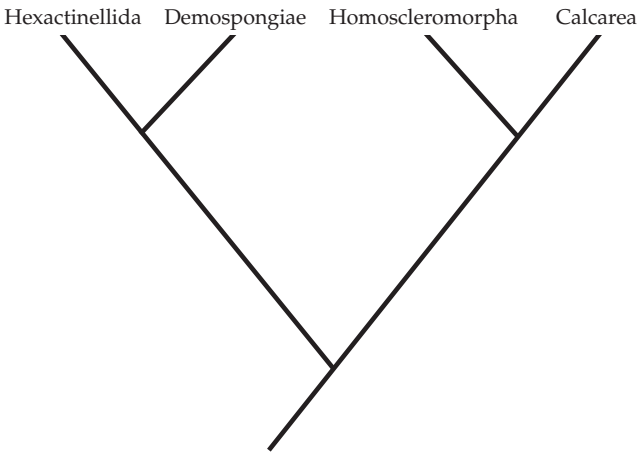

FIGURE 5.27 A modern view of poriferan phylogeny, based on phylogenomic analyses. Synapomorphies of the classes discussed in the text include the following: Hexactinellida with unique syncytial body anatomy, triaxon spicules, and a square axial filament; Homoscleromorpha never with a spongin skeleton; Calcarea with monocrystalline calcareous spicules; Demospongiae skeleton formed by monaxon and/or tetraxon spicules with an axial filament that is triangular or hexagonal, and/or spongin fibers (lost in some clades).

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Overall, relationships within the Demospongiae remain uncertain, although there is growing support for the three monophyletic subclasses used herein. Several phylogenies have been published using 18S and 28S rRNA, complete mitochondrial DNA sequence data, and housekeeping genes, but still some internal relationships remain unresolved. The most robustly supported relationships among demosponge orders are those of two spicule-less orders, Dendroceratida and Dictyoceratida, which were the earliest diverging group of demosponges. These sponges are now almost entirely limited to shallow-water coastal areas, where silicon is limiting due to large diatom populations. It is interesting then to see early demosponges without spicules, suggesting that the ability to make siliceous spicules was acquired by a more recently evolved group of demosponges. This is supported by the evidence of two very different enzymatic mechanisms to condense silica in hexactinellids and demosponges, which would render spicules as nonhomologous across siliceous sponges and would point to a later acquisition of a biomineralization mechanism in Demospongiae.

Chapter Summary

This chapter introduced you to the phylum Porifera, one of the earliest-appearing (perhaps *the* earliest-appearing), extant animal phyla. Sponges are characterized by having the following: some of the simplest of tissues and a high degree of cellular pluripotency; unique flagellated cells called choanocytes, nearly identical to choanoflagellate protists; motile, planktonic ciliated larvae; internal skeletal elements composed of calcium carbonate or silicon dioxide, and/or spongin fibers; and absence of a gut, organized nervous system, or any recognizable body organs. Major research areas that will dominate investigations of sponges over the coming decade include their precise phylogenetic placement in the tree of life, their ability to produce highly bioactive compounds, the nature of their symbiotic relationships with microbes and protists, their development, and their ecological role in the chemistry of our oceans.

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CHAPTER 6

Two Enigmatic Phyla

Placozoa and Ctenophora (The Comb Jellies)

In this chapter we discuss two unusual, marine, nonbilaterian animal phyla—Placozoa and Ctenophora. Although phylogenetic analyses show them to have diverged near the base of the metazoan tree of life, their precise relationships have eluded biologists for many decades and have long been at the center of phylogenetic debates. The phylum Placozoa was first discovered in 1883, and only a few species have been described. The bodies of these creatures are only a few millimeters in size, are just two cell layers thick, and lack both symmetry and organs. Once thought to be the sister group to all other animals due to their simplicity (e.g., few cell types), phylogenomics now places Placozoa as the sister group to Cnidaria or as the sister group to Cnidaria + Bilateria, with whom they constitute a clade that has been named Planulozoa. Members of the phylum Ctenophora are gelatinous and somewhat resemble jellyfish (phylum Cnidaria), although the two groups are not closely related and such resemblances largely reflect evolutionary convergences. Research on Ctenophora picked up in the late 2000s when a phylogenomic study suggested that they, and not Porifera, may be the sister group of all other Metazoa. Since then, dozens of high-profile papers have been published arguing back and forth whether sponges or ctenophores hold the honor of being the "first" Metazoa—although this is a misrepresentation because the debate is not about the first metazoan, but about the sister group relationship at the base of the animal tree of life. We consider this debate unsettled, yet it is now clear that Ctenophora are more basally placed in the metazoan tree than once thought, with the implication that complexity of tissues and a nervous system may have originated earlier than previously considered. Neither phylum (Placozoa or Ctenophora) has left a robust fossil record.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

Phylum Placozoa

Trichoplax adhaerens was discovered by F. E. Schulze in 1883 in a seawater aquarium at the Graz Zoological Institute in Austria. Specimens have subsequently been found throughout the world's tropical and subtropical seas, and two additional placozoan species were described in 2018 (*Hoilungia hongkongensis*) and 2019 (*Polyplacotoma mediterranea*). A species described in 1896, *Treptoplax reptans*, has not been seen since, and it is currently not accepted. These creatures remained a mystery until the great German protozoologist Karl Grell, director of the Zoology Institute at Tübingen, began working on them—although it remains unclear whether Grell's specimens, the source of what most people studied until recently, are conspecific with *T. adhaerens*. Molecular genetics of placozoans from around the world has suggested great genetic diversity, yet to be formalized taxonomically. Box 6A lists the major characteristics of Placozoa.

The body of *Trichoplax* is only 1 to 3 mm in diameter, although it consists of a few thousand cells, of only a few types, arranged as a simple double-layered plate (Figure 6.1) that may be polytomous (*P. mediterranea*). It lacks anterior–posterior polarity, symmetry, a mouth or gut, nervous system, muscles, or extracellular matrix, although a recent gene-expression study has suggested the existence of an oral–aboral axis that corresponds with the bottom–top of the animal. However, the cells of the upper (top) and lower (bottom) layers differ in shape, and there is a consistent orientation of the body relative to the substratum. Because the concepts of dorsal and ventral are generally taken to be characteristics of triploblastic animals, we will use the terms "upper-layer cells" and "lower-layer cells." The upper-layer cells are flattened and monociliate and epithelium-like, and they have curious extracellular structures, called **shiny spheres**, unique to placozoans. Long thought to be lipid inclusions, they appear to be easily dislodged and fall out of the cell layer. In 2007, Vicki Buchsbaum Pearse and Oliver Voight reported that gastropods, flatworms, and sabellid polychaetes recoil upon contact with placozoans, suggesting they might possess a chemical deterrent to predators. In 2009, Alexis Jackson and Leo Buss tested this hypothesis, finding that when individual *Trichoplax*

BOX 6A Characteristics of the Phylum Placozoa

1. Minute, flattened metazoans composed of ciliated upper and lower cell layers; ameboid and fibrous cells in a "gel" layer in between; adults discoidal and asymmetrical or with polytomous branching
2. With six somatic cell types
3. Cells with desmosome cell-cell connections
4. With unique shiny spheres, possibly defensive structures, in upper cell layer
5. Without a structural nervous system, muscles, or digestive system

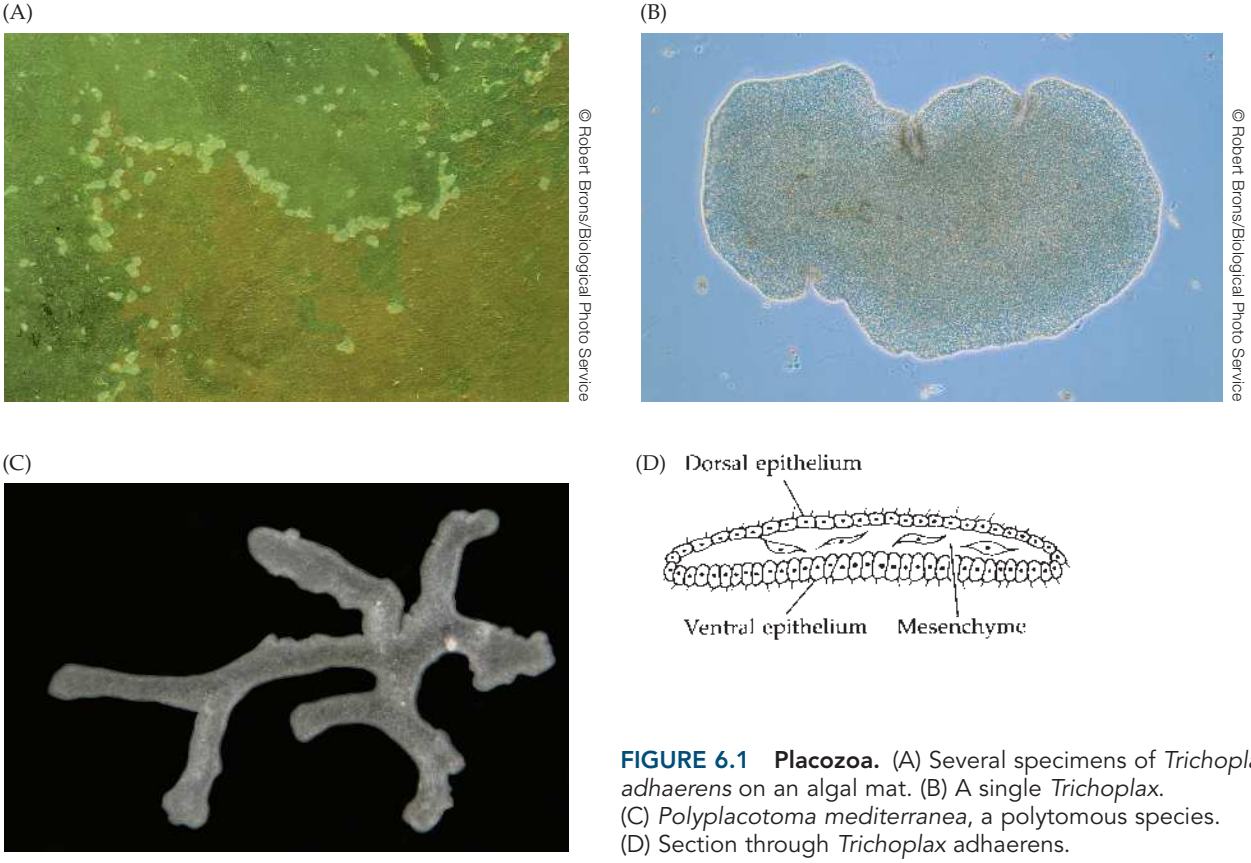

FIGURE 6.1 Placozoa. (A) Several specimens of *Trichoplax adhaerens* on an algal mat. (B) A single *Trichoplax*. (C) *Polyplacotoma mediterranea*, a polytomous species. (D) Section through *Trichoplax* adhaerens.

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were fed to the hydrozoan *Podocoryna carnea*, the polyps became paralyzed, suggesting that the peculiar shiny spheres might indeed be antipredator devices.

Most of the lower-layer cells are also monociliate, but they are all more columnar and lack distinct shiny spheres; "gland cells" may also occur on the lower surface. Fiber cells can be seen between the upper and lower cell layers. These internal cells have thin extensions that connect to each other in a network. Cellular material such as microtubules and microfilaments traverse the extensions from fiber cell to fiber cell. It has been suggested that this network plays a role in coordinating movement of the animal. Importantly, desmosomes, cell-cell junctions of extracellular cell adhesion proteins, have been found in placozoans, a feature not seen in Porifera but present in most other Metazoa.

The lower cell layer can be temporarily invaginated, presumably for feeding. This observation supports the notion that there are functional as well as structural differences between the two cell layers. Between these two cell layers (or epithelial sheets) is a mesenchymal layer of stellate ameboid cells embedded in a supportive gel matrix. Grell (1982) considered *Trichoplax* to be a true diploblastic metazoan and suggested that the upper and lower cell layers were true epithelia and might be homologous with ectoderm and endoderm, respectively. However, a basement membrane has not yet been identified beneath either layer, which suggests that *Trichoplax* may be closer to the Porifera in organization than it is to Cnidaria, Ctenophora, or the triploblastic Eumetazoa. No fossil placozoans have been found, but it has been suggested that the feeding tracks of the Ediacaran *Dickinsonia* are similar to those of placozoans, and an affinity between these was proposed.

Trichoplax moves by ciliary gliding along a solid surface, aided by irregular, ameba-like shape changes along the body edges. Very small, presumably young individuals can swim, while larger individuals seem to always crawl. *Trichoplax* apparently feeds by phagocytosis of organic detritus using the lower surface, which can contract to form a "feeding chamber." An elegant recent study showed that *T. adhaerens* is able to control feeding behavior and do this by responding to endomorphin-like peptides. A small number of sensory secretory cells lacking processes and synapses can evoke a wave of peptide secretion across the entire animal and even between individuals that are not in contact. These peptide secretions allow the animal to arrest ciliary beating and pause during feeding. Although there is no evidence of extracellular digestion, it is possible that *Trichoplax* secretes digestive enzymes onto its food within the lower digestive pocket. It is not known what these animals eat in nature, but lab cultures can be sustained on diets of flagellated protists (e.g., *Cryptomonas*, *Chlorella*).

Trichoplax reproduces asexually by fission of the entire body into two new individuals and also by a budding process that yields numerous multicellular flagellated "swarmers," each of which forms a new individual. It is also capable of regeneration from damage to the body, to the point that some have claimed that predation upon placozoans by rhodopemorph gastropods can contribute to asexual reproduction. Sexual reproduction is also known, followed by a developmental period of holoblastic cell division and growth. Eggs have been observed within the mesenchyme, but their origin is unknown.

With only six somatic cell types and a lack of defined symmetry or constant body axis, *Trichoplax* has the simplest body of any known metazoan. Over the years, it has been suggested that *Trichoplax* might be a secondarily reduced cnidarian (or a sister group to the Cnidaria). However, the more highly derived cnidarians (Scyphozoa, Hydrozoa, Cubozoa) all have a linear mtDNA molecule—a unique synapomorphy of that clade within Cnidaria—in contrast to the circular mtDNA of Anthozoa and all other Metazoa. *Trichoplax* also has circular mtDNA. Further, the secondary structure morphology of the mitochondrial 16S rRNA gene of *Trichoplax* differs markedly from that seen in cnidarians. Curiously, a shift from circular to linear mitochondrial genomes also occurred in a clade of calcareous sponges. But now we have more genomes than named species of placozoans available, and phylogenomic analyses have suggested two possible placements for Placozoa—either as sister group to cnidarians, or as sister group of Cnidaria + the bilaterian phyla.

Phylum Ctenophora

Ctenophores (Greek *cten*, "comb"; *phero*, "to bear")—commonly called comb jellies, sea gooseberries, or sea walnuts—are transparent, gelatinous animals. They are one of the earliest branching metazoan groups. Most of them are planktonic, living from surface waters to depths of at least 7,000 m, while a few species are benthic. Their transparency and fragile nature make them difficult to capture or observe by traditional sampling methods such as trawling with nets, and until the advent of manned submersibles and "blue water" scuba techniques, they were thought to be only modestly abundant. However, they are now known to form a major portion of the planktonic biomass in many areas of the world, and they may periodically be the predominant zooplankton in some regions. About 130 credible species have been described (90 planktonic, 40 benthic), plus there are an additional 40 species that remain uncertain, and there are many deep-sea forms yet to be discovered. Ctenophores have traditionally been illustrated with the oral side facing downward, and for this reason some people have probably confused them with cnidarian medusae.

Ctenophores have a form of radial symmetry, are probably diploblastic animals, and resemble cnidarians

The section on Ctenophora was revised by Steven Haddock.

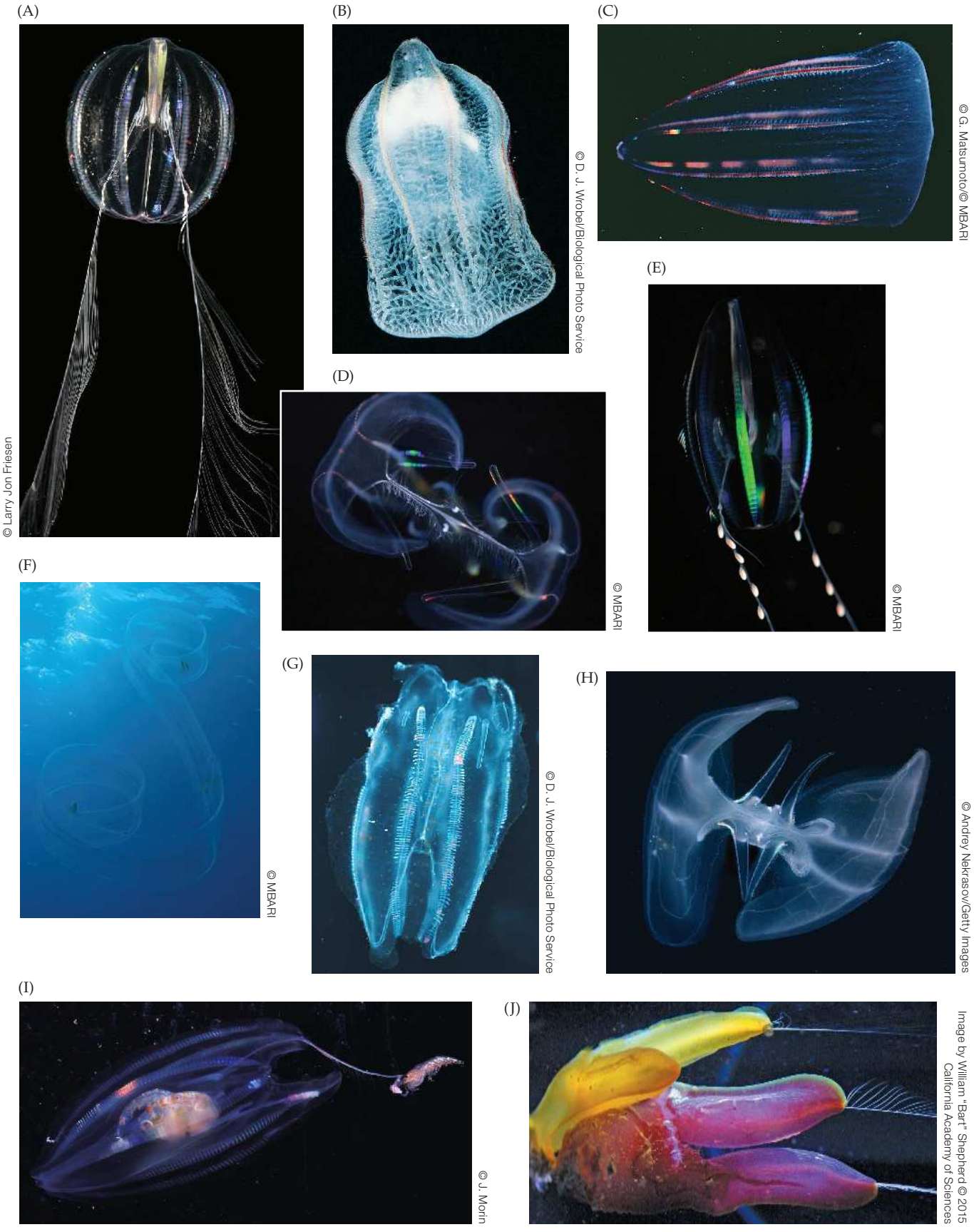

FIGURE 6.2 Representative ctenophores. (A) *Pleurobrachia* (order Cydippida). (B) *Beroe ovata* (order Beroida). (C) *Beroe*, showing iridescence in the comb rows. (D) *Eurhamphaea* (order Lobata). (E) The genus *Euplokamis* has coiled tentilla that can quickly wrap around prey. (F) *Velamen* (order Cestida). (G) *Leucothea* (order Lobata). (H) Warty comb jelly or sea walnut, *Mnemiopsis leidyi* (order Lobata), Crimea, Ukraine. (I) An Antarctic cydippid ctenophore with two krill in its gut, and a third one being captured. (J) *Lyrocteis imperatoris*, an Indo–West Pacific platyctenid ctenophore.

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in many—potentially superficial—respects. Some similarities include a gelatinous mesenchyme or collenchyme, the absence of a body cavity between the gut and the body wall, and a relatively simple, netlike nervous system. Zoologists, however, view these similarities as convergent features resulting from adaptations to pelagic lifestyles. Ctenophores are significantly different from cnidarians in their more extensively organized digestive system, their wholly mesenchymal musculature, and several other features (Box 6B). There remains uncertainty as to the origin of the ctenophoran mesenchyme, with developmental evidence favoring an endodermal origin. This might at first suggest developmental homology with the true mesoderm of bilaterians. However, sequencing of the genomes of *Pleurobrachia bachei* and *Mnemiopsis leidyi* have shown that many of the genes involved in mesoderm development in bilaterians appear to be absent in Ctenophora.

Ctenophores also differ fundamentally from cnidarians in that they are monomorphic throughout their life histories, are never colonial, lack any trace of an attached sessile stage, and lack cnidae. Ctenophores lack a hard skeleton, an excretory system, and a respiratory system. Most are simultaneous hermaphrodites capable of self-fertilization—an unusual quality among the Metazoa. A distinctive larval form, the **cydippid larva**, is usually produced. Ctenophores are exclusively marine. They display a wonderful variety of shapes, and they range in size from less than 1 cm in height to ribbon-shaped forms over a meter long (Figure 6.2). Some have evolved rather elaborate body forms, and a few have taken up a benthic creeping existence. They occur throughout the world oceans and at all latitudes. Battered specimens of the genus *Pleurobrachia* ("sea gooseberries") are often found washed ashore after storms, but most of the diversity is rarely seen. In their planktonic environment, ctenophores are some of the most elegant and graceful creatures in the sea, and observing them in their natural habitat is a memorable experience.

BOX 6B Characteristics of the Phylum Ctenophora

1. Diploblastic (or possibly triploblastic) Metazoa, with ectoderm and endoderm separated by a cellular mesenchyme; mesenchyme endodermal in origin
2. Biradial symmetry, with oral–aboral body axis
3. With adhesive exocytotic structures called colloblasts
4. Gastrovascular cavity (gut) as the only "body cavity"; gut with stomodeum and canals that branch complexly throughout body; gut ending in two small anal pores
5. Without discrete respiratory, excretory, or circulatory systems
6. Nervous system in the form of a nerve net or plexus, without true ganglia, but more specialized than that of cnidarians; some species with giant axons
7. With striated muscles, always formed of true mesenchymal cells
8. With eight rows of ciliary plates (combs or ctenes) at some stage in their life history; comb rows controlled by unique apical sense organ
9. Some adults and most juveniles with a pair of long tentacles, often retractable into sheaths
10. Monomorphic, without alternation of generations and without any kind of an attached sessile life stage
11. Most are hermaphroditic, and typically with a characteristic cydippid larval stage

Taxonomic History and Classification

Perhaps because many well-known ctenophores are brilliantly luminescent and are commonly seen from ships, the group has been known since ancient times. The first recognizable figures of ctenophores were drawn by a ship's doctor and naturalist in 1671. Linnaeus placed them in his group Zoophyta, along with various other "primitive" invertebrates. Cuvier classified them with medusae and anemones in Zoophytes. In the early nineteenth century, Johann Friedrich von Eschscholtz designed the first rational classification of pelagic medusae and ctenophores by creating the orders Ctenophorae (for comb jellies), Discophorae (for all the solitary cnidarian medusae), and Siphonophorae (for the colonial siphonophores and chondrophorans). Eschscholtz viewed these orders as subdivisions of the class Acalepha, regarding them as intermediate between Zoophytes and Echinodermata (on the basis of the common presence of radial symmetry). Recall that it was Leuckart who first separated the Coelenterata from the echinoderms in 1847, although his Coelenterata also included sponges and ctenophores. Raspailia Vosmaer (in 1877) was responsible for removing the sponges and Hatschek (in 1889) for removing the ctenophores as separate groups.

Until recently, two classes of ctenophores were recognized: Nuda, for species lacking tentacles (the single order Beroida), and Tentaculata, for those species with tentacles (all other orders). However, the monophyly of these two groups had been questioned even before genetic sequencing. Recent molecular analyses show that, while the Ctenophora overall are a monophyletic lineage, the presence or absence of tentacles provides some phylogenetic information but cannot constitute the basis for the main division of the phylum; Beroida (which may be monophyletic) are nested well within the phylum, suggesting an evolutionary loss of tentacles in the history of Ctenophora.

Until the taxonomy is revised, we largely follow Harbison and Madin (1982) in simply dividing the ctenophores into six orders (omitting Ganeshida) containing 18 families. Figures 6.2 and 6.3 illustrate the general anatomy of the major groups. The position of the Ctenophora among the early-diverging

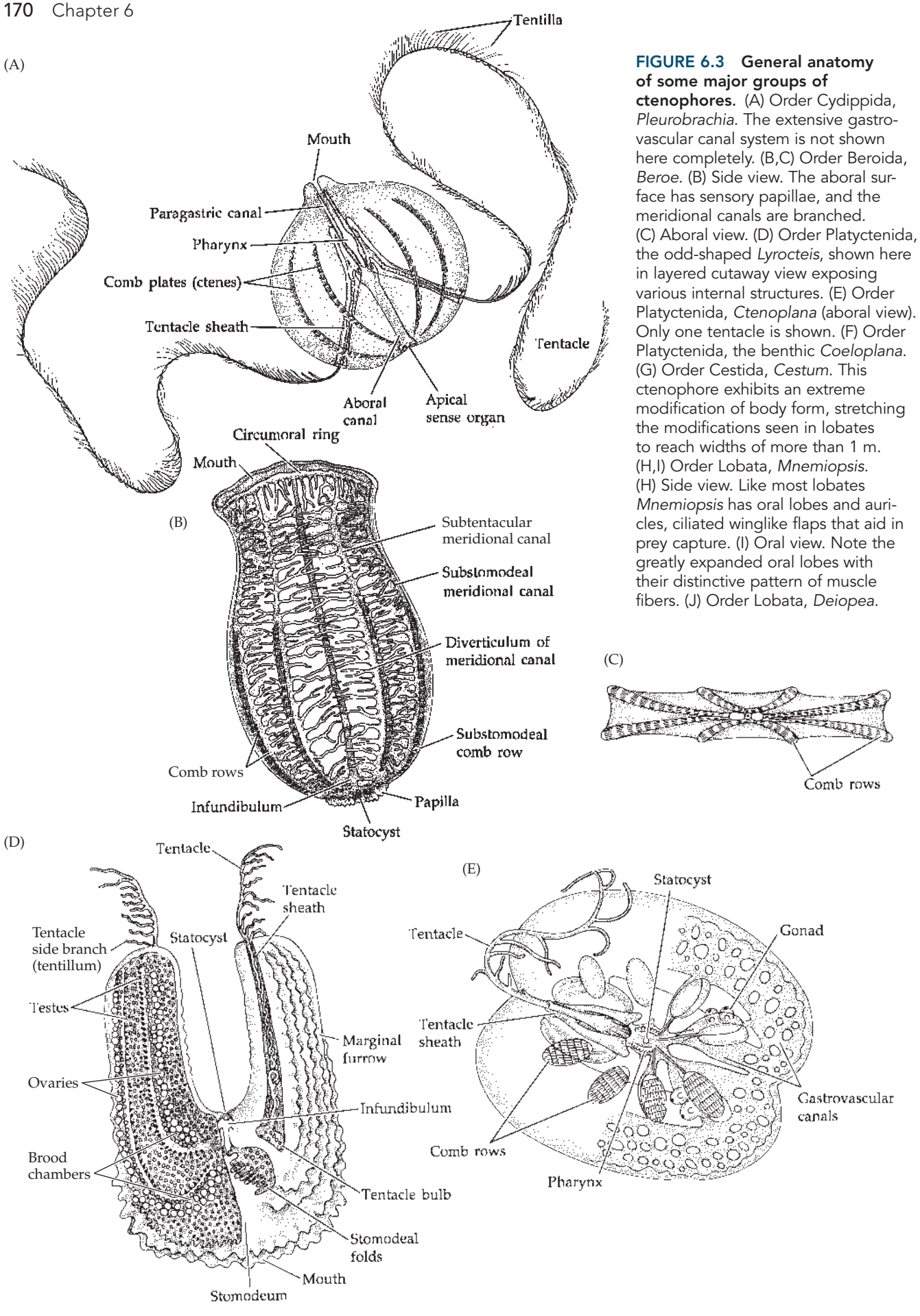

FIGURE 6.3 General anatomy of some major groups of ctenophores. (A) Order Cydippida, *Pleurobrachia*. The extensive gastrovascular canal system is not shown here completely. (B,C) Order Beroida, *Beroe*. (B) Side view. The aboral surface has sensory papillae, and the meridional canals are branched. (C) Aboral view. (D) Order Platyctenida, the odd-shaped *Lyrocteis*, shown here in layered cutaway view exposing various internal structures. (E) Order Platyctenida, *Ctenoplana* (aboral view). Only one tentacle is shown. (F) Order Platyctenida, the benthic *Coeloplana*. (G) Order Cestida, *Cestum*. This ctenophore exhibits an extreme modification of body form, stretching the modifications seen in lobates to reach widths of more than 1 m. (H,I) Order Lobata, *Mnemiopsis*. (H) Side view. Like most lobates *Mnemiopsis* has oral lobes and auricles, ciliated winglike flaps that aid in prey capture. (I) Oral view. Note the greatly expanded oral lobes with their distinctive pattern of muscle fibers. (J) Order Lobata, *Deiopea*.

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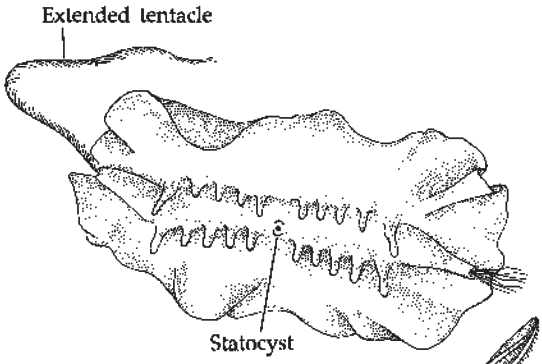

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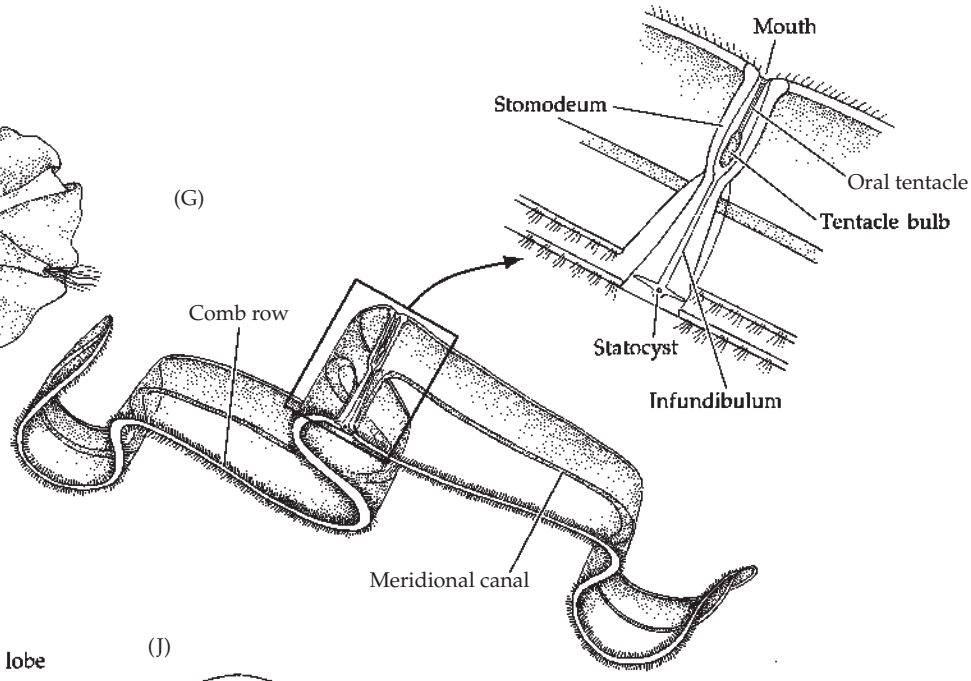

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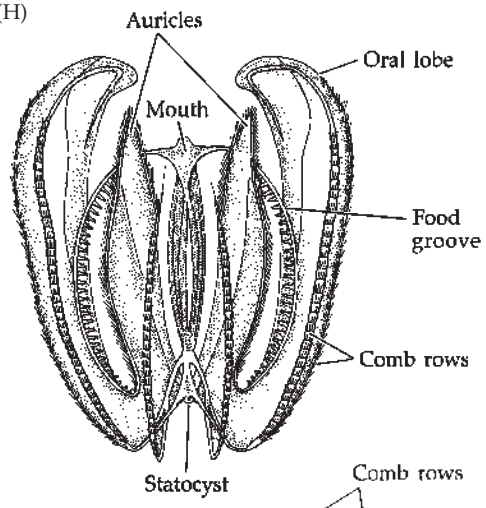

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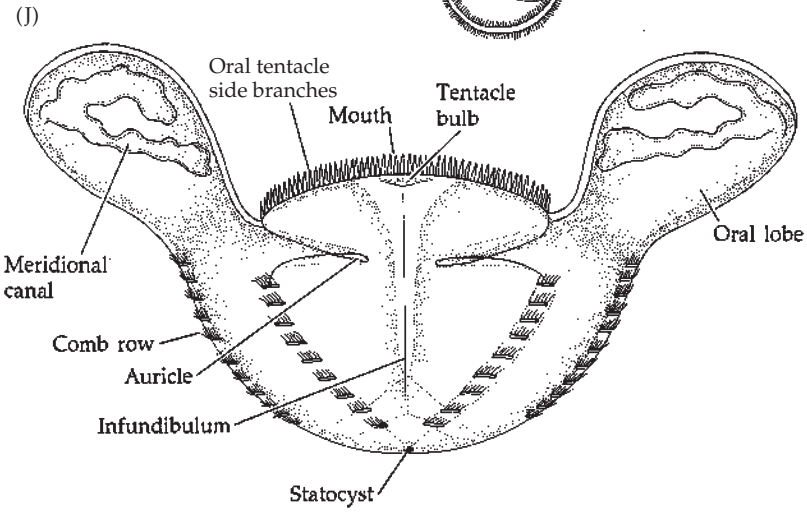

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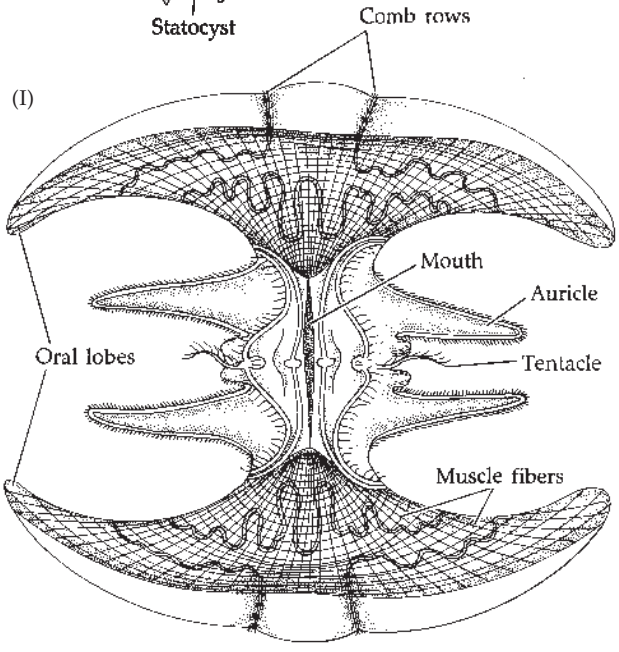

Metazoa is still under debate. Some molecular phylogenetic studies have suggested they might be the sister group to all other metazoans, while others recover the traditional view of Porifera diverging first. No modern molecular studies recover a monophyletic "Coelenterata" with ctenophores as sister group to cnidarians.

CLASSIFICATION OF CTENOPHORA

ORDER CYDIPPIDA (Figures 6.2A and 6.3A). Pelagic; with well-developed comb rows; tentacles long and retractable into sheaths; body globular or ovoid, occasionally flattened in the stomodeal (= sagittal) plane; meridional canals end blindly, paragastric canals (when present) end blindly at mouth. This order is widely viewed as polyphyletic and in need of revision. (e.g., *Aulacoctena*, *Bathyctena*, *Callianira*, *Dryodora*, *Euplokamis*, *Haeckelia*, *Hormiphora*, *Lampea*, *Mertensia*, *Pleurobrachia*, *Tinerfe*)

ORDER PLATYCTENIDA (Figure 6.3D–F). Benthic or epibenthic; comb rows reduced; most species greatly flattened, with part of stomodeum everted as a creeping sole; with oral adhesive organs; often with tentacle sheaths; tentacle canals bifid; gastrovascular system complex and anastomosing; most species possess anal pores; many are ectocommensals on other organisms (e.g., corals, echinoderms). Unlike in most ctenophores, fertilization is often internal, and many platyctenids brood their embryos to the larval stage; asexual reproduction is common. (e.g., *Coeloplana*, *Ctenoplana*, *Lyrocteis*, *Tjalfiella*, *Vallicula*)

ORDER CESTIDA (Figures 6.2E,F and 6.3G). Pelagic; body extremely compressed in tentacular plane, and greatly elongated in stomodeal plane, producing a ribbonlike form more than 1 m long in some species; substomodeal comb rows elongate, extending along entire aboral edge; subtentacular meridional canals arise near subtentacular comb rows (*Cestum*) or equatorially from interradial canals (*Velamen*); paragastric canals extend along oral edge and fuse with meridional canals; oral tentacles. Two genera: *Cestum* and *Velamen*.

ORDER LOBATA (Figures 6.2D,G,H and 6.3H–J). Pelagic; body compressed in tentacular plane; with a pair of characteristic oral lobes and 4 flaplike auricles; a ciliated auricular groove extends to base of auricles from each side of each tentacle base; paragastric and subtentacular meridional canals unite orally. (e.g., *Bolinopsis*, *Deiopea*, *Eurhamphaea*, *Leucothea*, *Mnemiopsis*, *Ocyropsis*)

ORDER THALASSOCALYCIDA (Figure 6.5). Pelagic; body extremely fragile, expanded orally into medusa-like bell, to 15 cm along tentacular axis; body slightly compressed in stomodeal plane; auricles and tentacle sheaths absent; tentacles arise near mouth and bear lateral filaments; comb rows short; mouth and pharynx borne on central conical peduncle; meridional canals long, describing complex patterns in bell; all meridional canals end blindly aborally. Monotypic: *Thalassocalyce inconstans*.

ORDER BEROIDA (Figures 6.2B,C and 6.3B,C). Pelagic; body cylindrical or thimble-shaped, sometimes strongly flattened in tentacular plane; tentacles and sheaths absent; aboral end rounded (*Beroe*) or with 2 prominent keels (*Neis*); stomodeum greatly enlarged; aboral sense organ well developed; meridional canals with numerous side branches; paragastric canals simple or with side branches. Without a cydippid larva phase. Two genera: *Beroe* (worldwide in distribution) and *Neis*.

The Ctenophoran Body Plan

Although ctenophores appear simply constructed, they do possess true tissues. Between the epidermis and the gastrodermis is a well-developed middle layer, which is always a cellular mesenchyme. Within this mesenchyme true muscle cells develop, a condition that also characterizes the triploblastic Metazoa, although by different developmental pathways.

As we noted in Chapter 3, a critical essence of the ctenophoran and cnidarian body plans is radiality (in one fashion or another) we explained some of the structural constraints and advantages that derive from this symmetry. Thus, predictably, the nervous system of ctenophores is in the form of a simple, noncentralized nerve net, and the locomotor structures are arranged radially about the body. Other features that characterize the Ctenophora include retractile **tentacles** and often **tentacle sheaths**; **anal pores**; adhesive prey-capturing structures called **colloblasts** (see Figures 6.7 and 6.8); locomotor structures called **ctenes** or comb plates, arranged in **comb rows**; and an **apical sense organ** containing a statolith that regulates the activity of the comb rows. The sheathed tentacles, colloblasts, comb plates, and nature of the apical sense organ are unique features of ctenophores. Figures 6.2 and 6.3 illustrate ctenophoran anatomy.

Many ctenophores are spherical or ovoid in shape, although some species have evolved flattened shapes through compression and elongation in one of the two primary planes of body symmetry (Figures 6.2E and 6.3I). The general body plan can best be understood by first examining an idealized cydippid ctenophore (Figure 6.4). Specialists have long considered the cydippids to be ancestral within the phylum, although molecular evidence shows that the order Cydippida is polyphyletic. Fossil evidence has framed the discussion in relation to an evolutionary gain or loss of tentacles, but the evidence from extant ctenophores shows tentacles being lost and reduced (loss of tentilla) as a derived state more than once.

As in cnidarians, the principal axis is oral–aboral. The mouth is at the oral pole; the aboral pole bears the apical sense organ. Unlike pelagic cnidarians, however, ctenophores encounter their world leading with the oral end, not with the mouth trailing like a medusa. There is a long and confounding tradition of illustrating

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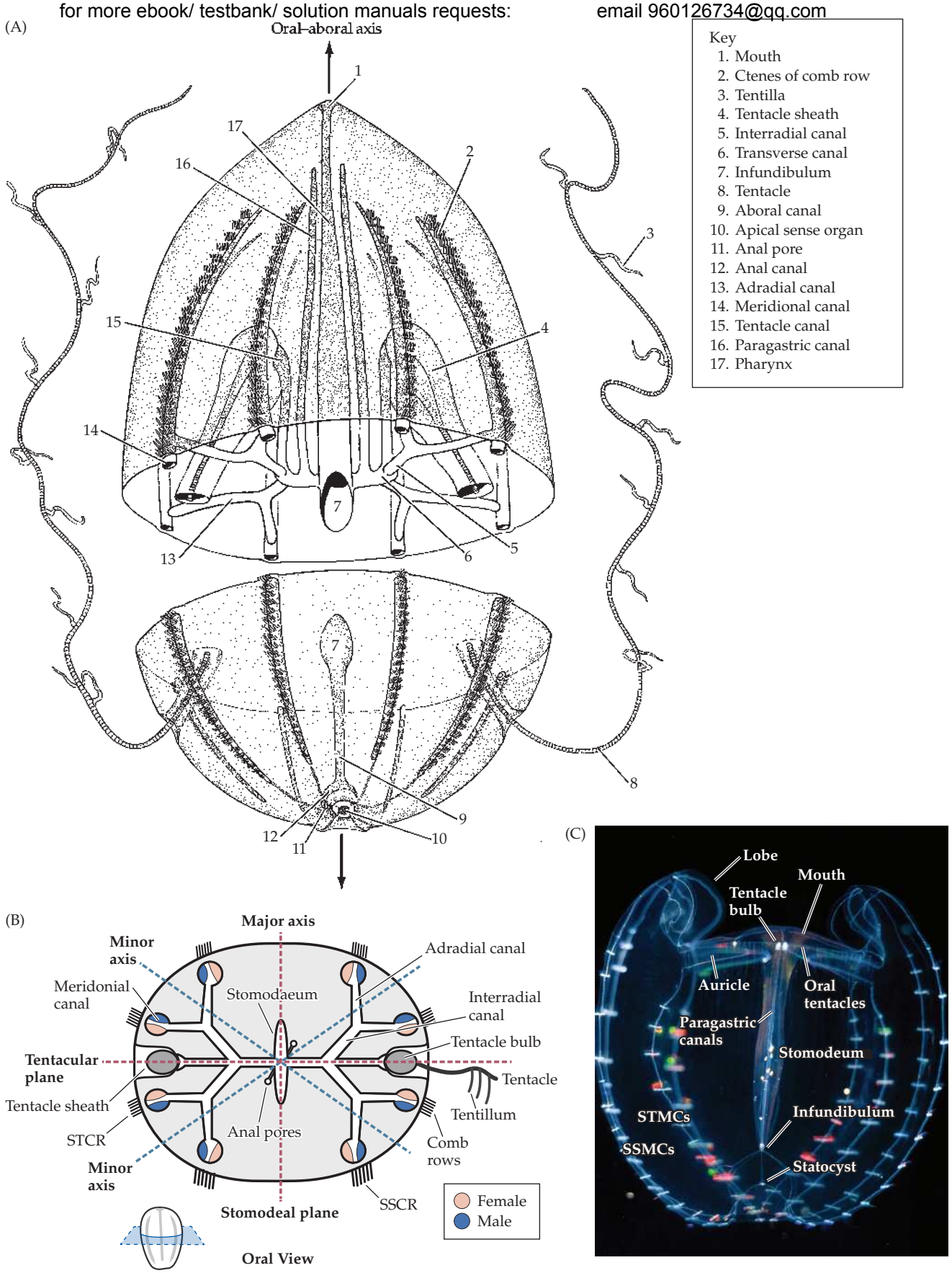


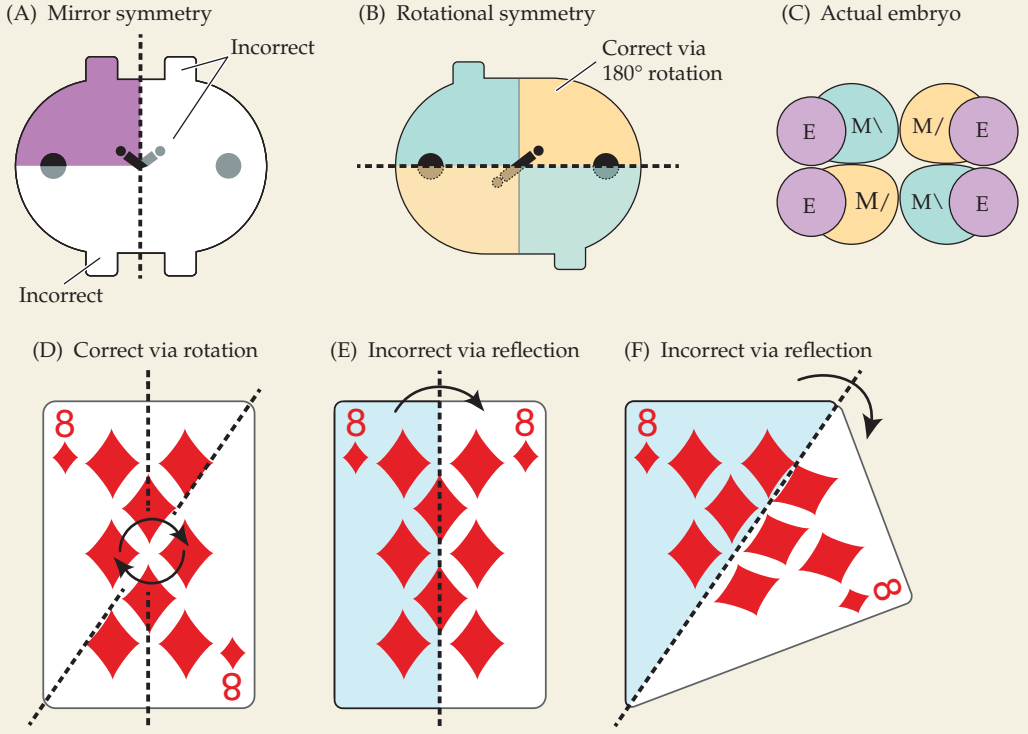
FIGURE 6.4 The ctenophoran body plan. (A) A cydippid ctenophore (cross section). (B) Ctenophoran biradiality and the planes of symmetry (oral view). (C) The lobate ctenophore, *Deiopea kaloktenota*, showing main anatomical features. SSMCs are the substomodeal meridional canals, and STMCs are the subtentacular canals, adjacent to the tentacular plane. SSCR, substomodeal comb row; STCR, subtentacular comb row.

them "upside down." On the surface of the body are eight equally spaced **meridional rows** of comb plates. Each comb plate, or ctene, is composed of a transverse band of long, fused, compound cilia. On each side of the body of many species is a deep, ciliated epidermal pouch (the tentacle sheath) from whose inner wall a tentacle arises. The tentacles are typically very long and contractile and bear lateral branches called filaments, or **tentilla**. The epidermis of both the tentacles and the lateral tentilla is richly armed with colloblasts (see Figure 6.8). Most species can retract the tentacles into the sheaths with muscles. It is the tentacles and certain aspects of the internal anatomy that give ctenophores a biradial symmetry (Box 6C). The elongate **stomodeum** lies on the oral–aboral axis of the body. It is distinctly flattened in one plane of body symmetry, the **stomodeal plane**, historically called the **sagittal plane** (Figure 6.4B). Bisecting the animal along the stomodeal plane separates the two tentacular halves of the body. The second major plane of body symmetry, called the **tentacular plane**, is defined by the position of the tentacle sheaths. At roughly 45° between these major planes, the body can also be divided into minor planes of symmetry. These are useful in describing the morphology because the female gonads lie on the side of the meridional canals adjacent to the major planes, while the male gonads and bioluminescent photocytes are found next to the minor axes (Figure 6.4).

Some variations of the basic ctenophoran body plan are illustrated in Figures 6.2 and 6.3. In members of

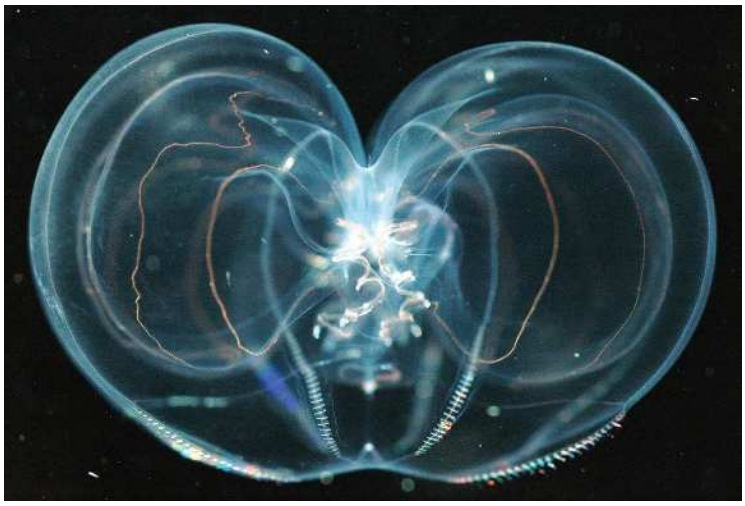
BOX 6C Ctenophore Symmetry

These "top-down" (oral) diagrammatic views of ctenophores (A,B) are shown looking down along the longitudinal axis of the body. The symmetry of ctenophores around their central axis is challenging to describe. The term "biradial symmetry" is frequently used, but by itself this does not explain the morphology. (A) At first glance it might appear that ctenophores can be described using mirror or reflectional symmetry. However, there are certain features—most conspicuously the diagonally offset anal pores—that mean you cannot get a correct representation by mirroring half or a fourth of a ctenophore across a central plane. (B) What is required to correctly reproduce a ctenophore is 180° rotation about the central axis. The half to be rotated does not have to be cut along the major horizontal or vertical axis; any slice that passes through the central point parallel to the long axis will create a suitable section for rotation. (C) Surprisingly, the diagonally offset quadrants may even be detected during the four- or eight-cell embryonic stage. Descendants of the end (E) and middle (M) micromeres form particular structures. Here, the two aqua-colored M\ cells are fated to form tissues such as the anal pores, while their counterpart brown M/ cells will form longitudinal muscles and other tissues (Martindale and Henry 1998). (D) A playing card provides a visual analogy of rotational symmetry. Any half may be rotated to reproduce the full card, but no reflections, either (E) along a major axis or (F) a diagonal, will recreate the true "morphology" of the card.



the diverse order Lobata (Figure 6.3H–J), the body is compressed in the tentacular plane, and the oral end is expanded on each side into rounded, contractile **oral lobes**. The mouth sits on an elongate region, the ends of which bear four long flaps called **auricles**. The tentacles are reduced and lack sheaths. From either side of each tentacle base, a ciliated **auricular groove** arises and extends around the perimeter of the auricles connecting with the subtentacular comb rows at the other side.

Members of the order Cestida (Figures 6.2E and 6.3G) are also compressed in the tentacular plane and extremely elongated in the stomodeal plane, giving these ctenophores a striking eel- or ribbonlike appearance—hence the common name Venus's girdle. The sheathed tentacles are reduced and shifted alongside the mouth with oral tentilla forming a fringe across the width of the body. Beroida are thimble shaped and either cylindrical or flattened in the stomodeal plane (Figures 6.2B,C and 6.3B,C) and lack tentacles and sheaths throughout their life. In the single species of Thalassocalycida (*Thalassocalyce inconstans*), the would-be lobes are fused around the mouth to form a medusa-like bell (Figure 6.5).



Courtesy of L. P. Madin/WHOI

FIGURE 6.5 ***Thalassocalyce inconstans*, in the monotypic order Thalassocalycida,** with its expanded oral lobes that form a medusa-like bell.

Members of the order Platyctenida (Figures 6.2I and 6.3D–F) look more like flatworms than their ctenophore kin. Platyctenids are benthic and small, often less than 1 cm in length; in contrast to most pelagic ctenophores, they are pigmented rather than transparent. The body is oval and markedly flattened, resembling a free-living flatworm. Despite these unusual features, early naturalists recognized them as ctenophores by the presence of an apical sense organ, comb rows, and a pair of tentacles. Detailed studies have shown that the flattened oral surface is actually an everted portion of the pharynx. The platyctenid pharynx was, in a sense, preadapted to serve a dual purpose as a creeping foot or sole by its intrinsic musculature. Many of these animals crawl about on the sea bottom and algae, while some are ectocommensals, attached like a flag on a flagpole to alcyonarian cnidarians, echinoderms, or sponges.

Support and Locomotion

Ctenophores rely primarily on their elastic mesenchyme for structural support. The watery gelatinous mesenchyme makes up most of the body mass; ctenophore dry weights are only about 4% of their live wet weights. The mesenchyme contains both elastic supportive cells and muscle cells, the general tonus of the latter being primarily responsible for maintaining body shape. Figure 6.6 shows a highly stylized cutaway section of a cydippid ctenophore and illustrates the arrangement of the supportive mesenchymal muscle fibers. Tension in the looped muscles tends to maintain the body geometry. Action of the radial muscles diminishes the radius and hence the circumference and also serves to open the pharynx. These two muscle sets are antagonistic.

Most ctenophores are pelagic. The gelatinous body and low specific gravity maintain relatively neutral buoyancy, allowing these creatures to float about with the ocean currents. Neutral buoyancy appears to be maintained by passive osmotic accommodation. Because buoyancy adjustments take time, ctenophores may temporarily accumulate at discontinuity layers in the sea, where a water mass of one density overlies a water mass of a slightly different density.

The beating of the ctenes provides most of the locomotory power that allows ctenophores to move up and down in the water column and to locate richer feeding sites or preferred environmental conditions. Some, like *Thalassocalyce* species may be motionless in the water,

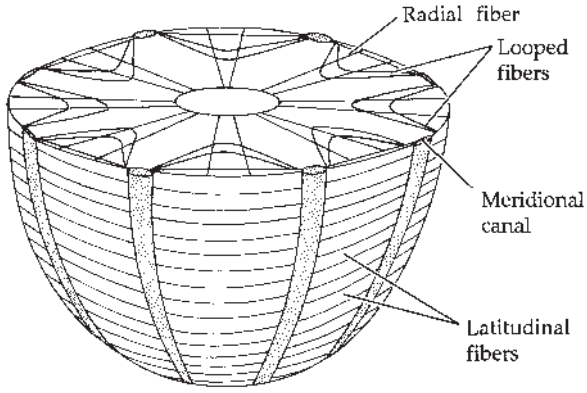


FIGURE 6.6 Stereogram of the arrangement of muscle fibers in *Pleurobrachia*, a cydippid ctenophore. The diagram depicts a transverse section through the region of the pharynx; the gastrovascular system and tentacle sheaths have been omitted for clarity.

lobates like *Leucothea* and *Eurhamphaea* cruise slowly forward to increase encounters with prey, and others like *Euplokamis* have giant ctenes that can propel them at many body lengths per second during escape swimming. Each comb row comprises many ctenes. Each ctene consists of a transverse band of hundreds of very long, partly fused cilia (to 3.5 mm in length) that beat together as a unit (see Figure 6.11D). Ctenophores are the largest animals known to use cilia for locomotion. Each cilium has a typical 9+2 microtubule structure, but each also possesses a unique set of lamellae at the 3 and 8 doublets; these lamellae protrude to link together the adjacent cilia.

Ctenophores are beautiful animals to observe in life because their beating comb rows appear iridescent over a wide range of light intensities. This feature of ctenophoran movement appears to be caused by the dense and highly regular packing of ciliary elements at the base of each comb row. Because of their size, ctenophore ctene plates move at low Reynolds numbers, where fluid flow is smoother but where water viscosity can impede ciliary movement. In contrast, the bodies of ctenophores move at higher Reynolds numbers, where viscosity is less important but water turbulence can impede or enhance animal movement through the medium.

As noted previously, mesenchymal musculature is used to maintain body shape and assist in feeding; it is involved in behaviors such as prey swallowing, pharyngeal contractions, and tentacle movements. Usually both longitudinal and circular muscles are present just beneath the epidermis. In the benthic and epifaunal platyctenids, stomodeal musculature facilitates a creeping locomotion. In the snakelike cestids, body muscles may generate graceful swimming undulations. Swimming in the lobate ctenophores is assisted by muscular flapping of their two oral lobes, especially in active species like *Ocyropsis maculata*, whose lobes appear frosty white due to the density of musculature. The lobate *Leucothea* (Figure 6.2G) can swim either by typical slow ctene propulsion or by rapid ctene propulsion; the latter is accomplished by coiling the lobes and increasing ciliary beat to produce a vortex wake, resulting in jet propulsion. Giant smooth muscle fibers—the first to be discovered in ctenophores—have been found in *Beroe*.

Feeding and Digestion

Comb jellies, so far as is known, are mostly predatory in their habits, and none are true parasites. The long tentacles of cydippids (and of the larvae of most other forms) have a muscular core with a colloblast-laden epidermal covering (Figure 6.7). The tentacles trail passively, are deployed in repeatable patterns, or are "fished" by various jigging motions. Upon contact with zooplankton prey, the adhesive granules in the colloblasts (sometimes called **lasso cells**) burst and discharge a strong adhesive

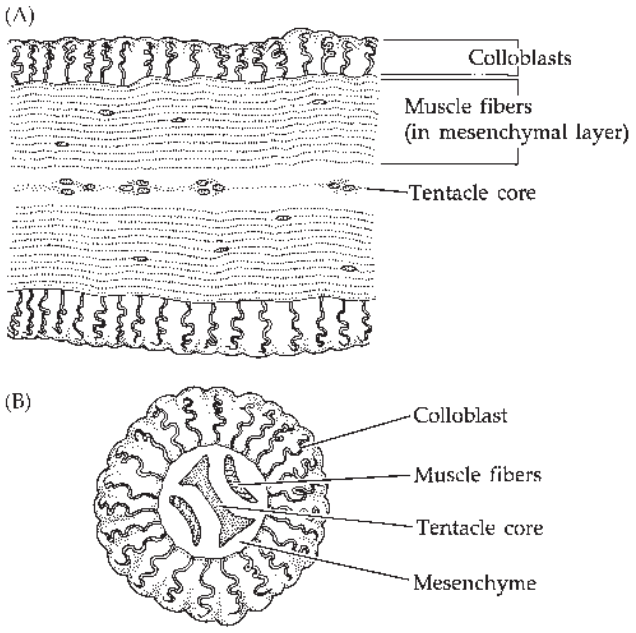


FIGURE 6.7 Ctenophore tentacle structure. (A) Longitudinal section of tentacle. (B) Cross section of a lateral filament (tentilla) of a tentacle.

material. Each multicellular colloblast develops from a single cell and consists of a hemispherical mass of secretory granules attached to the muscular core of the tentacle by a spiral filament coiled around a straight filament (Figure 6.8). The straight filament is actually the highly modified nucleus of the colloblast cell. The end of the spiral filament, which extends like a spring, adheres to the prey by the sticky material produced in the secretory granules. As the tentacles accumulate prey, they are periodically wiped across the mouth by muscular contractions or partially consumed, in some species combined with a coordinated somersaulting action of the animal that brings the mouth to the trailing tentacle. In members of the orders Lobata and Cestida, which bear very short tentacles, small zooplankton are trapped in mucus on the body or lobe surface and then carried to the mouth by ciliary currents (along the ciliated **auricular grooves** in lobate forms and ciliated **oral grooves** in cestids). Most of the benthic platyctenids also feed by capturing zooplankton in a somewhat similar fashion or using long trailing tentacles.

In some areas of the world's seas, ctenophores may be the dominant macrozooplankters and planktonic predators (e.g., *Mertensia ovum* in the Arctic region). *Mnemiopsis leidyi* is a highly effective predator and captures prey (e.g., microplankton, copepods, fish larvae) at rates comparable to predatory copepods and fish; early life stages may consume both zooplankton and phytoplankton. Many ctenophores consume crustaceans, fish larvae, and other plankton. The lobate ctenophore *Bolinopsis infundibulum* feeds primarily on copepods, which may sink to water layers near the seafloor during diapause and where *B. infundibulum*

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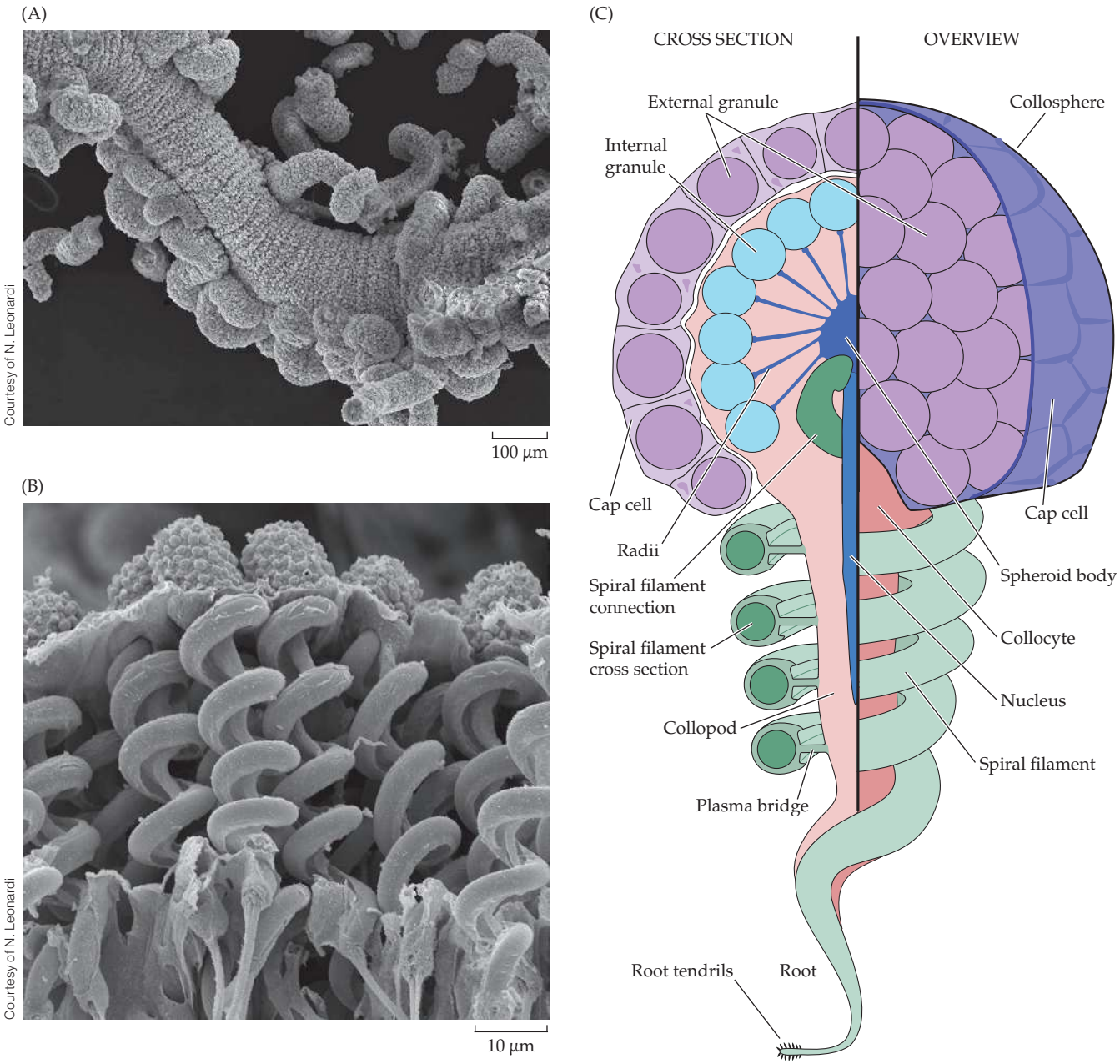
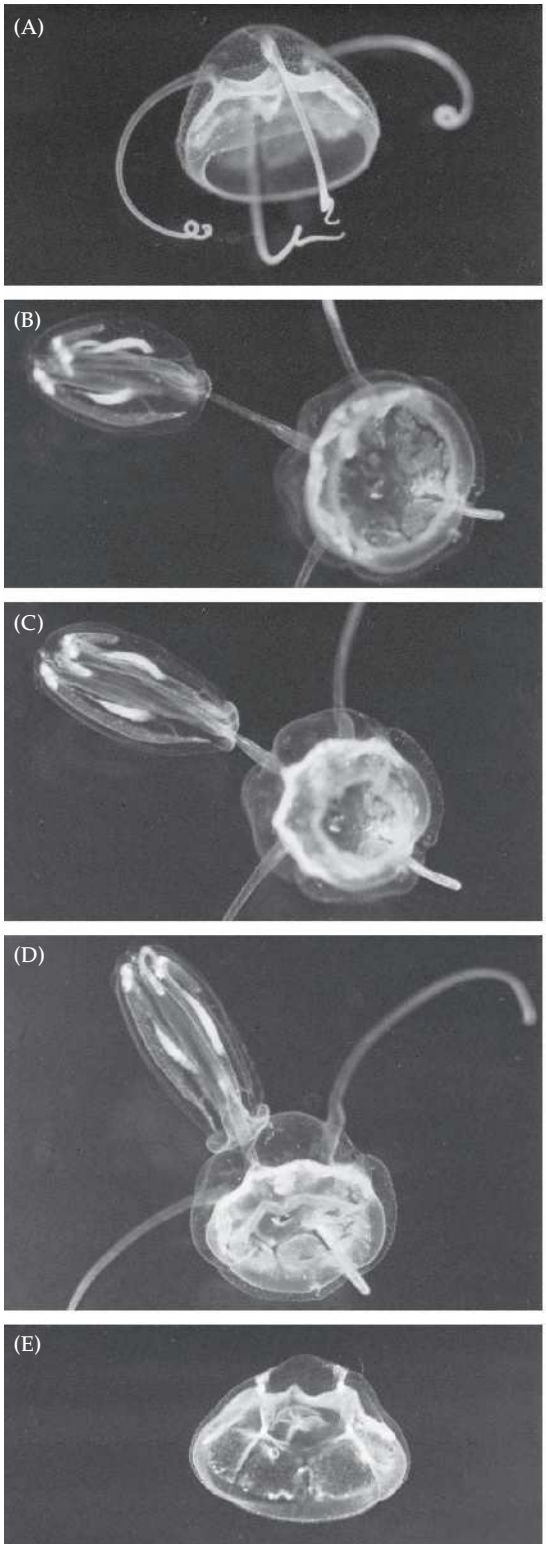


FIGURE 6.8 Colloblasts. (A) Tentacle of *Pleurobrachia bachei* covered with colloblasts. (B) Elongated colloblasts from *Aulacoctena* sp. showing (top to bottom) the cap cell with embedded adhesive granules, the spiral filament, and the root. (C) Diagram of the major structural and functional parts of a colloblast.

may form large aggregations to feed on this abundant source of carbon. The tendency of ctenophores to form aggregations near food sources or at the water's surface may contribute to their patchy distribution in nature.

Some ctenophores prey on larger animals, especially gelatinous forms. For example, as an adult the cydippid *Lampea* engulfs pelagic tunicates (salps, doliolids); but as larvae and juveniles, when they are too small to consume the whole salp, they adhere to the side with their open mouth, giving the impression of a parasite. Figure 6.9 is a series of remarkable photographs showing the cydippid ctenophore *Haeckelia* eating the tentacles of the narcomedusa *Aegina*. After consuming the tentacles one by one, *Haeckelia* retains the prey's unfired nematocysts, incorporates them into its epidermis, and uses them for its own defense. This phenomenon, known as **kleptocnidism**, occurs in several unrelated animal groups that prey on cnidarians (see Chapter 7). Because narcomedusae feed on other carnivorous jellies, this suggests that tiny 1 cm *Haeckelia* may be four trophic stages removed from the phytoplankton at the base of many marine food webs.



From C. E. Mills and R. L. Miller. 1984. *Mar Biol* 78: 215–221; https://link.springer.com/article/10.1007/BF00394704

FIGURE 6.9 The cydippid ctenophore *Haeckelia rubra* (= *Euchlora rubra*) feeding on the trachyline hydromedusa *Aegina citrea*. (A) Intact specimen of *Aegina*, with all four tentacles present. (B) *Haeckelia* begins to consume one of *Aegina*'s tentacles. (C) Most of the first tentacle of the medusa has been ingested. (D) Same animals, 2 minutes after feeding began. (E) *Aegina* has lost all four of its tentacles to *Haeckelia*, which goes on to incorporate the nematocysts into its own simple tentacles.

Ctenophores were center stage in an ecological drama that played out in the Black Sea near the end of the twentieth century. In the 1980s, the predatory northwest Atlantic ctenophore *Mnemiopsis leidyi* was accidentally introduced into the Black Sea from ship ballast water. The few invaders quickly underwent explosive population growth, reaching biomass levels in excess of 1 kg/m^3 by 1989, devastating the food web of the entire Black Sea basin and causing a collapse of the anchovy fishery (anchovy is one of the favored prey of *M. leidyi*). Then, in 1997, another ctenophore, *Beroe ovata*, was accidentally introduced to the Black Sea, probably also from ballast water. *Beroe ovata* readily feeds on *Mnemiopsis*, and its introduction resulted in a precipitous decline (perhaps extirpation) of *M. leidyi* in the sea, followed at last by the disappearance of *Beroe* itself. Introduced ctenophores continue to present a threat to local fisheries in many parts of the world, and their numbers are now monitored closely, particularly in the Mediterranean Sea. In recent years, *M. leidyi* has invaded the Caspian, Baltic, and Adriatic Seas, eastern Mediterranean, and parts of the North Sea and in every case has led to decreases in zooplankton abundances and diversity.

The ctenophoran mouth opens into an elongate, flattened, muscular, stomodeal pharynx. The epithelium of the pharynx is richly endowed with gland cells that produce digestive juices. Large food items are tumbled within the pharynx by ciliary action. Digestion takes place extracellularly, mostly in the pharynx. The largely digested food passes via a small chamber (the **infundibulum**, funnel, or stomach) from the pharynx into a complex system of radiating gastrovascular canals (Figures 6.3 and 6.4), eventually being evacuated through the anal pores or mouth. The details of the arrangement of the canals vary among different groups; the following description applies to the arrangement in a cydippid.

Two **paragastric** or **pharyngeal canals** recurve and lie parallel to the pharynx. Two **transverse canals** depart at right angles to the stomodeal plane and divide into three more branches. The middle branch of each triplet, the **tentacle canal**, leads to the base of the tentacle sheath. Although there is considerable diversity in ctenophore "plumbing," typically each of the other two branches (the **interradial canals**) bifurcates to form a total of four **adradial canals** on each side of the animal. These in turn connect to the eight **meridional canals**, one beneath each comb row. Depending on the morphology of the species, these canals can have diverticula or elaborations which allow them to serve lobes and internal structures that are not adjacent to the comb rows. Finally, an **aboral canal** passes from the infundibulum to the aboral pole, where it divides beneath the apical sense organ into four short canals, two ending blindly and two diagonally opposed (the anal canals) opening to the outside via small **anal pores**. These pores may open and seal intermittently, becoming undetectable when not in use. They serve as

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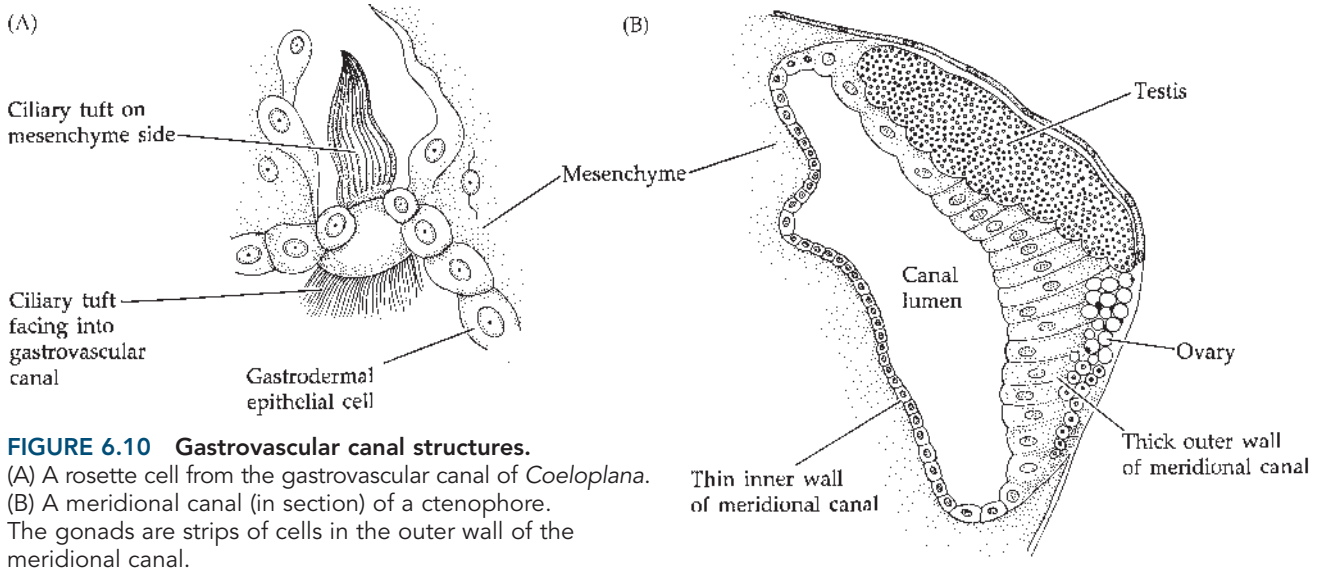

FIGURE 6.10 Gastrovascular canal structures.
(A) A rosette cell from the gastrovascular canal of *Coeloplana*. (B) A meridional canal (in section) of a ctenophore. The gonads are strips of cells in the outer wall of the meridional canal.

a rudimentary anus, assisting the mouth in the voiding of indigestible material and digested waste.

Within this very complicated gastrovascular canal system, digestion is completed, nutrients are distributed through the body, and absorption takes place. Minute pores lead from the various canals into the mesenchyme (Figure 6.10). Surrounding these pores are circlets of ciliated gastrodermal cells called **cell rosettes**, which appear to regulate the flow of the digestive soup and perhaps also play a role in excretion. Except for the stomodeal pharynx, the gastrovascular system is lined by a simple epithelium of endodermal origin.

Circulation, Excretion, Gas Exchange, and Osmoregulation

There is no independent circulatory system in ctenophores; as in cnidarians, the gastrovascular canal system serves in this role by distributing nutrients to most parts of the body. The gastrovascular system probably also picks up metabolic wastes from the mesenchyme for eventual expulsion out of the mouth or anal pores. The cell rosettes may also transport wastes to the gut. Gas exchange occurs across the general body surface and across the walls of the gastrovascular system. All of these activities are augmented by diffusion through the gelatinous mesenchyme. Movement of water over the body surface is enhanced by the beating of the comb plates. Thus, the extensive canal system and the ciliary bands help to overcome the problem of long diffusion distances. In genera with larger-bodied species and smaller surface-to-volume ratios, such as *Beroe* and *Aulacoctena* (length to 20 cm), diverticula from the meridional canals penetrate the mesoglea and distribute nutrients throughout the body. It has even been shown that the gel of ctenophores may sequester oxygen and provide a reservoir that buffers the animals from intermittent exposure to hypoxia.

Nervous System and Sense Organs

Although the nervous systems of both ctenophores and cnidarians are noncentralized nerve nets, there are certain important differences. In ctenophores, nonpolar neurons form a diffuse **subepidermal plexus**. Beneath the comb rows, the neurons form an **elongate plexus** or meshes such that they produce nervelike strands. The bases of the ctenes are thus in contact with a rich array of nerve cells. A similar concentrated plexus surrounds the mouth. However, as in cnidarians, no true ganglia occur, a condition that contrasts markedly with the presence of a centralized nervous system in bilateral Metazoa (the Bilateria).

The nerve nets of ctenophores consist of polygonal nerve cords spread under the ectodermal epithelium; these nerve nets show high levels of regional specialization and concentrations associated with the apical sensory organ/polar fields and tentacle bulbs—structures without clear homologues in any other animal group. In the genus *Euplokamis,* which displays rapid swimming and bioluminescent flashes, giant axons underlying the comb rows provide rapid neural conduction.

Within the apical sense organ is a **statocyst**, in which is a **statolith** that functions in balance and orientation. The statolith contains magnesium and calcium carbonates (possibly phosphates) and is made up of clusters of concretion-bearing cells called **lithocytes**, supported by four long tufts of cilia called **balancers** (Figure 6.11). The whole structure is enclosed in a transparent **dome** that is also derived from cilia. From each balancer arises a pair of **ciliated furrows** (= **ciliated grooves**), each of which connects with one comb row. Thus, each balancer innervates the two comb rows of its particular quadrant. Tilting the animal causes the statolith to press more heavily on the downside balancers, and the resulting stimulus elicits a vigorous beating of the corresponding comb rows to right the body. Depending on the "mood" of the individual (often associated with

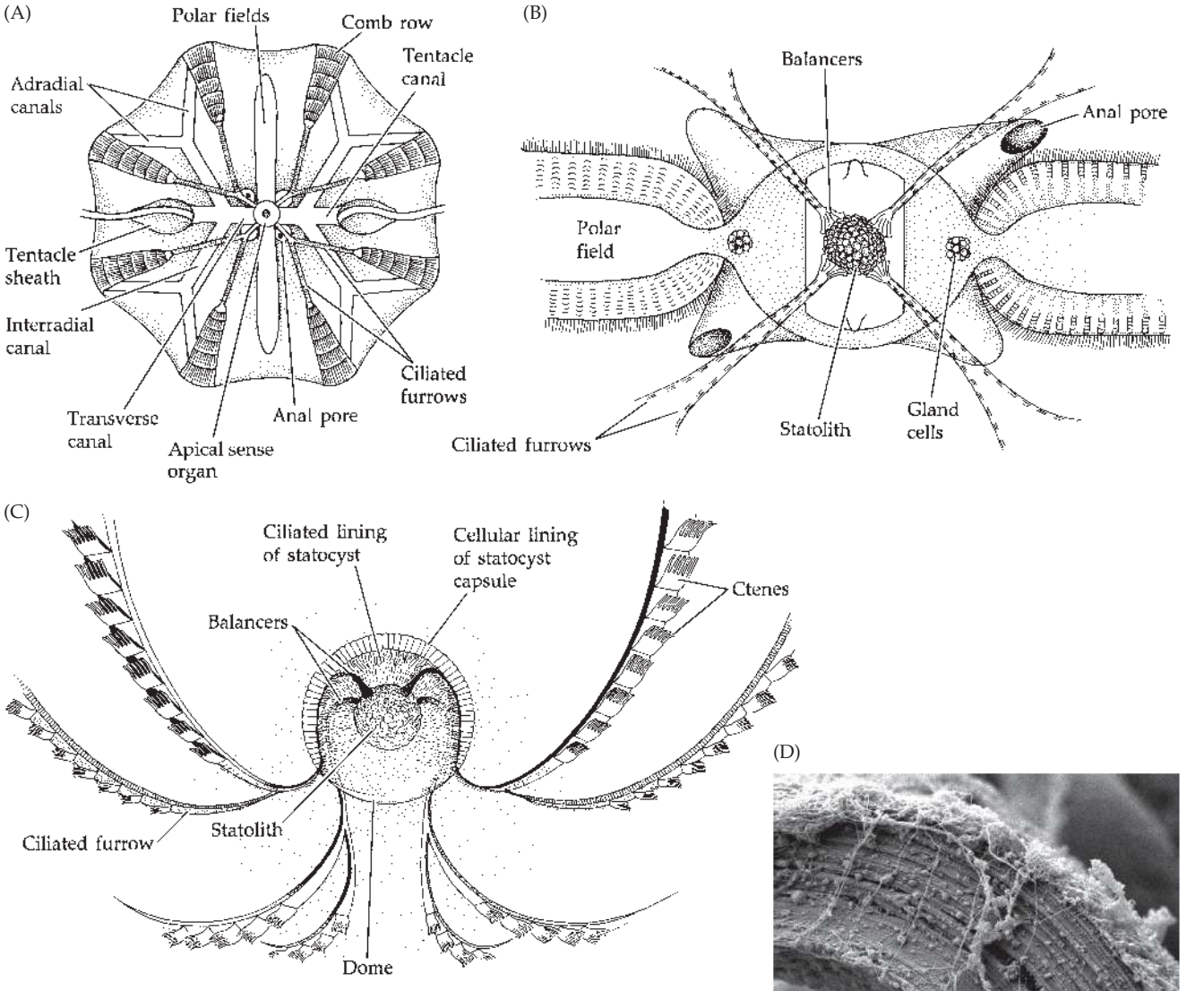

FIGURE 6.11 The ctenophore apical sense organ. (A) *Pleurobrachia* (aboral view). Note the relationship of the statocyst to the comb rows, the ciliated furrows, and the gastrovascular canals. (B) Apical sense organ of the cydippid *Hormiphora*. (C) Apical sense organ and its relationship to the eight comb rows. (D) Scanning electron micrograph showing the side view of a ctene from *Beroe forskalii*. The plate has been split along its axis to reveal the long bundles of cilia.

light-dark cycles), tilting might induce downward- or upward-directed swimming.

The two comb rows in each quadrant, connected to a single ciliated furrow, beat synchronously. If a ciliated furrow is cut, the beating of the two corresponding comb rows becomes asynchronous. The normal direction of ciliary power strokes is toward the aboral pole, so the animal is driven forward oral end first. The beat in each row, however, begins at the aboral end of the comb row and proceeds in metachronal waves toward the oral end (i.e., antiplectic metachrony). Stimulation of the oral end reverses the direction of both the wave and the power stroke. Removal of the apical sense organ or statolith results in an overall lack of coordination of the comb rows, and the injured ctenophore loses its ability to maintain a vertical position. The comb rows are very sensitive to contact; when a comb row is touched, some species partially retract it into a groove formed in the jellylike body.

In cydippids and beroids, the stimulation for any given ctene to beat is triggered mechanically by hydrodynamic forces arising from the movements of the preceding plate. However, in the lobate ctenophores, the ctenes are not coordinated in this

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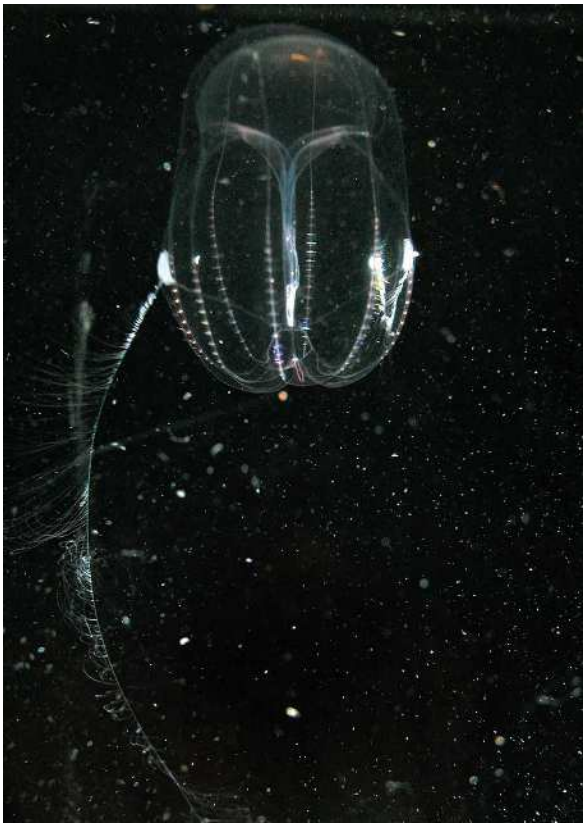
mechanical fashion. In these animals a narrow tract of shorter cilia—the **interplate ciliated groove**—runs between successive ctenes and is responsible for coordinating their activity. It is not known how the cilia of the groove are coordinated or how the grooves stimulate the appropriate comb row, so these actions may also be mechanical. The interplate ciliated grooves develop only as the lobate ctenophores mature to adulthood; the free-swimming larvae resemble cydippids and lack the grooves.

In most ctenophores, two oval tracts of cilia called polar fields lie on the stomodeal plane of the aboral surface (Figure 6.11B). These structures are thought to be sensory in function.

Reproduction and Development

Asexual reproduction and regeneration Many ctenophores (to a lesser extent in beroids) can regenerate virtually any lost part, including the apical sense organ. Entire quadrants and even whole halves will regenerate. Platyctenids reproduce asexually by a process that resembles pedal laceration in sea anemones; small fragments break free as the animal crawls, and each piece can regenerate into a complete adult.

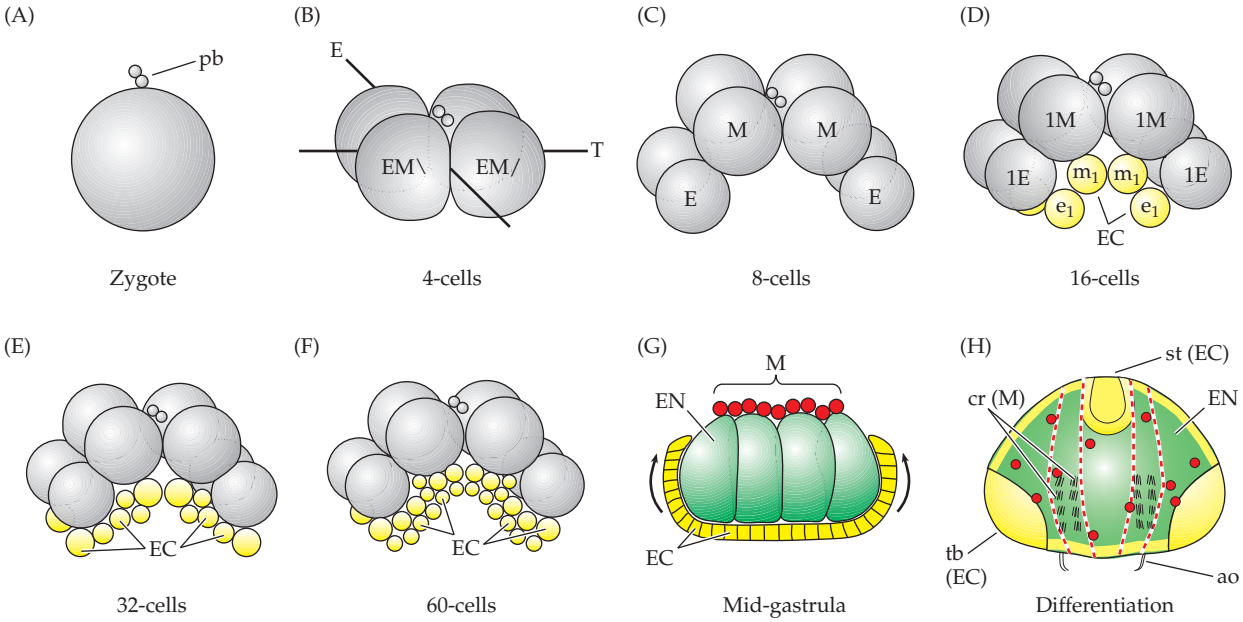
Sexual reproduction and development Most ctenophores are hermaphroditic, but a few gonochoristic species are known (e.g., members of the genus *Ocyropsis*). The gonads arise on the walls of the meridional canals (Figure 6.10B), with eggs arranged on the side adjacent to the major axes and with sperm next to the minor axes. Pelagic ctenophores generally shed their gametes via the mouth into the surrounding seawater, where either self-fertilization or cross-fertilization takes place. Fertilization appears to take place within the meridional canals in *Pleurobrachia*. Special sperm ducts occur in at least some platyctenid species. The eggs are centrolecithal and formed in association with nurse cell complexes. Polyspermy is known to occur in some ctenophores. Those that free-spawn typically produce embryos that grow quickly to planktotrophic **cydippid larvae** (Figure 6.12), although species in the order Beroida lack this larval phase. Development is thus usually indirect, although growth to the adult is gradual rather than metamorphic. Some ctenophores are known to reproduce sexually before they have completed their larval development, a condition known as **dissogeny**. Precocious reproduction is known in at least two orders (Lobata: *Mnemiopsis leidyi*; Cydippida: *Pleurobrachia bachei*) and may reflect an evolutionary history favoring early reproduction, possibly because food supplies are only intermittently available or because predation rates are high. In the benthic *Coeloplana* and *Tjalfiella*, and in a few pelagic species, fertilization is internal and embryos are brooded until a cydippid larva is formed and released. This mixed life history provides a means of dispersal for these benthic, sedentary animals.

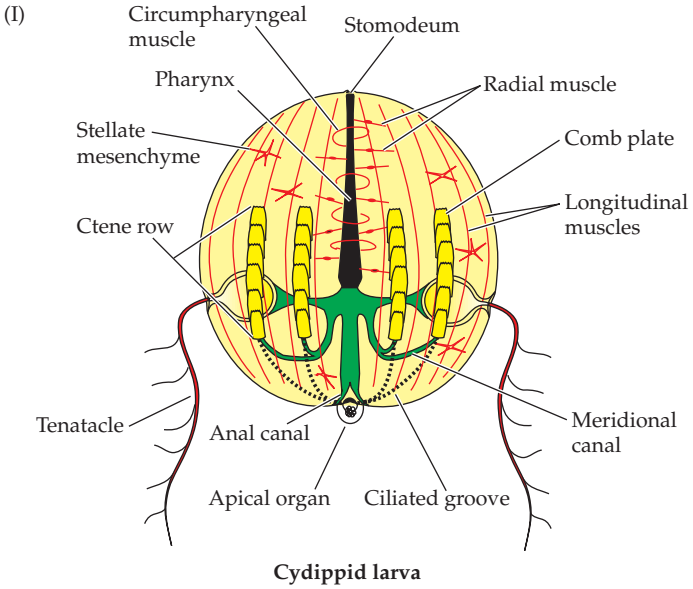


Courtesy of S. Haddock

FIGURE 6.12 A typical young cydippid larva of the lobate *Bolinopsis*, which will shortly take on its adult lobate body form.

Ctenophoran cleavage cannot easily be classified as either spiral or radial (Figure 6.13). During early cleavage, the first four blastomeres arise by the usual two meridional cleavages, which mark the adult planes of symmetry. Even at this stage, corresponding quadrants are diagonally opposed, suggestive of their rotational symmetry. The third division is also nearly vertical and results in a curved plate of eight cells (with four macromeres). The next division is latitudinal and unequal, giving rise to micromeres on the concave side of the macromere plate. The micromeres continue to divide and spread by epiboly over the aboral pole and eventually over the macromeres. The latter also invaginate, so the gastrula arises through a combination of epiboly and invagination. Thus, the micromeres become ectoderm and the macromeres become endoderm. Just prior to gastrulation, the macromeres divide and produce additional micromeres on the oral side of the embryo. Whereas the aboral micromeres become ectoderm, these oral micromeres are incorporated into the endoderm and, in at least some species, give rise to photoreceptor cells. There





Tentacular axis (T)
Esophageal axis (E)
Apical organ precursors (ao)
Ctene row precursors (cr)
Polar bodies (pb)
Tentacle bulb precursors (tb)
Stomodeum (st)

Cells give rise to ectoderm (EC)
Cells give rise to endoderm (EN)
Cells give rise to mesechymal/mesodermal structures (M)

FIGURE 6.13 Ctenophore embryogeny: schematic diagram and fate map of ctenophore development. (A) Lateral view of the fertilized egg. The polar bodies (pb) mark the animal pole, which represents the future oral end of the animal in all illustrations. (B) At second cleavage each blastomere divides asymmetrically to give rise to an EM/ and an EM\ cell. The EM/ and EM\ cells lie in opposite, not adjacent, locations in the embryo. (C) At third cleavage, two distinct cell lineages are born, the E (end) and M (middle) blastomeres. (D) At the 16-cell stage, small micromeres arise that are given subscript numerals to indicate the order of their birth (e.g., e_1). Their sister macromeres are given ordinal numbers for ease of identification. (E) At the next round of divisions, the 1E and 1M macromeres give rise to another round of micromeres and each micromere also divides. (F) The 60-cell stage arises as all cells divide one additional time except for the 2M macromeres. (G) As gastrulation by epiboly begins, a distinct set of micromeres is born at the oral pole. These will give rise to the mesodermal derivatives. (H) The tentacle bulbs thicken prior to their invagination, the comb row cilia begin to beat, muscle and mesenchymal cells appear, and the apical organ begins to coalesce as components from all four quadrants move toward the aboral pole. (I) By approximately 24 hr, a fully functional cydippid-stage animal is formed. Cells colored in yellow give rise to ectoderm, cells colored green give rise to endoderm, and cells in red give rise to mesenchymal/mesodermal structures.

is some question about the fate of all of these oral micromeres. Metschnikoff (1885) suggested that these cells may contribute to the mesenchyme and may thus be viewed as true endomesoderm. Martindale and Henry (1999) mapped the fate of embryonic cells and showed that the mesenchyme is derived from endoderm. However, as mentioned previously, the genomes of *Mnemiopsis leidyi* and *Pleurobrachia bachei* show important genetic differences in the pathways for ctenophoran mesenchyme and the mesoderm of true triploblastic bilaterians.

As the micromeres cover the embryo to form the epidermis, four interradial bands of small, rapidly dividing cells become apparent. Eventually, each of

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these thickened ectodermal bands differentiates into two of the comb rows. The aboral ectoderm differentiates into the apical sense organ and its related parts; the oral ectoderm invaginates to form the stomodeum. The gastrovascular system develops from endodermal outgrowths, and the tentacle sheaths arise as ectodermal invaginations from the points where the tentacles sprout. The embryo eventually develops into a free-swimming cydippid larva (Figures 6.12 and 6.13) that closely resembles adult ctenophores of the order Cydippida. Given the transformation, it is tempting to invoke Haeckel's "ontology recapitulates phylogeny" and conclude that Cydippida houses the most primitive lineage of extant ctenophores.

The development of ctenophores differs markedly from that of cnidarians. In the latter group, early cleavage results in an irregular mass of cells whose fates are not clearly predictable until later development, and the mesenchyme is strictly ectodermal in origin. In the ctenophores, on the other hand, development is determinate and a very precise cleavage pattern unfolds, in which the ultimate morphology is definitely mapped. For example, if the two blastomeres of a two-cell embryo are experimentally separated, the "half-embryos" develop into adults with exactly half the normal set of adult structures. Such results indicate that blastomere fate is highly determined, but they also suggest that inductive processes among embryonic cells and tissues are important in ctenophore embryogenesis, as is true in many bilaterian Metazoa. Additional data suggest that such processes can lead to more variation in cell fate than was previously suspected. Ctenophores produce a cydippid larval type having no counterpart among other metazoans.

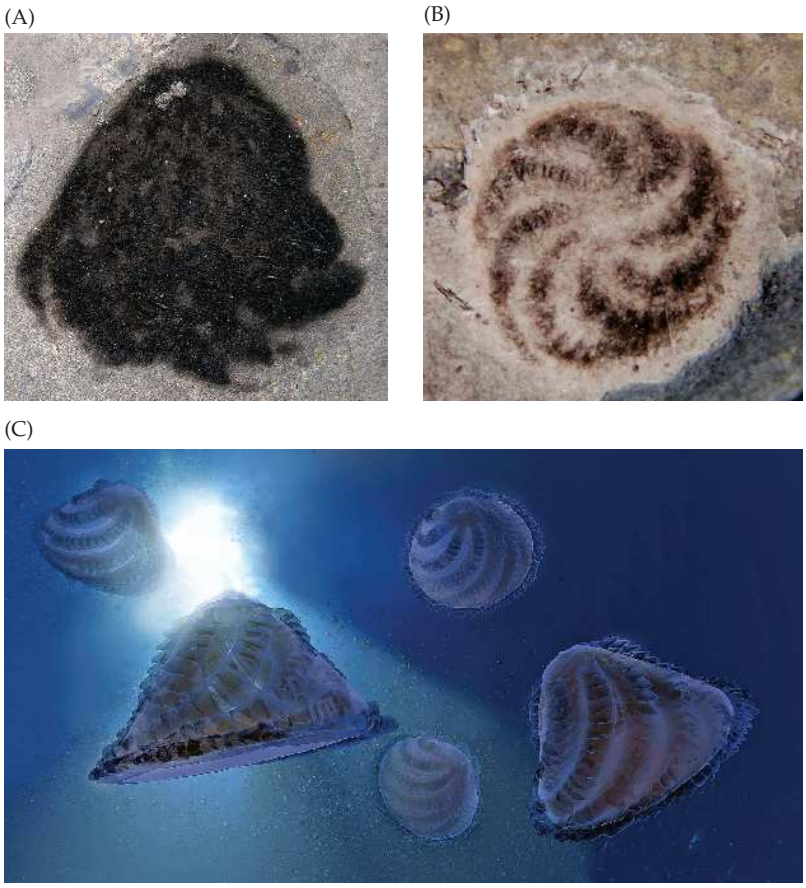
Ctenophoran Phylogeny

Even though the ctenophores and hydrozoan cnidarians share superficial traits such as cellular mesenchyme and transparency, there are no robust affinities between ctenophores and any cnidarian group, with the exception of unipolar cleavage. The early concept of "Coelenterata" is not currently considered accurate nor particularly useful. Many of the similarities between ctenophores and cnidarian medusae are likely to be convergences reflecting adaptations to their similar lifestyles, and in fact, many gelatinous zooplankters from across metazoan diversity show superficial similarities in body form and construction. Benthic ctenophores (e.g., *Ctenoplana* and *Coeloplana*), which are flattened and creep along substrates, show some similarities with flatworms (Platyhelminthes; Chapter 17), but again this is convergence.

It is not just the affinities of ctenophores, but their phylogenetic relationships to other nonbilaterian Metazoa (Porifera, Placozoa, Cnidaria) that remain enigmatic. Some molecular phylogenies have placed the Ctenophora as sister group to the rest of the animals (including Porifera), as the earliest-diverging animal phylum. Perhaps supporting this hypothesis are phylogenomic studies that have shown the genomes of ctenophores and sponges to lack several homeobox-containing genes that are present within the genomes of placozoans, cnidarians, and bilaterians. Further, ctenophore genomes are unique in many respects. For example, they lack microRNA and microRNA-processing machinery, and their mitochondrial genomes are reduced. The debate between the "Porifera-first" and "Ctenophora-first" scenarios continues even in the presence of more comprehensive sampling of the diversity of each group, and better-quality data sets. However, methodological studies have shown that the choice of evolutionary model, outgroup taxa, and even inclusion of a particular handful of genes can sway the outcome. Resolving this question remains challenging because of the relatively small branch lengths separating the divergence of sponges and ctenophores, the long branches from that point to extant taxa, and the potential for saturation of the genetic signal due to great ages of origin, even with full genomes in hand.

Phylogenetic relationships within the Ctenophora have been challenged by limited gene data until recently, with phylogenomic analyses representing the main lineages of ctenophores. Molecular data show that the tentaculate condition is primitive and the atentaculate lineage (the order Beroida) arose from within the tentaculate groups. This placed the former class Nuda well nested within the former class Tentaculata. Furthermore, the Haeckeliidae, which have simple tentacles lacking side branches, has been shown to be the sister group to Beroidae, suggesting a progressive loss of tentacles. Molecular phylogenetic studies have also suggested that the cydippid family Mertensiidae might be the sister group to all other ctenophores, that Cydippida is clearly not monophyletic, and that some of the other orders are likely nested within the Lobata.

The fossil record for ctenophores faces several challenges, given the rare fossilization of these diaphanous organisms. In only a few cases can the features of a fossil be said to clearly correspond to the anatomy of extant ctenophores. Therefore, when a specimen has traits reminiscent of ctenophores but differs in other ways, it is hard to interpret whether this means early ctenophores were fundamentally different from modern ones, or whether the fossil may in fact not be a ctenophore ancestor at all. The fossils suggesting stalked ctenophores, or skeletonized meridional canals, are unlikely to actually be ctenophore progenitors. Cambrian fossils that have been ascribed to ctenophores typically lack tentacles, leading to the



A and B from F. S. Tang et al. 2011. *Evol Dev* 13: 408–414. © 2011 Wiley Periodicals, Inc.

Courtesy of Javier Herboso

FIGURE 6.14 The Ediacaran fossil *Eoandromeda octobrachiata* from the Doushantuo Formation (580–551 Ma) in southern China. (A,B) Carbonaceous impressions from the Institute of Geology, Chinese Academy of Geological Sciences, Bejing. (C) Artist's rendering of live *Eoandromeda*.

"atentaculate primitive" hypothesis. If this is correct, then modern atentaculate ctenophores will have secondarily lost tentacles, because even before molecular evidence, it was considered that they are well nested within the tentaculate forms. The modern eight-comb rows appear to have stabilized in fossil forms long ago, including the first ctenophore fossil described in 1983. The enigmatic Ediacaran *Eoandromeda*, with octoradiate symmetry (generally equated with four pairs of comb plates), may have been an atentaculate ctenophore whose comb rows spiraled down the length of its cone-shaped body (Figure 6.14).

Chapter Summary

This chapter introduced you to two unusual, marine animal phyla, Placozoa and Ctenophora. Both are nonbilaterian, basally positioned clades in the animal tree of life, although their precise phylogenetic relationships remain elusive. Placozoans were first discovered in 1883, and only a few additional species have been described since. The bodies of these creatures are but a few millimeters in size, just two cell layers thick, and lack both symmetry and organs. They reproduce both sexually and asexually (by fragmentation or fission). Ctenophores are gelatinous creatures with biradial symmetry that are found floating in the open sea or on the seafloor. Although only about 130 species have been described, they can be quite common and abundant predators in the world's seas. Neither placozoans nor ctenophores have left a robust fossil record.

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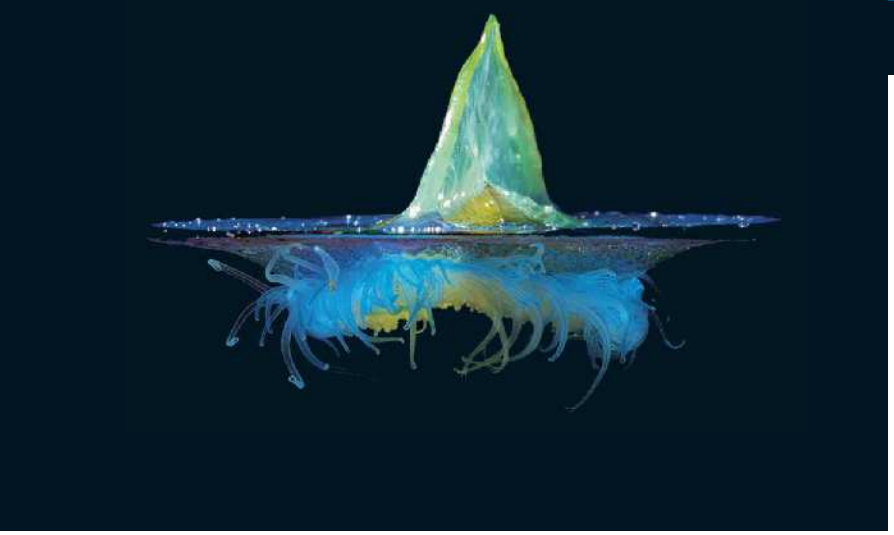

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CHAPTER 7

Phylum Cnidaria

Anemones, Corals, Jellyfish, and Their Kin

The phylum Cnidaria is a highly diverse assemblage that includes jellyfish, sea anemones, corals, and the common laboratory *Hydra*, as well as many less familiar forms such as hydroids, sea fans, siphonophores, zoantharians, and the endoparasitic Endocnidozoa (Box 7A, Figure 7.1). There are about 13,300 described living species, all of which are predators (or highly modified parasites). Much of the striking diversity seen in this phylum results from three fundamental aspects of their natural history. First is the possession of **cnidae**—unique, tubular structures contained within cellular capsules that aid in prey capture, defense, locomotion, and attachment. No other animal group produces cnidae, and all cnidarians produce them. Second is the tendency to form colonies or assemblages of individuals by asexual reproduction; the colony can achieve dimensions and forms unattainable by single, nonmodular individuals. Third, many species of cnidarians exhibit a dimorphic life cycle that can include two entirely different morphologies: a **polypoid** form and a sexual **medusoid** form, in addition to a larval form as in many marine animals. The dimorphic life cycle has major evolutionary implications touching on nearly every aspect of cnidarian biology.[1] The polyp form of Cnidaria, planula larvae, stinging or adhesive cnidae, unique epitheliomuscular cells, and ectodermal-endodermal nerve nets are some of the key anatomical synapomorphies that define the phylum (Figure 7.44).

Cnidarians are **diploblastic** metazoans, at the tissue grade of construction. They possess radial symmetry (the body axes being in an oral–aboral plane), tentacles, an endodermally derived incomplete **gastrovascular cavity** as their only "body cavity," and a

[1] When both polyp and medusa phases are present in a species' life cycle, it is said to undergo **alternation of generations**, or as it is sometimes called, "**metagenesis**."

Classification of The Animal Kingdom (Metazoa)

- PHYLUM PORIFERA
- PHYLUM CTENOPHORA
- PHYLUM PLACOZOA
- PHYLUM CNIDARIA

Bilateria (a.k.a. triploblasts)
- PHYLUM XENACOELOMORPHA

Nephrozoa

PROTOSTOMIA

Spiralia
- PHYLUM DICYEMIDA (=RHOMBOZOA)

GNATHIFERA
- PHYLUM CHAETOGNATHA
- PHYLUM GNATHOSTOMULIDA
- PHYLUM ROTIFERA
- PHYLUM MICROGNATHOZOA

PLATYTROCHOZOA
- PHYLUM ENTOPROCTA
- PHYLUM CYCLIOPHORA

Lophotrochozoa
- PHYLUM MOLLUSCA
- PHYLUM NEMERTEA
- PHYLUM ANNELIDA*

LOPHOPHORATA
- PHYLUM PHORONIDA
- PHYLUM BRYOZOA (=ECTOPROCTA)
- PHYLUM BRACHIOPODA

Rouphozoa
- PHYLUM GASTROTRICHA
- PHYLUM PLATYHELMINTHES

Ecdysozoa

SCALIDOPHORA**
- PHYLUM KINORHYNCHA
- PHYLUM PRIAPULA
- PHYLUM LORICIFERA

NEMATOIDA
- PHYLUM NEMATODA
- PHYLUM NEMATOMORPHA

PANARTHROPODA
- PHYLUM TARDIGRADA
- PHYLUM ONYCHOPHORA
- PHYLUM ARTHROPODA
  - SUBPHYLUM CHELICERATA
  - MANDIBULATA
    - SUBPHYLUM MYRIAPODA
    - PANCRUSTACEA
      - SUBPHYLUM CRUSTACEA***
      - SUBPHYLUM HEXAPODA

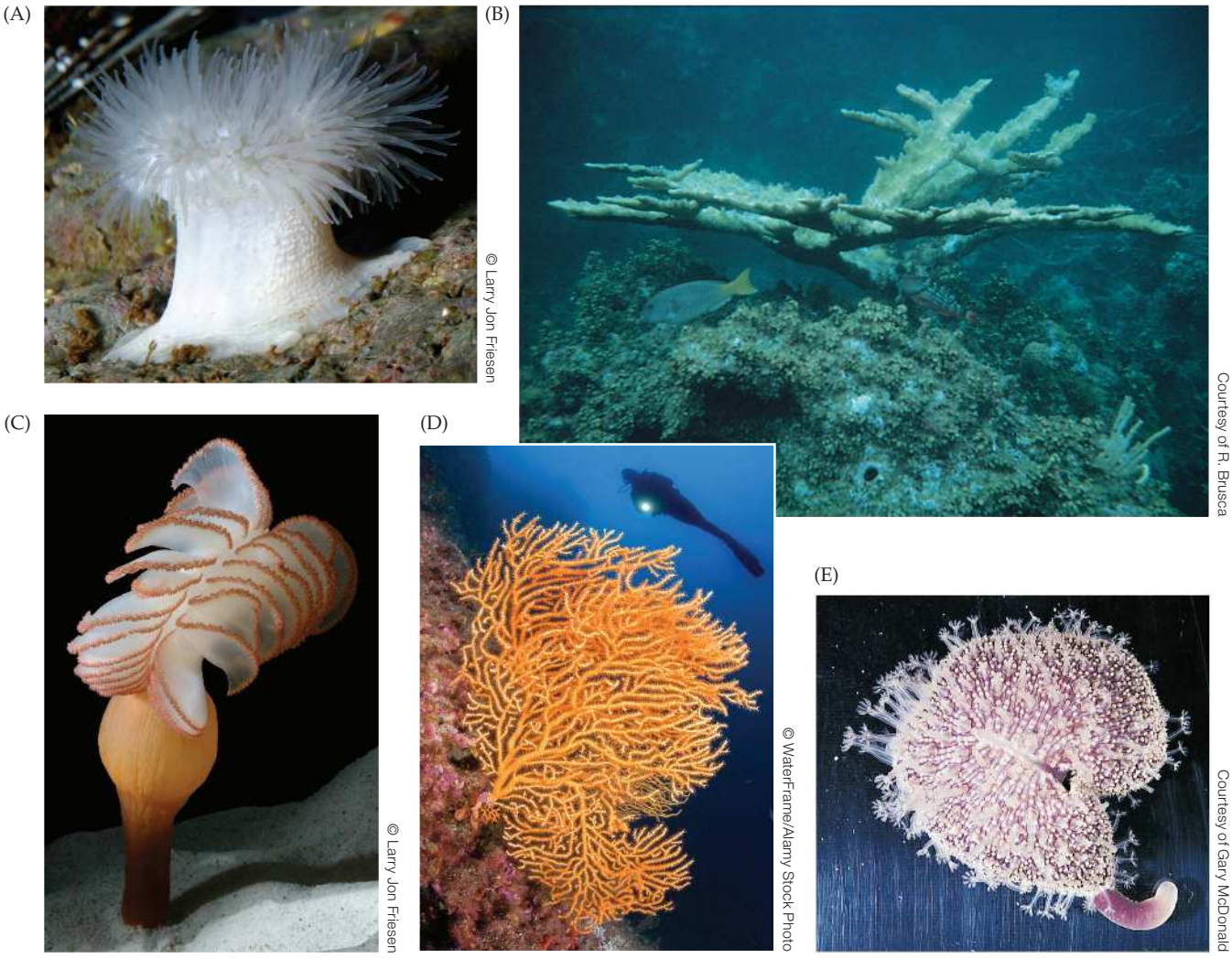
DEUTEROSTOMIA
- PHYLUM CHORDATA

AMBULACRARIA
- PHYLUM HEMICHORDATA
- PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida

** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent

*** Paraphyletic (excludes Hexapoda)



middle layer (called mesenchyme, or mesoglea) derived primarily from ectoderm.[2] They lack cephalization, a centralized nervous system, and discrete respiratory, circulatory, and excretory organs (Box 7B). This basic body plan is retained in both the polypoid and medusoid forms (Figure 7.2). In most, the radial symmetry is modified as biradial or tetraradial or by other degrees of radiality (animal symmetry was discussed in Chapter 3).

[2]There is a suite of terms in zoological literature that apply to non-triploblastic species that is frequently confused, misused, and generally messy. These terms include "mesenchyme," "mesoglea," "mesohyl," "collenchyme," "parenchyme," and "coenenchyme." In this book, these terms are used in the following ways. **Mesenchyme** (Greek, literally "middle juices") refers to a primitive connective tissue located between the outermost and innermost cell layers (e.g., epidermis and gastrodermis) and derived wholly or in large part from embryological ectoderm (and its derivatives). Mesenchyme generally consists of two components: a noncellular, jellylike matrix called **mesoglea**, and various cells and cell products (e.g., fibers). When no (or very little) cellular material is present, this layer is simply called mesoglea. Mesenchyme is the typical middle layer of sponges, between the pinacoderm and the choanoderm (where it is called the **mesohyl**), and of members of the diploblastic phyla Cnidaria and Ctenophora, between the endoderm (gastrodermis) and the ectoderm (epidermis). When cellular material is sparse or densely packed, mesenchyme may sometimes be designated as **collenchyme** or **parenchyme**, respectively. The term "parenchyme" is also sometimes used for the mesenchymal layer of triploblastic acoelomate animals (such as platyhelminths and xenacoelomorphans), in which the dense layer includes tissues derived from both ecto- and endomesoderm.

In some colonial cnidarians, particularly anthozoan polyps, the individuals are embedded in and arise from a mass of mesenchyme perforated with gastrovascular channels that are continuous among the members of the colony. The term coenenchyme refers to this entire matrix of common basal material, which is itself covered by a layer of epidermis.

Adding to the potential confusion, the term "mesenchyme" is used in a second, very different way by some biologists. Vertebrate embryologists sometimes use the term to refer to that part of true (endo-) mesoderm from which all connective tissues, blood vessels, blood cells, the lymphatic system, and the heart are derived. Thus, to a vertebrate embryologist, the term "mesenchymal cell" often denotes any undifferentiated cell found in the embryonic mesoderm that is capable of differentiating into such tissues. Occasionally, one also sees the term "mesenchyme" used in this way by echinoderm embryologists and non–vertebrate chordate specialists. In these latter cases, researchers are generally referring to cells that are destined to become mesodermal, and thus a better term might be "proto-" or "incipient mesodermal cells." Because of this confusion, some authors prefer to use the term "mesoglea" in lieu of "mesenchyme" when referring to the middle layers of sponges and diploblastic Metazoa. However, we adhere to the former definition of "mesenchyme" and hope that this note will lessen rather than add to the muddle.

A word of caution regarding spelling: the meanings of some of these terms can be altered by changing the terminal *e* to an *a*. The termination "-chyme" is preferred for animals, "-chyma" for plants. Thus, "mesenchyma" refers to tissue lying between the xylem and phloem in plant roots; "collenchyma" refers to certain primordial leaf tissues. "Parenchyma" is a very general botanical term used in reference to various supportive tissues. Unfortunately, the same spelling is occasionally (improperly) used by zoologists.

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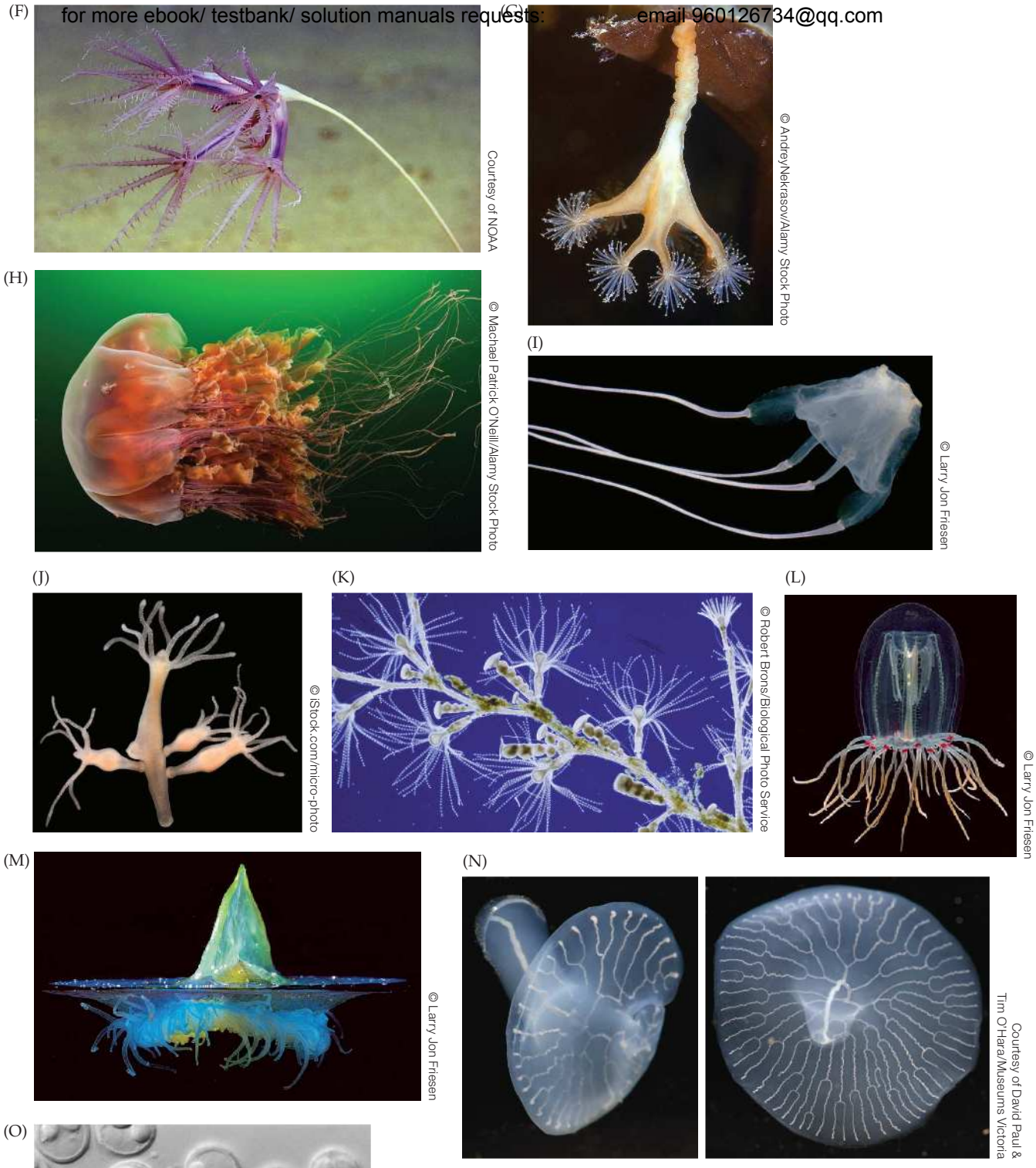

FIGURE 7.1 **Some cnidarians.** (A–F) Anthozoa. (A) An actiniarian, the sea anemone *Metridium senile*. (B) A Caribbean elkhorn coral, *Acropora palmata*. (C) A sea pen, *Ptilosarcus gurneyi* (Pennatulacea). (D) The yellow gorgonian *Eunicella cavolini* (Mediterranean Sea, Italy). (E) *Renilla amethystina*, a sea pansy (Pennatulacea). (F) The bizarre octocorallian *Umbellula* (Gulf of Mexico). (G–I) Medusozoa. (G) *Lucernaria*, a staurozoan (White Sea, Russia). (H) A lion's mane jellyfish, *Cyanea capillata*, a semaeostoman scyphozoan from the northeast Pacific Ocean. (I) *Carybdea marsupialis*, a cubozoan; (J–M) Hydrozoa. (J) *Hydra*, an aberrant freshwater anthomedusan (shown here budding). (K) A colony of the leptomedusan *Gonothyraea*. (L) The medusa of *Polyorchis*, an anthomedusan. (M) A colonial hydrozoan, *Velella* ("by-the-wind sailor"). (N) *Dendrogramma enigmatica*, bracts (with radial canals). (O) *Myxobolus cerebralis*, myxozoan spores from an infected trout.

BOX 7A Classification of the Phylum Cnidaria

SUBPHYLUM ANTHOZOA

- Class Anthozoa. Anemones, sea pens, gorgonians, corals
  - Subclass Octocorallia. Octocorals
    - Order Helioporacea
    - Order Alcyonacea
      - Suborder Protoalcyonaria
      - Suborder Stolonifera
      - Suborder Alcyoniina
      - Suborder Scleraxonia
      - Suborder Calcaxonia
    - Order Holaxonia
    - Order Pennatulacea
  - Subclass Hexacorallia. Anemones and stony corals
    - Order Zoantharia
    - Order Actiniaria
    - Order Antipatharia
    - Order Corallimorpharia
    - Order Scleractinia
  - Subclass Ceriantharia

SUBPHYLUM ENDOCNIDOZOA Parasites of annelids, bryozoans, and aquatic vertebrates

- Class Polypodiozoa (monotypic: *Polypodium hydriforme*)
- Class Myxozoa
  - Subclass Myxosporea
    - Order Bivalvulida
    - Order Malacosporea

SUBPHYLUM MEDUSOZOA

- Class Hydrozoa. Hydroids and hydromedusae
  - Subclass Trachylina
    - Order Limnomedusae
    - Order Trachymedusae
    - Order Narcomedusae
    - Order Actinulida
  - Subclass Hydroidolina
    - Order Thecata (= Leptomedusae, Calyptoblastea)
    - Order Athecata (= Anthomedusae, Gymnoblastea)
      - Suborder Capitata
      - Suborder Aplanulata
      - Suborder Filifera
    - Order Siphonophora
      - Suborder Cystonecta
      - Suborder Codonophora
- Class Staurozoa. Stalked jellyfish
- Class Cubozoa. Sea wasps and box jellyfish
  - Order Chirodropida
  - Order Carybdeida
- Class Scyphozoa. Jellyfish
  - Order Coronatae
  - Order Semaeostomeae
  - Order Rhizostomeae

Cnidaria are marine, except for some Hydrozoa and some Endocnidozoa; only a few dozen species have been described from inland waters. Most are sessile (polyps) or planktonic (medusae) predators, although some employ suspension feeding and many species harbor symbiotic intracellular "algae" (e.g., dinoflagellates, cyanobacteria) from which they may secondarily derive energy, and one clade (Endocnidozoa) is strictly parasitic. Free-living cnidarians range in size from nearly microscopic polyps and medusae, to individual jellyfish 2 m wide and with tentacles 25 m long. Colonies, such as corals and siphonophores, may be many meters in size. The phylum probably dates back to the Precambrian but is known with greater confidence from the earliest Cambrian. Its members have played important roles in various ecological settings throughout their long history, just as they do today.

In Asia, jellyfish are routinely consumed by humans, and they have been a regular part of Chinese cuisine for centuries. About 35 species are eaten, most from the order Rhizostomeae, which tend to have more rigid bodies and produce the desired crunchiness when cooked. Recently, jellyfish fisheries (for export to Asia) have also started up in the New World, from Canada to Peru and

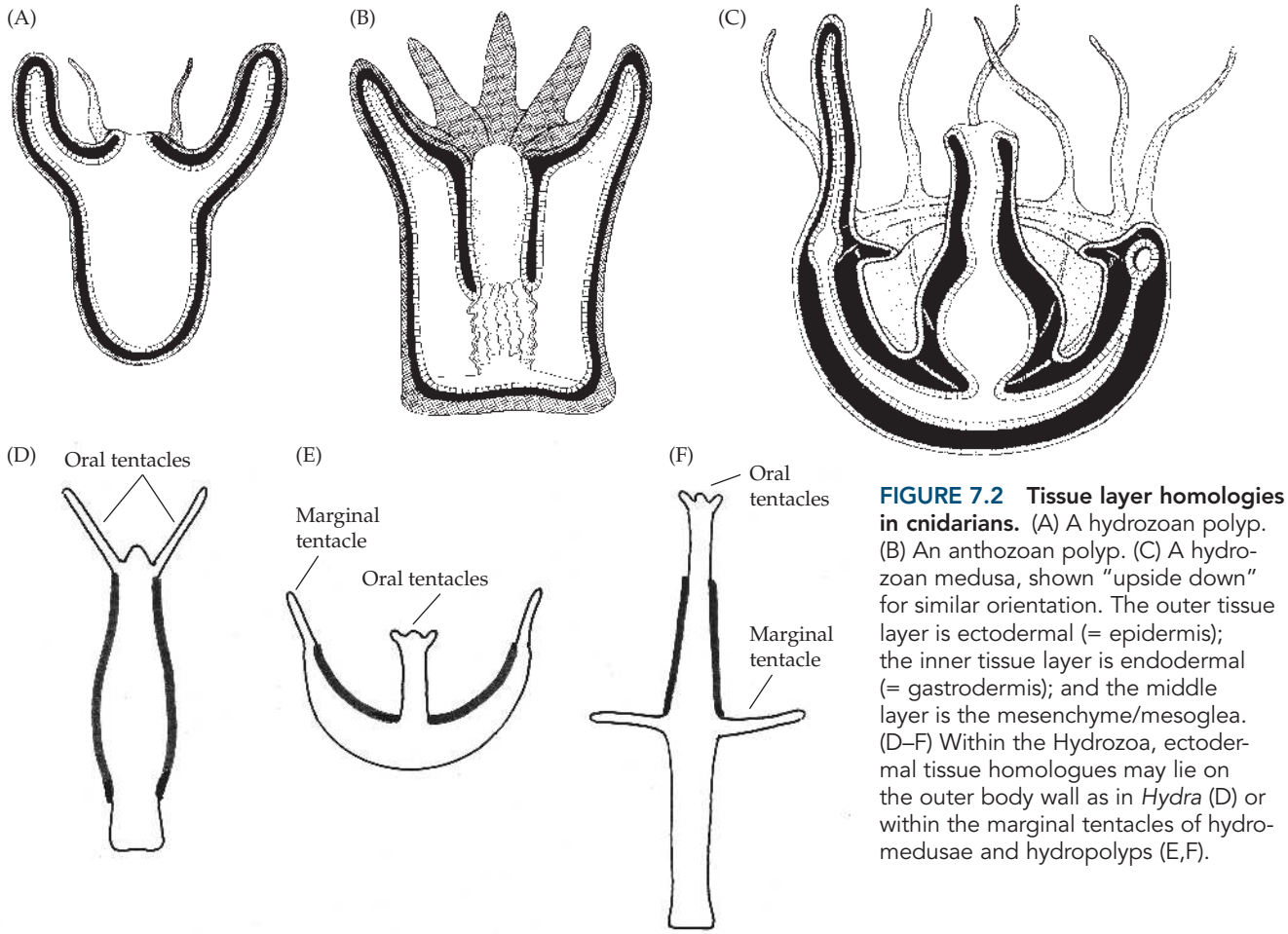

FIGURE 7.2 Tissue layer homologies in cnidarians. (A) A hydrozoan polyp. (B) An anthozoan polyp. (C) A hydrozoan medusa, shown "upside down" for similar orientation. The outer tissue layer is ectodermal (= epidermis); the inner tissue layer is endodermal (= gastrodermis); and the middle layer is the mesenchyme/mesoglea. (D–F) Within the Hydrozoa, ectodermal tissue homologues may lie on the outer body wall as in *Hydra* (D) or within the marginal tentacles of hydromedusae and hydropolyps (E,F).

Argentina. Most fisheries operations process the catch into semidried, rather than freeze-processed, products. In Asia, jellyfish are often touted as a traditional Chinese medicine that is beneficial for treating arthritis, high blood pressure, cancer, ulcers, and a myriad of other ailments. However, mild to severe allergic reactions have also been observed in humans eating jellyfish. In Russia, jellyfish have been added to cement to increase its strength. Sea turtles, penguins, ocean sunfish, and other fishes are all significant predators on jellyfish.

Cnidarians play numerous roles in folklore around the world. In Samoa, the corallimorpharian anemone

BOX 7B Characteristics of the Phylum Cnidaria

1. Diploblastic Metazoa with ectoderm and endoderm separated by a (primarily) ectodermally derived acellular mesoglea or partly cellular mesenchyme
2. With primary radial symmetry, often modified as biradial or quadriradial or with other variations on the radial theme, and an oral–aboral primary body axis
3. With unique stinging or adhesive structures called cnidae, the most common being called nematocysts, with each cnida residing in and produced by one cell, the cnidocyte
4. Musculature formed largely of myoepithelial cells (= epitheliomuscular cells and nutritive-muscular cells), derived from ectoderm and endoderm (adult epidermis and gastrodermis)
5. Alternating asexual polypoid and sexual medusoid generations, but with many variations on this basic theme (e.g., no medusoid stage in the class Anthozoa)
6. With a single "body cavity," the endodermally derived gastrovascular cavity (coelenteron), which is saclike, partitioned, or branched but with only a single opening serving as both mouth and anus
7. With no head, centralized nervous system, or discrete gas exchange, excretory, or circulatory structures
8. With a simple nerve net(s) of naked and largely nonpolar neurons as the nervous system
9. Typically with a planula larva (ciliated, motile, gastrula larva)

Rhodactis howesii, known as *mata-malu*, is served boiled as a festive holiday dish. Eaten raw, however, *mata-malu* causes death and is a traditional device in Samoan suicide. Hawaiians refer to the zoantharian *Palythoa toxica* as *limu-make-o-Hana* ("the deadly seaweed of Hana"). Hawaiians used to smear their spear tips with this cnidarian, the toxin from which is called **palytoxin**. Interestingly, palytoxin may be produced by an unidentified symbiotic bacterium, not by the cnidarian itself. It is one of the most powerful toxins known, being deadlier than that of poison arrow frogs (batrachotoxin) and paralytic shellfish toxin (saxitoxin).

Taxonomic History and Classification

As is the case with sponges, the nature of cnidarians was long debated. In reference to their stinging tentacles, Aristotle called the medusae *Acalephae* (*akalephe*) and the polyps *Cnidae* (*knide*), both names derived from terms meaning "nettle." Renaissance scholars considered them plants, and it was not until the eighteenth century that the animal nature of cnidarians was widely recognized. Eighteenth-century naturalists classified them along with the sponges and a few other groups under Linnaeus's Zoophytes, a category for organisms deemed somewhere between plants and animals. Lamarck instituted the group Radiata (or "Radiaires") for medusoid cnidarians, ctenophores, and echinoderms.

In the early nineteenth century the great Norwegian naturalist Michael Sars demonstrated that medusae and polyps were merely different forms of the same group of organisms. Sars also demonstrated that the genera *Scyphistoma*, *Strobila*, and *Ephyra* actually represented stages in the life history of certain jellyfish (scyphozoans). The names have been retained and are now used to identify these stages in the life cycle. The German zoologist Rudolph Leuckart eventually recognized the fundamental differences between the two great "radiate" groups, the Porifera/Cnidaria/Ctenophora and the Echinodermata, and in 1847 he created the name Coelenterata (Greek *koilos*, "cavity"; *enteron*, "intestine") for the former group in his recognition of the "intestine" as the sole body cavity. In 1888 the Austrian zoologist Berthold Hatschek split Leuckart's Coelenterata into the three phyla recognized today: Porifera, Cnidaria, and Ctenophora. Cnidarians and ctenophores are now universally recognized as distinct phyla, a view upheld by molecular analyses.

An important recent major advance in cnidarian systematics was confirmation that the myxozoans, formerly classified as protists, are in fact, highly derived, parasitic cnidarians. Myxozoans had been considered protists until 1899 when the Czech zoologist Antonín Štolc proposed they should be considered reduced cnidarians because of the nematocyst-like architecture of their spores. Over time, the multicellular nature of Myxozoa, and the structural and developmental similarity of their polar capsules to cnidarian nematocysts, gradually came to be recognized. And, since the early 2000s, molecular data have supported the classification of Myxozoa as cnidarians. In 2002, the enigmatic metazoan *Buddenbrockia plumatellae,* first discovered in 1850, was reinterpreted as a myxozoan. *Buddenbrockia* is a motile vermiform creature that inhabits the body cavity of freshwater bryozoans. It possesses four bands of longitudinal muscle cords, a cuticle-like body surface, no digestive tract, a cnidarian-like complement of polar capsules, and myxozoan-like infective spores (including polar capsules) that form inside the body cavity. Shortly after its rediscovery, it became clear that *Buddenbrockia plumatellae* is the same creature as *Tetracapsula bryozoides*, a known malacosporean (also described as *Myxosporidium bryozoides*), and furthermore, that another myxozoan, *Tetracapsula bryosalmonae*, was responsible for proliferative kidney disease (PKD) in salmonid fishes. The class Polypodiozoa comprises a single known species (*Polypodium hydriforme*), an intracellular parasite of acipenseriform fishes (sturgeons and paddlefishes); once thought to be allied with the class Hydrozoa, Polypodiozoa has been shown to be the sister group of Myxozoa, the two forming a clade of parasites called Endocnidozoa (Box 7A, and see below).

The Cnidaria thus comprise three major lineages: Anthozoa, a polypoid lineage lacking medusae; Medusozoa, a diverse clade including species exhibiting primarily motile medusoid forms as well as forms with both medusoid and polypoid life stages; and Endocnidozoa, a clade of highly simplified obligate endoparasites.

CLASSIFICATION OF PHYLUM CNIDARIA

SUBPHYLUM ANTHOZOA Class Anthozoa. Marine. Anemones, sea pens, soft corals, gorgonians, organ-pipe corals, and stony corals (Figure 7.1A–F).[3] Solitary or colonial; without a medusoid stage (individuals all polypoid); cnidae epidermal and gastrodermal; coelenteron divided by longitudinal (oral–aboral) mesenteries, the free edges of which form thick, cordlike mesenterial filaments; mesenchyme thick; tentacles number 8 (Octocorallia) or occur in multiples of 6 (Hexacorallia) and contain extensions of the coelenteron; stomodeal pharynx (= actinopharynx) extends from the mouth into the coelenteron and bears one or more ciliated grooves (siphonoglyphs); polyps may reproduce both sexually and asexually; gametes arise from gastrodermis. About 7,200 described living species divided into three subclasses: Octocorallia, Hexacorallia, and Ceriantharia.

[3] We use the term "anemone" in a general sense for any solitary anthozoan polyps, but we restrict the term "sea anemone" to the anemones of the order Actiniaria.

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SUBCLASS OCTOCORALLIA Octocorals. Polyps with 8 hollow, marginal, pinnate tentacles, and 8 complete (perfect) mesenteries, each with retractor muscle on the sulcal side (facing the single siphonoglyph); most species with free or fused calcareous sclerites embedded in mesenchyme, although sclerites lacking in some species; stolons or coenenchyme connect the polyps. Four orders are currently recognized, but considerable revision of subordinal groups is likely, particularly within the Alcyonacea.

ORDER HELIOPORACEA Helioporaceans. Colonies produce massive, rigid calcareous skeletons of aragonite crystals (not fused sclerites) similar to those of milleporid hydrozoans and stony corals; polyps monomorphic. Two families (Lithotelestidae and Helioporidae) and three genera (*Epiphaxum, Nanipora*, and *Heliopora*, "blue coral").

ORDER ALCYONACEA Soft gorgonians and organ-pipe corals. Colonies encrusting or erect, often massive; usually fleshy and flexible, although the coenenchyme is sclerite-filled; polyps monomorphic or dimorphic; fleshy distal portions of polyps usually retractable into more compact basal portion; skeletal elements composed of calcite and gorgonin. With 29 recognized families, classified in 5 heterogeneous suborders that may be little more than morphological grades.

SUBORDER PROTOALCYONARIA Deep-water octocorals with solitary polyps that reproduce exclusively by sexual means (e.g., *Ignis*, *Taiaroa*, and possibly *Haimea*).

SUBORDER STOLONIFERA Stoloniferans. Simple polyps arise separately from ribbon-like stolons that form an encrusting sheet or network; oral disc and tentacles retractable into a calyx (stiff proximal portion of polyp); mesenchyme with or without sclerites; in some (e.g., Cornulariidae) a thin, horny external skeleton may cover polyps and stolons (e.g., *Bathytelesto*, *Clavularia*, *Coelogorgia*, *Cornularia*, *Pseudogorgia, Sarcodictyon*, *Telesto*, *Tubipora*, the organ-pipe or pipe-organ "corals").

SUBORDER SCLERAXONIA Encrusting or upright, branched colonies with an inner axis (or axial-like layer) consisting mainly of fused sclerites. Includes *Corallium*, one of the precious corals used to make jewelry (also *Briareum*, *Melithaea*, *Paragorgia*, *Parisis*).

SUBORDER CALCAXONIA Gorgonians. Upright, branched or unbranched colonies with an inner axis consisting of scleroproteinous gorgonin without hollow cross-chambered central core, with large amounts of nonscleritic $CaCO_3$ as internodes or embedded in the gorgonin. Mostly found in the deep sea (e.g., *Australogorgia*, *Callogorgia*, *Chrysogorgia*, *Dendrobrachia*, *Helicogorgia*, *Isis, Plumarella*, *Plumigorgia*, *Primnoa*, *Verrucella*).

SUBORDER ALCYONIINA Soft corals. Polyps united within a mass of fleshy coenenchyme; coenenchyme usually with sclerites, but lacking an axis (e.g., *Alcyonium*, *Nidalia*, *Sarcophyton*, *Studeriotes*, *Umbellulifera*, *Xenia*).

SUBORDER HOLAXONIA Gorgonians. Upright, branched colonies with an inner axis consisting of scleroproteinous gorgonin without free spicules, with hollow cross-chambered central core, often with small amounts of embedded nonscleritic $CaCO_3$ (e.g., *Acanthogorgia*, *Eugorgia*, *Eunicea*, *Gorgonia*, *Ideogorgia*, *Muricea*, *Pseudopterogorgia, Swiftia*).

ORDER PENNATULACEA Sea pens and sea pansies. Colonies complex and polymorphic; adapted for life on soft benthic substrata; often bioluminescent; elongate primary axial polyp extends length of the colony (to 1 m) and consists of a basal bulb or peduncle for anchorage and a distal stalk, the latter giving rise to dimorphic secondary polyps; coelenteron of axial polyp with skeletal axis of calcified horny material in canals (e.g., *Anthoptilum*, *Cavernularia*, *Funiculina*, *Halipteris*, *Pennatula*, *Ptilosarcus*, *Renilla*, *Sarcoptilus, Stylatula*, *Umbellula*, *Virgularia*).

SUBCLASS HEXACORALLIA Anemones and stony corals. Solitary or colonial; naked, or with calcareous skeleton or chitinous cuticle, but never with isolated sclerites; mesenteries usually paired and in multiples of 6; mesenteries bear longitudinal retractor muscles arranged so that those of each pair either face toward each other or away from each other; mesenterial filaments typically trilobed, with two ciliated bands flanking a central one bearing cnidocytes and gland cells; one to several circles of hollow tentacles arise from endocoels (the spaces between the members of each mesentery pair) and exocoels (the spaces between 2 mesenteries of different pairs); pharynx may have 0, 1, 2, or many siphonoglyphs; cnidae very diverse; endodermal zooxanthellae may be profuse.

ORDER ACTINIARIA The sea anemones. Solitary or clonal; calcareous skeleton lacking, although some species secrete a chitinous cuticle; some harbor zooxanthellae; column often with specialized structures, such as warts or verrucae, acrorhagi, pseudotentacles, or vesicles; oral tentacles conical, digitiform, or branched, usually hexamerously arrayed in 1 or more circles; typically with 2 siphonoglyphs. A highly successful group with at least 1,000 living species in 41 families, the largest being the Actiniidae (e.g., *Actinia*, *Adamsia*, *Aiptasia*, *Alicia*, *Anemonia*, *Anthopleura*, *Calliactis*, *Diadumene*, *Edwardsia*, *Epiactis*, *Halcampa*, *Heteractis*, *Liponema*,

Metridium, *Nematostella*, *Peachia*, *Ptychodactis*, *Stichodactyla*, *Stomphia*, *Triactis*).

ORDER SCLERACTINIA (= MADREPORARIA) Stony corals. Colonial or solitary; polyp morphology almost identical to that of Actiniaria, except lacking siphonoglyphs and ciliated lobes on the mesenterial filaments; zooxanthellae present in about half the known species; colonies form delicate to massive calcareous (aragonite) exoskeletons, with platelike skeletal extensions (septa). Many species harbor symbiotic zooxanthellae of the genus *Symbiodinium*.[4] Over 1,300 extant species, in 24 families[5] (e.g., *Acropora*, *Agaricia*, *Astrangia*, *Balanophyllia*, *Dendrogyra*, *Flabellum*, *Fungia*, *Goniopora*, *Leptopsammia*, *Lophelia*, *Meandrina*, *Montipora*, *Oculina*, *Pachyseris*, *Porites*, *Psammocora*, *Siderastrea*, *Stylophora*).

ORDER ZOANTHARIA Zoantharians. Colonial polyps arise from a basal mat or stolon containing gastrodermal solenia or canals; new polyps bud from gastrodermal solenia of stolons; pharynx flattened, with one siphonoglyph; mesenteries numerous, but with weak musculature; without intrinsic skeleton, but many species incorporate sand, sponge spicules, or other debris into the thick body wall; most with a thick cuticle; zooxanthellae abundant in some species; many species epizootic (e.g., *Epizoanthus*, *Isaurus*, *Isozoanthus*, *Palythoa*, *Parazoanthus*, *Thoracactis*, *Zoanthus*).

ORDER ANTIPATHARIA Black or thorny corals. Upright, branched or whiplike colonies up to 6 m tall; calcareous axial skeleton, usually brown or black and covered by a thin coenosarc bearing small polyps, usually with 6 (but up to 24) nonretractable tentacles; with feeble mesenteries; skeleton produces thorns on its surface (e.g., *Antipathes*, *Bathypathes*, *Leiopathes*).

ORDER CORALLIMORPHARIA Corallimorpharians are solitary polyps, without a skeleton and lacking siphonoglyphs; with ciliated bands on mesenterial filaments, and muscles in the pedal disc (e.g., *Amplexidiscus*, *Corynactis*, *Rhodactis*, *Ricordea*).

SUBCLASS CERIANTHARIA Ceriantharians or tube anemones. Mesenteries complete, but with feeble musculature; with 6 primary mesenteries (as in Hexacorallia). Large, solitary, elongate polyps living in vertical tubes in soft sediments; tube constructed of interwoven specialized cnidae (ptychocysts) and mucus; aboral end lacks a pedal disc and possesses a terminal pore; long, thin tentacles arise from margin of oral disc, fewer shorter labial tentacles encircle mouth; mesenteries complete; gonads occur only on alternate mesenteries; protandric hermaphrodites. Two orders usually recognized, Penicillaria and Spirularia (e.g., *Arachnanthus*, *Botruanthus*, *Ceriantheomorphe*, *Ceriantheopsis*, *Cerianthus*, *Pachycerianthus*). Until recently, considered an order of Hexacorallia.

SUBPHYLUM ENDOCNIDOZOA Marine, brackish, and freshwater. Intracellular parasites of poikilotherm vertebrates, annelids, and bryozoans; possessing myxospores, cnidalike structures with 2 or more shell valves and polar capsules containing nematocyst-like filaments. This subphylum contains 2 clades (Polypodiozoa and Myxozoa), well supported by molecular phylogenetic analyses. About 2,200 described species.

CLASS POLYPODIOZOA Parasites of the oocytes of acipenseriform fishes. Worm shaped, without epithelial muscle cells, but with smooth muscle cells in mesoglea. Binucleate cells within fish oocytes develop into inverted planuliform larvae, which evert during host spawning into tentaculate stolons that possess cnidae and fragment when released into fresh water, dispersing as asexually reproducing medusoids whose gametes infect host fish. A single known species, *Polypodium hydriforme*.

CLASS MYXOZOA

SUBCLASS MYXOSPOREA Marine and freshwater species, usually with hard valves; life cycles include a myxosporean phase in vertebrates and an actinosporean phase within marine annelids. About 2,200 described species (Figure 7.1O).

ORDER BIVALVULIDA Possessing 2 valves per myxospore; gut and tissue parasites (e.g., *Ceratomyxa*, *Henneguya*, *Myxidium*, *Myxobolus*, *Sphaerospora*; the genus *Myxidium* appears to be polyphyletic).

[4] Coral reef ecosystems, to a great extent, owe their success to obligate mutualistic symbioses involving various invertebrates, particularly corals, and photosynthetic dinoflagellate symbionts. These single-celled algae, commonly referred to as zooxanthellae and predominantly belonging to the family Symbiodiniaceae, occur as symbionts with numerous species of Cnidaria, Porifera, Acoela, and Mollusca and with some other protists. In most cases, the algae are intracellular, residing in complex host-derived vacuoles, but in some cases (e.g., the bivalves *Tridacna* and *Hippopus*) they are intercellular. Photosynthetically fixed carbon, typically in the form of glycerol and other simple molecules, is translocated from the alga at a rate and volume often capable of meeting the host's respiratory demands. The presence of Symbiodiniaceae also facilitates the assimilation and conservation of nitrogen, a limiting resource in most coral reef ecosystems. Vertical transmission of the symbiont (the alga is passed from parent to progeny) is common, but in a majority of cases the offspring must be infected from environmental pools of the alga (horizontal transmission). The latter process potentially offers host progeny an opportunity to associate with symbiodiniacean types best adapted to local environmental conditions. Recent molecular genetic studies have revealed a half dozen or so "types" or clades within the former genus *Symbiodinium*, which has now been split into seven genera: *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium*, *Effrenium*, *Fugacium*, and *Gerakladium*.

[5] The taxonomy of the Scleractinia is in a state of confusion, and many taxa, from genus and higher, appear to be nonmonophyletic. About 700 coral species live in deep water and do not form symbiotic relationships with zooxanthellae, and about two dozen of these build reef structures.

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ORDER MULTIVALVULIDA Possessing more than 2 valves per myxospore (e.g., *Kudoa*, *Trilospora*).

SUBCLASS MALACOSPOREA With a single order, Malacovalvulida, and a single family, Saccosporidae. Freshwater parasites of bryozoans; characterized by soft-walled spores, and spore formation within a saclike body form (e.g., *Buddenbrockia*, *Tetracapsuloides*).

SUBPHYLUM MEDUSOZOA Medusozoans. Marine and freshwater; free-swimming and sessile forms; medusae produced through lateral budding and growth of the entocodon; epidermal gonads; loss of intramesogleal muscles, associated with 4 peristomial pits; loss of primary polyp tentacles, transformed into hollow structures; gastric filaments and coronal muscles absent. Body typically tetraradial or, rarely, pentaradial. About 3,900 described living species in 4 classes.

CLASS STAUROZOA Stalked jellyfish (Figures 7.1G and 7.15E). Small, sessile individuals that develop from benthic, nonciliated planula larvae and have complex but poorly understood life cycles; the planula develops into a sessile stauropolyp, and this into a stauromedusa with a stalked adhesive disc by which individuals attach to substratum (a highly motile medusa stage does not exist); stauromedusae have 8 tentacle-bearing "arms" and lack a velum; sexual reproduction may be dominant in most species, although asexual reproduction is known in at least one (*Haliclystus antarcticus*). About 50 species, most in the Northern Hemisphere (e.g., *Calvadosia*, *Haliclystus*, *Lucernaria*). Molecular phylogenetic analyses indicate that despite considerable morphological convergence with trachyline hydrozoans, the minute Antarctic species, *Microhydrula limopsicola*, formerly identified within the Limnomedusae, is in fact a life stage within the life cycle of *Haliclystus antarcticus*.

CLASS CUBOZOA Sea wasps and box jellyfish (Figures 7.1I and 7.15A). Medusae 1–30 cm, largely colorless; polyps each produce a single medusa by complete metamorphosis (strobilation does not occur), medusa bell nearly square in cross section; rhopalia with complex visual structures; hollow interradial tentacle(s) hang from bladelike pedalia, one at each corner of umbrella; unfrilled bell margin drawn inward to form a velumlike structure (the velarium) into which diverticula of the gut extend. Cnidae of the nematocyst type only; the sting is very toxic, in some cases fatal to humans, hence the name "sea wasps." Cubozoans are strong swimmers that occur in all tropical seas (and a few temperate regions, e.g., the west coast of South Africa and Namibia) but are especially abundant in the Indo-Pacific region.

ORDER CHIRODROPIDA Pedalia branch into handlike structure with each branch giving rise to a tentacle; externally fertilizing species including known deadly genera, although toxicity is variable within this order due to differences in tentacle surface area and means of venom delivery (e.g., *Chironex*, *Chiropsalmus*, *Chiropsella*).

ORDER CARYBDEIDA Ovoviviparous species; venom can induce Irukandji syndrome, a usually not-life-threatening but physically and psychologically uncomfortable set of symptoms following envenomation. Five families: the pelagic Alatinidae (*Alatina, Keesingia*, *Manokia*), whose rhopaliar openings are T shaped; two families that lack rhopaliar horns and have rhopaliar openings that are frown shaped, the Carukiidae (*Carukia*, *Gerongia*, *Malo, Morbakka*) and the Tamoyidae (e.g., *Tamoya*), which also lack gastric filaments; the Carybdeidae (*Carybdea*), whose rhopaliar openings are heart shaped; and the Tripedaliidae (*Tripedalia*, *Copula*), which engage in courtship and "copulatory" behavior.

CLASS SCYPHOZOA Jellyfish (Figures 7.1H and 7.15B–D). Polypoid individuals (scyphistomae) are small and inconspicuous but often long-lived; polyps lacking in some species; when present, polyps produce medusae by asexual budding (strobilation); coelenteron divided by 4 longitudinal (oral–aboral) mesenteries; medusae acraspedote (without a velum), typically with a thick mesogleal (or collenchymal) layer, distinct pigmentation, filiform or capitate tentacles, and marginal notches producing lappets; sense organs occur in notches and alternate with tentacles; rhopalia with complex visual structures; gametes arise from gastrodermis; cnidae present in epidermis and gastrodermis, nematocysts only; mouth may or may not be on a manubrium; usually without a ring canal. Scyphozoans are exclusively marine; planktonic, demersal, or attached. About 200 species, divided into three orders.

ORDER CORONATAE High bell divided into upper and lower regions by a coronal groove encircling exumbrella; margin of bell deeply scalloped by gelatinous thickenings termed "pedalia," which give rise to tentacles, rhopalia, and marginal lappets; gonads present on the 4 gastrovascular septa. Small to moderate in size; primarily bathypelagic; some contain zooxanthellae (e.g., *Atolla*, *Linuche*, *Nausithoe*, *Periphylla*, *Stephanoscyphistoma*).

ORDER SEMAEOSTOMEAE Corners of mouth drawn out into 4 broad, gelatinous, frilly lobes; stomach with gastric filaments; hollow marginal tentacles contain extensions of radial canals; without coronal furrow or pedalia; gonads on folds of gastrodermis. This order contains most of the typical jellyfish of temperate and tropical seas; moderate to very large forms (some with a bell reaching several meters in diameter) (e.g., *Aurelia*, *Chrysaora*, *Cyanea*, *Pelagia*, *Phacellophora*, *Sanderia*, *Stygiomedusa*).

ORDER RHIZOSTOMEAE Lacking a central mouth; frilled edges of the four oral lobes are fused over the mouth so that many suctorial "mouths"

(ostioles) open from a complicated canal system on 8 branching armlike appendages; bell without marginal tentacles or pedalia; stomach without gastric filaments; gonads on folds of gastrodermis. Small to large jellyfish that swim vigorously using a well-developed subumbrellar musculature; primarily occur in low latitudes (e.g., *Cassiopea*, *Cephea*, *Eupilema*, *Mastigias*, *Rhizostoma*, *Stomolophus*).

CLASS HYDROZOA Hydroids, fire coral, and hydromedusae (Figures 7.1J–M and 7.8). Alternation of generations occurs in most genera (typically asexual benthic polyps alternate with sexual planktonic medusae), although one or the other generation may be suppressed or lacking; medusae produced through lateral budding of the entocodon; medusoids often retained on the polyp; polyps usually colonial, with interconnected coelenteron; often polymorphic, with individual polyps modified for various functions (e.g., gastrozooids feed, gonozooids are reproductive, dactylozooids are for defense and prey capture, etc.); exoskeleton, when present, usually of chitin or occasionally calcium carbonate (in the families Milleporidae and Stylasteridae); coelenteron of polyps and medusae lacks a pharynx and mesenteries; mesoglea acellular; tentacles solid or hollow; cnidae occur only in epidermis; gametes arise from epidermal cells; medusae mostly small and transparent, nearly always craspedote (with a velum) and with a ring canal; mouth typically borne on pendant manubrium; medusae lack rhopalia. A highly diverse group of about 3,500 described species, in 6 orders, including several dozen species from inland waters. Although the taxonomy of Hydrozoa is currently in a state of revision (and debate), there is considerable support for the existence of two monophyletic groups classified as subclasses, the Trachylina and the Hydroidolina. The Siphonophora has previously been regarded as its own subclass, but it now appears likely to be part of the subclass Hydroidolina.

SUBCLASS TRACHYLINA Trachyline medusae. Polypoid generation minute or absent; medusae produce planula larvae that usually develop directly into actinula larvae, which metamorphose into adult medusae; medusae craspedote, with tentacles often arising from exumbrellar surface, well above bell margin; medusae mostly gonochoristic; over 150 known species, in 4 orders.

ORDER LIMNOMEDUSAE (Figure 7.13A–C). Freshwater and marine hydromedusae with ecto-endodermal statocysts, hollow tentacles, and 4 (rarely 6) radial canals. The close relationship among freshwater genera suggests that freshwater species may share a common ancestor; these species are the only trachylines with true polyps, tiny structures that bud sexual medusae or asexual frustules that creep away to generate more polyps. Limnomedusae includes 6 families and numerous genera (e.g., *Astrohydra, Craspedacusta*, *Geryonia, Gonionemus*, *Limnocnida, Liriope, Monobrachium*, *Olindias*).

ORDER TRACHYMEDUSAE Exclusively marine hydromedusae, usually with 8 radial canals and solid tentacles; includes 4 families—Halicreatidae, Petasidae, Ptychogastriidae, and Rhopalonematidae. A large, possibly nonmonophyletic order with 6 families and many genera (e.g., *Aglantha*, *Botrynema, Ptychogastria*).

ORDER NARCOMEDUSAE Pelagic or bathypelagic hydromedusae lacking radial canals, with lobed umbrella margins, broad, pouched stomach, solid tentacles. Includes 7 families and numerous genera (e.g., *Aegina*, *Cunina*, *Pegantha*, the wormlike *Tetraplatia* formerly considered a coronate scyphozoan).

ORDER ACTINULIDA Two marine families, Halammohydridae (e.g., *Halammohydra*) and Otohydridae (e.g., *Otohydra*).

SUBCLASS HYDROIDOLINA (Figures 7.5 and 7.13D–F). Hydroids and their medusae, and siphonophores. Polypoid generation often predominant; polyps may have a chitinous exoskeleton; oral tentacles filiform or capitate, rarely branched or absent; colonies often polymorphic; many do not release free medusae but release gametes from sporosacs or sessile attached medusoids (= medusoid buds, or gonophores) on polypoid colony; colonies gonochoristic. A large group, with over 75 described families and over 3,220 species. Hydroids occur at all depths; the polypoid forms are very common in the littoral zone.

ORDER THECATA (= LEPTOMEDUSAE, CALYPTOBLASTEA, OR LEPTOTHECATA) A diverse group of hydroids with polyps, always colonial; hydranths and gonozooids encased in exoskeleton; free medusae usually absent, but when present flattened and with statocysts; medusae form gametes on subumbrella, beneath radial canals; gonozooids (= gonangia) with blastostyle that produces medusa buds. Monophyly of Thecata seems likely, but relationships within this order await further study. These are some of the most common species of hydrozoans in the marine littoral zone (e.g., *Abietinaria*, *Aequorea*, *Aglaophenia*, *Bonneviella*, *Campanularia*, *Cuvieria*, *Gonothyraea* [Figure 7.1K], *Lovenella*, *Obelia*, *Plumularia*, *Sertularia*).

ORDER ATHECATA (= ANTHOMEDUSAE, GYMNOBLASTEA, OR ANTHOATHECATA) Polyps solitary or colonial; hydranths and gonozooids lack exoskeleton; gonozooids produce free or sessile medusae; some groups produce gametes in transient sporosacs; free medusae tall and bell shaped, without statocysts, with or without ocelli; medusae form gametes on subumbrella or manubrium. Current research suggests this order is poly- or paraphyletic, and the three suborders here listed are provisional.

SUBORDER CAPITATA A diverse (and probably nonmonophyletic) group of hydroids

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possessing stenotele nematocysts and tentacles with rounded (capitate) tips at some stage in the life cycle; many have medusae with complex, cup-shaped ocelli. Current research suggests there may be two clades, Zancleida and Corynida. Zancleida includes well-known polypoid forms (e.g., *Pennaria*, the Christmas tree hydroids) and the fire corals or milleporids (known for their calcium carbonate skeleton and their potent stinging nematocysts). Milleporidae is a small family of about 13 species, all living in shallow tropical seas. Distinguished by massive or encrusting calcareous coral-like skeletons, the calcareous matrix covered by thin epidermal layer; gastrozooids with short capitate tentacles, each gastrozooid surrounded by 4–8 dactylozooid-like tentacles, each tentacle in a separate skeletal cup; gonophores housed in pits (ampullae) in skeleton; and, in the small free medusae, lack of mouth, tentacles, and velum. Like the stony corals, milleporids rely on a commensal relationship with zooxanthellae and are thus restricted to the photic zone. Zancleida also includes well-known medusoid forms, formerly known as "chondrophorans," whose colonies may consist of gastrozooids, gonozooids, and dactylozooids; or may be solitary but highly specialized polypoid individuals. Chondrophoran "zooids" are attached to a chitinous, multichambered, disclike float that may or may not have an oblique sail (e.g., *Porpita*, *Velella* [Figure 7.1M]); their "gonozooids" bear medusiform gonophores that are released and shed gametes; and most are richly supplied with zooxanthellae. The Corynida includes well-known medusoid forms such as *Coryne, Polyorchis* (Figure 7.1L), *Sarsia*, and *Slabberia*. The status and generic relationships of Corynida are unclear.

SUBORDER APLANULATA Members of this taxon lack a ciliated planula stage, hence their name; the group is well supported by molecular phylogenetic analyses. This suborder includes *Corymorpha*, *Tubularia*, *Hydra,* and *Candelabrum*. *Hydra*, while often used to exemplify the Cnidaria, is actually rather unusual in life cycle and morphology.

SUBORDER FILIFERA This heterogeneous (and probably nonmonophyletic) taxon is currently divided into around 26 families, in 4 major groups (Filifera I, II, III, and IV). Filifera I is typified by the family Eudendriidae, which is distinguished from other filiferans by the absence of desmoneme nematocysts, the presence of a styloid-shaped gonophore, and a trumpet-shaped hypostome. Filifera II is less distinct but shares a solid ring canal and macrobasic eurytele cnidae, as well as reduction in hydranth tentacles. Many species in this group live on other invertebrates (e.g., *Hydrichthella* on octocorals; *Brinckmannia* within hexactinellid sponges; *Proboscidactyla* on sabellid polychaete tubes). Filifera III is typified by the families Hydractiniidae (e.g., *Clava*, *Hydractinia*) and Stylasteridae (e.g., *Stylaster*). Members of these families have polymorphic polyps and perisarc- or skeleton-covered stolons that can be colorful. With over 300 living species in 30 genera, Stylasteridae is one of the most species-rich hydrozoan families. The stylasterid skeleton is secreted within the epidermis and covered by a thick epidermal layer; a calcareous style often rises from the base of the polyp cup, hence the name "stylasterid"; polyps may have tentacles; free medusae are not produced, but sessile medusoid gonophores are retained in shallow chambers (ampullae) of the colony; several dactylozooids surround each gastrozooid, although polyp pits are joined. Filifera IV includes the families Bougainvilliidae (e.g., *Bougainvillia*, *Dicoryne*), Cordylophoridae (e.g., *Cordylophora*), Pandeidae (e.g., *Pandea*), Rathkeidae (e.g., *Rathkea*), and Oceaniidae (e.g., *Turritopsis*, the "immortal jellyfish"), which all bear gonophores on structures other than hydranths.

ORDER SIPHONOPHORA Siphonophores comprise a diverse clade of about 190 named species of polymorphic colonies, with a number of distinct types of polyps and attached modified medusae (Figures 7.1N, 7.8F,H,I, and 7.9). Most species planktonic, but some are benthic and tethered to the sea bottom (Codonophora: Rhodaliidae) at depths up to 4,300 m. They are well known for their ability to produce bioluminescence, fluorescence, and structurally based colors (especially the nectophores). All are colonial, each zooid being homologous with a solitary animal though physiologically integrated. Zooids are specialized for a range of functions, including feeding, reproduction, protection, swimming, and flotation. Some species have numerous zooid types, for example, nectophore, gastrozooid, palpon, several types of bracts, and gonophores. Gonophores are male or female sexual medusae that produce gametes. Some species are hermaphroditic (male and female gonophores occur on the same colony), but most are gonochoristic (male and female gonophores are on different colonies). Gastrozooids are feeding polyps that have a single tentacle attached to the base of the zooid used for prey capture (with the exception of *Physalia physalis*, the Portuguese man-of-war, which has separate zooids for feeding and prey capture, and rhodaliids, which have some tentacles used to anchor to the substratum). Gastrozooids carry nematocyst batteries. Nectophores are highly specialized nonreproductive propulsive medusae of the nectosome region. Bracts are greatly reduced zooids (unique to codonophoran siphonophores)

that function for protection of the other zooids and help maintain neutral buoyancy; they usually have extensions of a gastrovascular or radial canal system. The role of palpons is not well understood, but they might function in circulation of gastrovascular content, digestion, and/or defense; each bears a single tentacle with nematocysts. All these zooid types bud from one or two restricted growth zones at the base of the nectosome, creating long chains of highly organized zooids (the siphosome region) in repeating groups called cormidia and typically containing a helmet-shaped bract, a gastrozooid, and one or more gonophores. The pneumatophore (when present) is a gas-filled float located at the "anterior" end of the colony, which helps the colony maintain its orientation in the water column and can play a role in flotation (it is not a zooid but is formed by invagination at the aboral end of the planula during early development). The term "anterior" in this case is strictly a legacy convention and does not imply an anatomical anterior–posterior axis in the colony. Siphonophores are major oceanic predators, some colonies reaching tens of meters in length (in 2020 a spectacular colony was seen off the west coast of Australia, estimated to be 50 m in length); a majority of the species is bioluminescent. Historically divided into three groups based on body structure, but molecular phylogenetic research now suggests the existence of two major clades—Cystonectae and Codonophora. The benthic, deep-sea *Dendrogramma enigmatica*, from southern Australian seabeds at 400 to 2,900 m depth (Figure 7.1N), once thought to be a medusozoan, is now believed to be the detached bracts of a benthic codonophoran siphonophore.

SUBORDER CYSTONECTA Possessing an anterior gas-filled float or pneumatophore, with a posterior, zooid-bearing siphosome (e.g., *Physalia*, *Rhizophysa*).

SUBORDER CODONOPHORA Structurally the more complex siphonophores, this suborder includes the monophyletic Calycophorae and the paraphyletic Physonectae. The former includes most siphonophore species, which possess an anterior nectosome, composed of nectophores, swimming elements that propel the colony, and a posterior zooid-bearing siphosome but no pneumatophore (e.g., *Diphyes*, *Hippopodius*, *Sphaeronectes*). "Physonectans" possess an apical (aboral) gas-filled float, or pneumatophore, that is probably not a medusa nor of medusoid origin (the float is filled mainly with carbon monoxide, and the cavity is lined by ectoderm); they are currently divided into a few clades, including Apolemiidae and Pyrostephidae (e.g., *Agalma*, *Apolemia*, *Bargmannia*, *Dendrogramma*, *Nanomia*, *Physophora*).

The Cnidarian Body Plan

Although showing marked advances over Porifera and Placozoa, cnidarians still possess only two embryonic germ layers—the ectoderm and the endoderm—which become the adult epidermis and gastrodermis, respectively. The middle mesoglea or mesenchyme in adults is derived largely from ectoderm and never produces the complex organs seen in triploblastic Metazoa (i.e., the Bilateria).

Whether or not a true basement membrane (= basal lamina) exists in cnidarians is debatable. We define a **basement membrane** as a thin sheet of extracellular matrix upon which an epithelial layer may rest; it contains collagen and other proteins, and it helps hold the epithelial cells in place. By this definition, placozoans lack a basement membrane, cnidarians and ctenophores possess one by way of the mesenchyme, and the Bilateria possess a well-developed, highly proteinaceous basement membrane. And, as we have seen, basement membranes also occur in some sponges.

The essence of the cnidarian body plan is radial symmetry (Figure 7.3). As discussed in Chapter 3, radial symmetry is associated with various architectural and strategic constraints. Cnidarians are sessile, sedentary, or pelagic, and they do not engage in the active unidirectional movement seen in bilateral, cephalized creatures. Radial symmetry demands certain anatomical arrangements, particularly of those parts that interact directly with the environment, such as feeding structures and sensory receptors. Thus, we typically find a ring of tentacles encircling the body that can collect food from any direction, and a diffuse, noncentralized nerve net with radially distributed sense organs. These and other implications of radial symmetry are explored further throughout this chapter. Although polypoid and medusoid forms are often represented as inverted forms of one another (Figure 7.2A–C), studies of gene expression in cnidarians show that the oral tentacles of polyps and the marginal tentacles of medusae may not necessarily be homologous structures (Figure 7.2D–F). As we will see, differences between polyps and medusae go well beyond how animals appear to be oriented along their oral–aboral axis.

In spite of the limitations of a diploblastic, radially symmetrical body plan, cnidarians are a highly successful and extraordinarily diverse group. Much of their success has been attributed to the possession of cnidae and the diversity of different dimorphic life histories. Although polyps and medusae are very different in appearance, they are really variations on the basic cnidarian body plan (Figure 7.2). And yet, the two stages are vastly different ecologically, and their presence in a single life history allows an individual species to exploit different environments and resources, leading a "double life."

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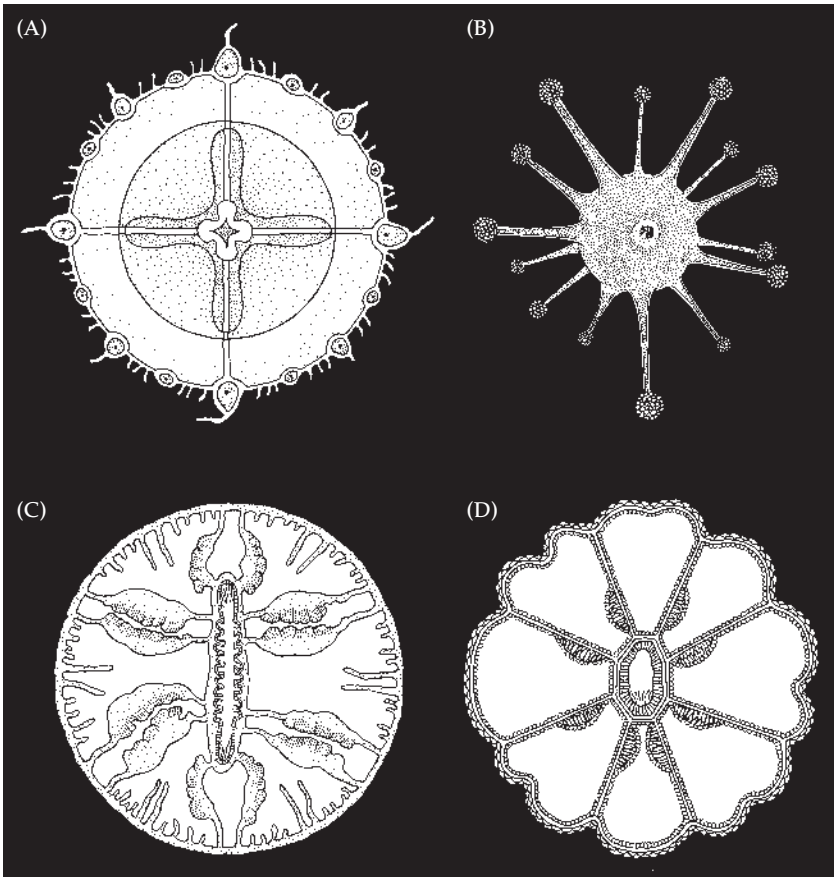

FIGURE 7.3 Cnidarian radial symmetries. (A) Quadriradial symmetry of a hydromedusa. (B) Radial symmetry of a hydrozoan polyp. (C) Biradial symmetry of an actiniarian polyp (a sea anemone). (D) Biradial symmetry of an octocoral polyp (Anthozoa).

The Body Wall

Cnidarian epithelia—the outer epidermis and the inner gastrodermis—include **myoepithelial cells** (Figures 7.4 and 7.19), which are capable of performing both epithelial and muscular functions. These columnar cells bear flattened, contractile, basal extensions called **myonemes** (Figure 7.19). In the epidermis, these cells are referred to as **epitheliomuscular cells**, and in the gastrodermis they are called **nutritive-muscular cells**. The myonemes rest against the middle mesoglea or mesenchyme, and the opposite ends of the cells form the outer body and gut surfaces. The myonemes run parallel to free surfaces and contain contractile myofibrils. Myonemes of neighboring cells are interconnected, often forming longitudinal and circular sheets capable of contracting like typical muscle layers of the triploblastic phyla.

Molecular studies of germ layer formation in anthozoans show that virtually all of the genes involved in endomesoderm formation in bilaterian embryos, including the core genes identified as components of an evolutionarily conserved endomesoderm ("kernel") gene regulatory network, are expressed in cnidarian epithelial tissue that lines the gastric cavity or the pharynx. This conservation in components of the endomesodermal gene regulatory network provides compelling evidence that the endodermal and pharyngeal tissue of cnidarians (and probably ctenophores) is homologous with that of the gut and oral ectoderm of bilaterians, and that both endoderm and mesoderm of bilaterians evolved from an ancestral endomesodermal layer. Fate mapping experiments have shown that the definitive endoderm is generated from the oral pole/animal hemisphere in both anthozoan cnidarians and ctenophore embryos. They also show that the primary opening to the cnidarian and ctenophoran gut arises from the same region of the embryo (the animal hemisphere) that forms the mouth in all bilaterians. This suggests that the oral pole of adult ctenophores and cnidarians is homologous with the anterior pole of bilaterians and that the gastrovascular opening/mouth is homologous with the mouth of bilaterians. This relationship is also supported by molecular data. Thus, the mouths of all animals appear to be homologous, with the possible exception of the chordates. (The mouth of chordates does not express the same suite of genes seen in other metazoans, and its position forms independently of a circumoral component of the nervous system shared by most other metazoans.)

Some cnidarians also possess subepidermal mesenchymal muscles, apparently derived from the contractile elements of the myoepithelial cells. In anemones, for example, cordlike sphincters are sunk below the epithelium and reside as distinct muscles wholly within the mesenchyme. In addition to epitheliomuscular cells, the epidermis contains sensory cells, cnida-bearing cells called cnidocytes, gland cells, and interstitial cells. The last are undifferentiated and capable of developing into other cell types. The gastrodermis is histologically somewhat similar to the epidermis (Figure 7.4). Along with the nutritive-muscular cells, it also contains cnidocytes (except in the Hydrozoa) and gland cells.

In medusozoans, the middle layer is a rather simple, gel-like, largely acellular mesoglea. Scyphomedusae have a very thick mesogleal layer with scattered cells. In stauromedusans, cubozoans, and hydrozoans, the mesoglea is noncellular. In anthozoans the middle layer is often a thick and richly cellular mesenchyme (see footnote 2, earlier in the chapter). Myxozoans are primarily small and cellular without clearly defined

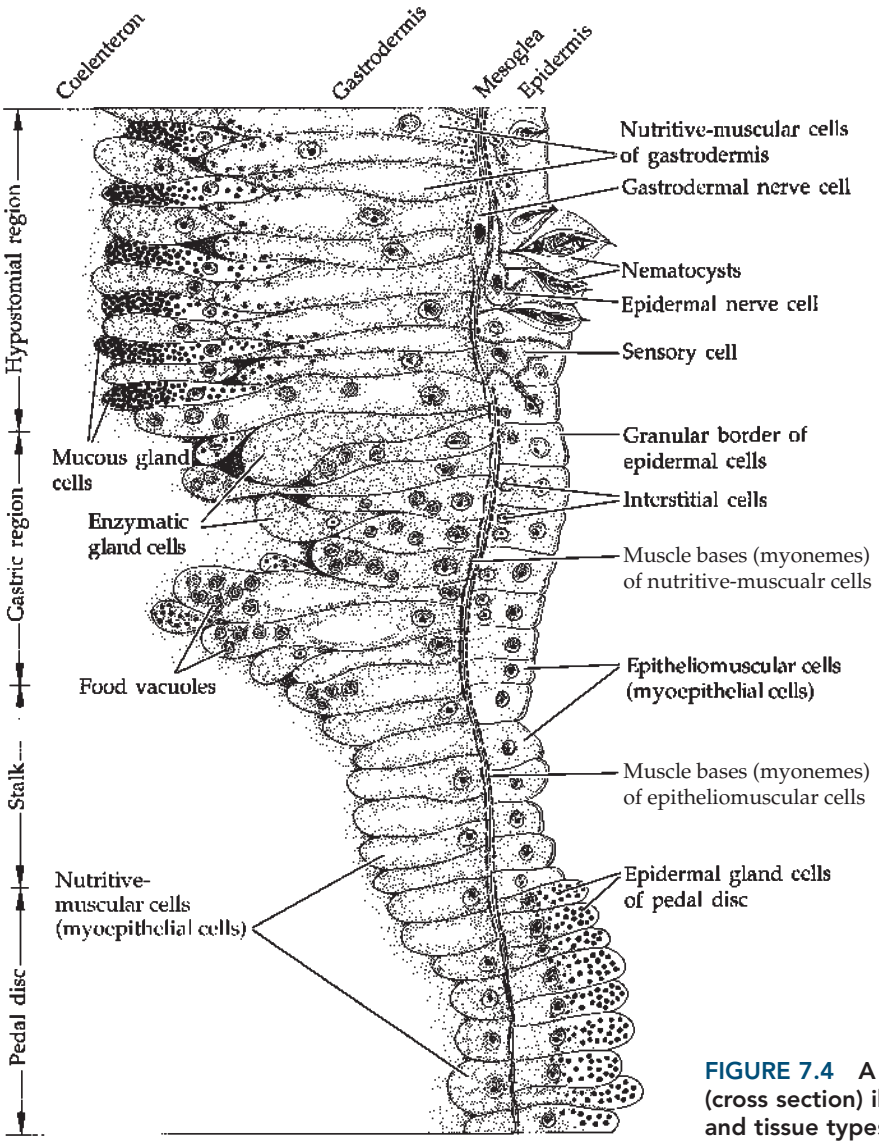

FIGURE 7.4 **A hydrozoan polyp column wall (cross section) illustrates the basic cnidarian cell and tissue types.**

body walls, with a few exceptions. The actinosporan larva of many myxosporeans has rays composed of single cells that are used to attach to the mucous membranes of vertebrate hosts. The wormlike *Buddenbrockia* has four blocks of longitudinal musculature that lie beneath the epidermis and surround a hollow, gut-free body cavity.

The polypoid form Polyp stages are much more diverse than are medusae, largely as a result of their capacities for asexual reproduction and colony formation (Figures 7.5–7.12). This diversity of form has led to an extensive lexicon of terms for the parts of polyps. This expansive terminology may at first seem a bit overwhelming, but bear with us—we won't give you anything unnecessary here. The polypoid stage occurs in the subphyla Anthozoa and Medusozoa, although it is greatly modified in the Scyphozoa, Cubozoa, and Staurozoa. A clearly defined polypoid stage appears to be lacking in the subphylum Myxozoa. Polyps are tubular structures with an outer epidermis, an inner gut sac (coelenteron) lined with gastrodermis, and a layer of jellylike mesoglea or mesenchyme in between. Most polyps are small, but the polyps of some species of sea anemones get quite large; the largest is the monstrous tropical Indo-Pacific *Stichodactyla mertensii*, which can exceed a meter in diameter, and the beautiful northeast Pacific *Metridium farcimen*, which can extend its column to a meter in height.

The fundamental polypoid symmetry is radial, although as a result of subtle modifications most species possess a biradial or quadriradial symmetry. The main body axis runs longitudinally through the mouth (oral end) to the base (aboral end) of the polyp. The aboral end may form a **pedal disc** for attaching to hard substrata (as in most common sea anemones); it may be a rounded structure—called a **physa**—adapted for digging and anchoring in soft substrata

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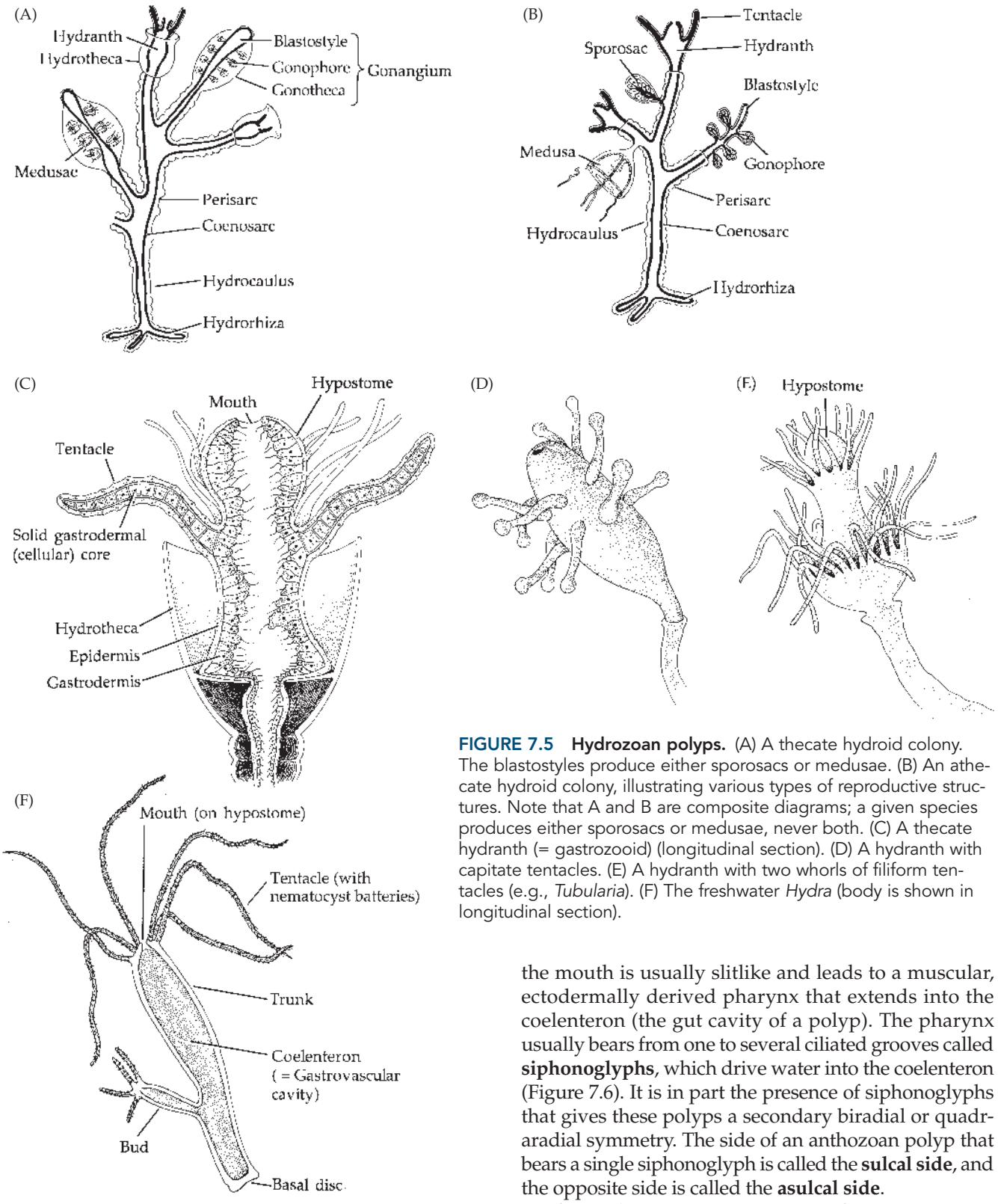
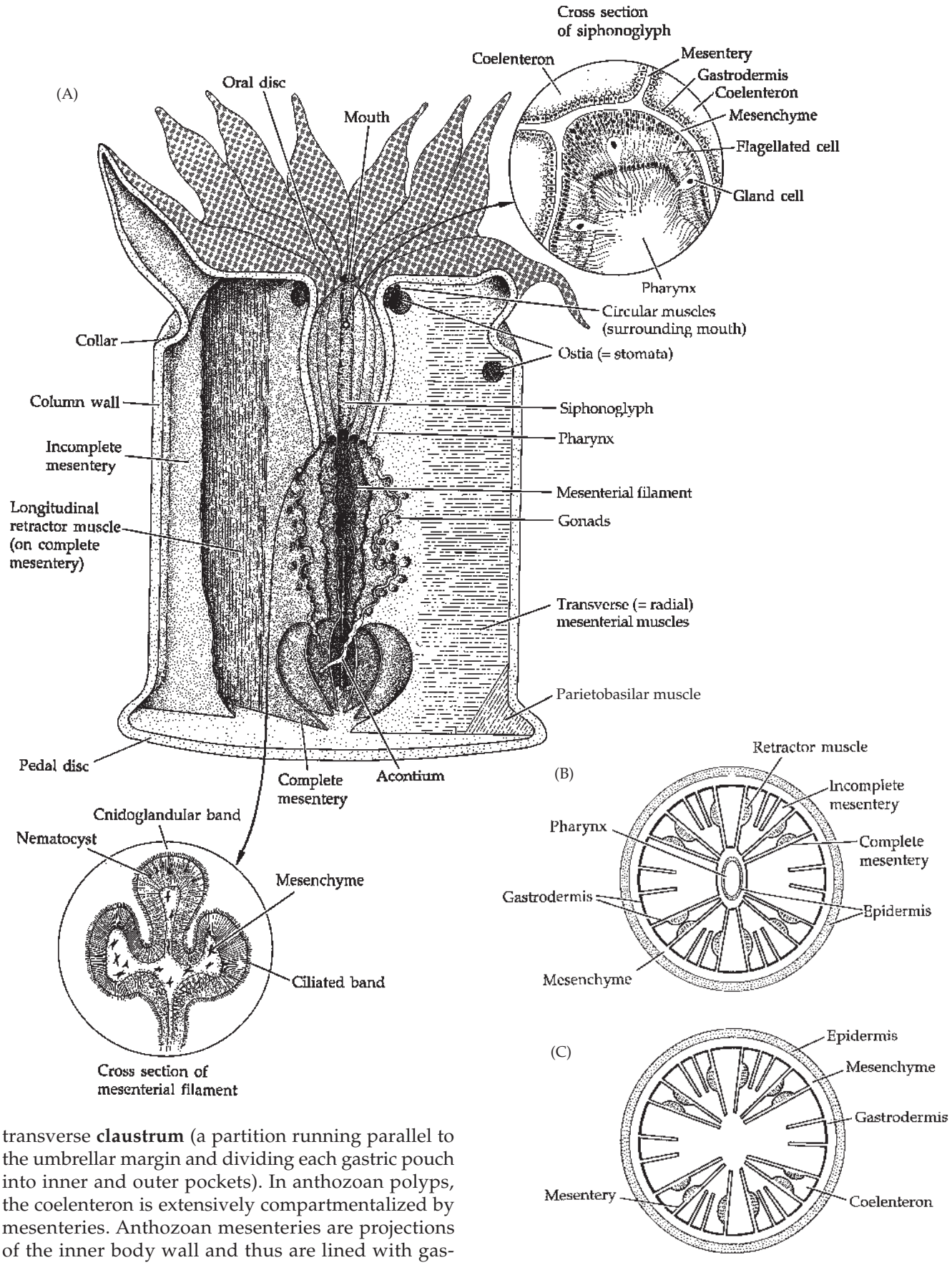


FIGURE 7.5 Hydrozoan polyps. (A) A thecate hydroid colony. The blastostyles produce either sporosacs or medusae. (B) An athecate hydroid colony, illustrating various types of reproductive structures. Note that A and B are composite diagrams; a given species produces either sporosacs or medusae, never both. (C) A thecate hydranth (= gastrozooid) (longitudinal section). (D) A hydranth with capitate tentacles. (E) A hydranth with two whorls of filiform tentacles (e.g., *Tubularia*). (F) The freshwater *Hydra* (body is shown in longitudinal section).

(as in burrowing anemones); or it may arise from a common mat, stalk, or stolon in colonial forms.

The mouth may be set on an elevated **hypostome** or **manubrium** as in hydrozoans, or it may be on a flat **oral disc** as in anthozoans (Figures 7.5 and 7.6). In anthozoans the mouth is usually slitlike and leads to a muscular, ectodermally derived pharynx that extends into the coelenteron (the gut cavity of a polyp). The pharynx usually bears from one to several ciliated grooves called **siphonoglyphs**, which drive water into the coelenteron (Figure 7.6). It is in part the presence of siphonoglyphs that gives these polyps a secondary biradial or quadraradial symmetry. The side of an anthozoan polyp that bears a single siphonoglyph is called the **sulcal side**, and the opposite side is called the **asulcal side**.

The **coelenteron**, or gastrovascular cavity, serves for circulation as well as digestion and distribution of food. In hydrozoan polyps, the coelenteron is a single, uncompartmentalized tube. In scyphozoan (scyphistomae) and staurozoan polyps, it is partially subdivided by four longitudinal, ridgelike mesenteries, and in some staurozoans and cubozoans, additionally by a



transverse **claustrum** (a partition running parallel to the umbrellar margin and dividing each gastric pouch into inner and outer pockets). In anthozoan polyps, the coelenteron is extensively compartmentalized by mesenteries. Anthozoan mesenteries are projections of the inner body wall and thus are lined with gastrodermis and filled with mesenchyme. They extend from the inner body wall toward the pharynx, some or all of them fusing with it as **complete mesenteries**. Those that do not connect to the pharynx are called

FIGURE 7.6 An anthozoan polyp. (A) A sea anemone (longitudinal section). (B) Cross section taken at the level of the pharynx. (C) Cross section taken below level of the pharynx.

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incomplete mesenteries. In anthozoan polyps, the free inner edge of each mesentery below the pharynx has a thickened, cordlike margin armed with cnidae, cilia, and gland cells and is called the **mesenterial filament** (Figures 7.6 and 7.20). In some sea anemones these filaments give rise to long threads, called **acontia**, that hang free in the gastrovascular cavity. Acontia function in defense and feeding (see the Feeding and Digestion section). In most colonial anthozoans the cellular mesenchyme unites individual polyps (Figure 7.12). In some, such as the soft corals, gastrovascular cavities are connected to one another by canals called **solenia**.

The tentacles that surround the mouth contain hollow extensions of the coelenteron in anthozoans, whereas they house a solid core of packed gastrodermal cells in most hydrozoans. Tentacles may taper to a point (filiform tentacles) or may terminate in a conspicuous knob containing cnidae (capitate tentacles). In some polyps the tentacles are branched, often as pinnately arranged pinnules (e.g., in the octocorals).

Branched hydrozoan colonies, the individual polyps of which are called **hydropolyps**, grow in two patterns (Figure 7.7). In **monopodial growth**, the first polyp elongates continuously from a growth zone at the distal end of the simple or branched stem of the colony, the **hydrocaulus.** This primary (axial) polyp may even lose its hydranth (feeding zooid) and persist merely as a stalk. The primary hydrocaulus gives rise to secondary polyps by lateral budding. These secondary polyps grow and may give rise to lateral tertiary polyps in the same fashion. In hydrozoan colonies developing by **sympodial growth**, the primary polyp does not continue to elongate but produces one or more lateral polyps by budding and then stops growing. The new polyps extend the colony upward some distance, then stop growing and give rise to more new polyps by budding. In these colonies the main stem or axis actually represents the combined hydrocauli of many polyps, and the age of the polyps decreases from base to tip along each branch.

Most marine hydroids are surrounded, at least in part, by a nonliving protein-chitin exoskeleton secreted by the epidermis and called the **perisarc** (Figure 7.5). Interestingly, this outer covering is absent in freshwater hydroids. The living tissue inside the perisarc is termed the **coenosarc**. The perisarc may extend around each hydranth and gonozooid as a **hydrotheca** and **gonotheca**, respectively. When this occurs, the hydroids are said to be **thecate**; hydroids whose perisarcs do not extend around the zooids are **athecate**.

A complex terminology has been developed to describe hydrozoan polyps, or "hydroids" as they are commonly called (Figures 7.5 and 7.7). The reason for this special nomenclature is that hydroid colonies are usually polymorphic, containing more than one kind of polyp, or zooid. The terms **hydranth** and **gastrozooid** refer to feeding zooids, which typically bear tentacles and a mouth. Other commonly occurring polyp types include

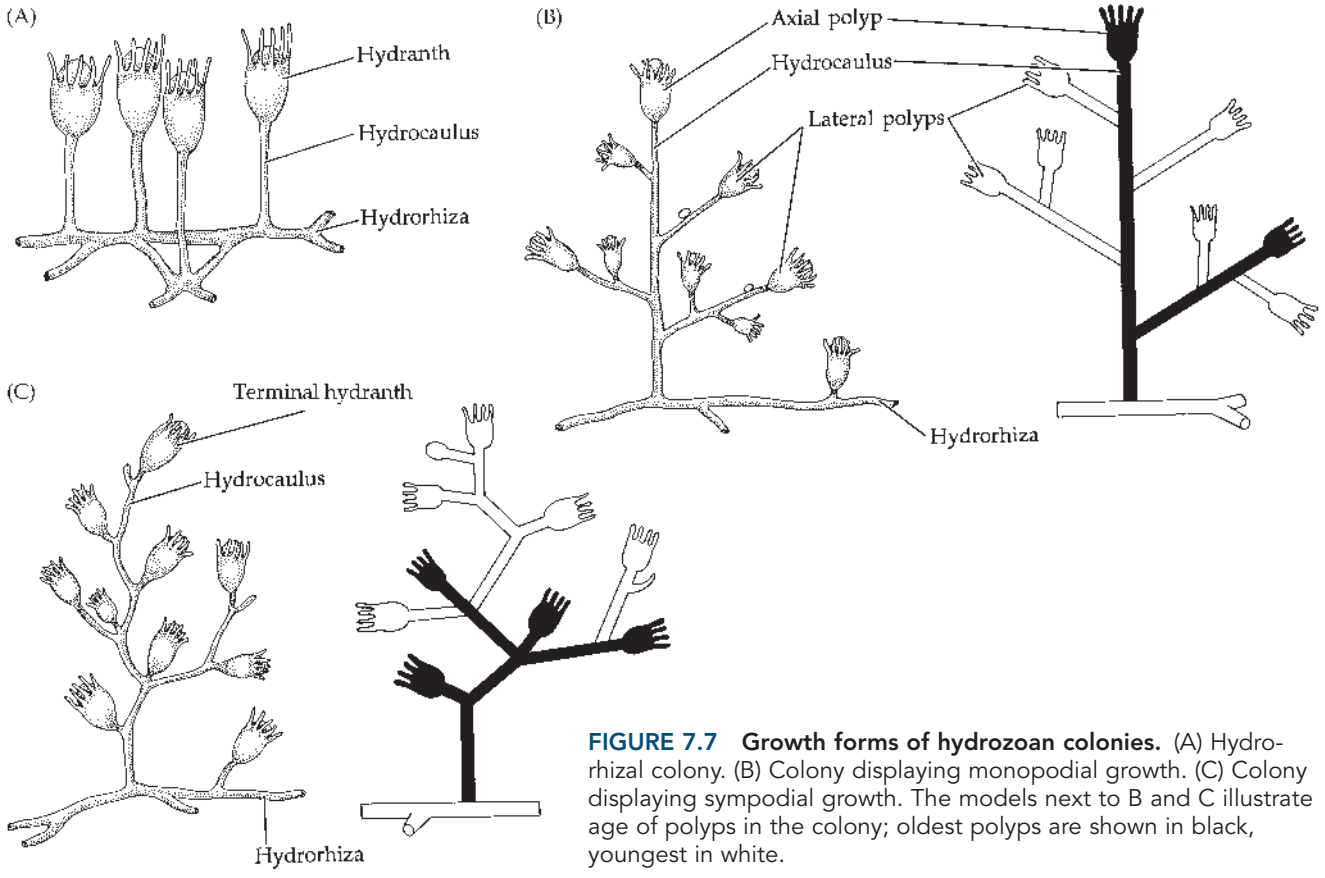

FIGURE 7.7 Growth forms of hydrozoan colonies. (A) Hydrorhizal colony. (B) Colony displaying monopodial growth. (C) Colony displaying sympodial growth. The models next to B and C illustrate age of polyps in the colony; oldest polyps are shown in black, youngest in white.

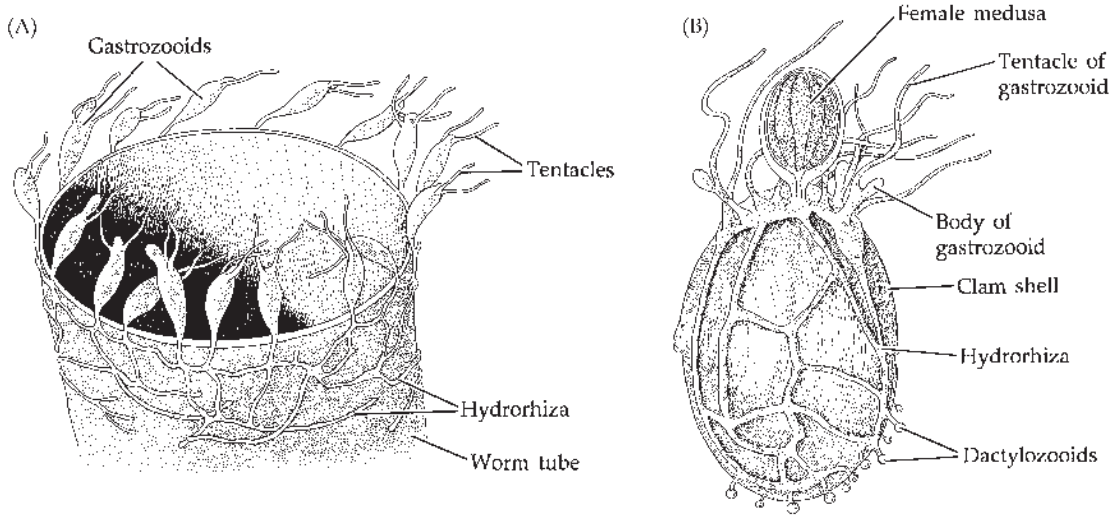

FIGURE 7.8 Diversity of form among the colonial Hydrozoa. (A) *Proboscidactyla*, a two-tentacled hydroid that lives around the open end of polychaete worm tubes. (B) *Monobrachium*, a one-tentacled hydroid that lives on clam shells. (C) *Hydractinia*, a colonial hydroid commensal on shells inhabited by hermit crabs. (D) The "chondrophoran" *Porpita* (aboral view). (E) A colony of the calcareous milleporid hydrocoral *Millepora* (fire corals). (F) A siphonophore, *Physalia* ("Portuguese man-of-war"). (G) A colony of the calcareous stylasterid hydrocoral *Stylaster*. (H) *Praya dubia*, a colonial calycophoran siphonophore from California. (I) Another siphonophore.

defensive polyps (**dactylozooids**) and reproductive polyps (**gonozooids** or **gonangia**). Each zooid typically arises from a stalk, called a **hydrocaulus** (pl. hydrocauli). In most colonial hydrozoans, the individual polyps are anchored in a rootlike stolon called a **hydrorhiza**, which grows over the substratum. From the hydrorhiza arise the hydrocauli, bearing polyps singly or in clusters.

Gastrozooids capture and ingest prey and provide energy and nutrients to the rest of the colony. Dactylozooids, which occur in a variety of sizes and shapes, are heavily armed with cnidae. Often several dactylozooids surround each gastrozooid and serve for both defense and food capture. Gonozooids produce medusa buds called **gonophores** that are either released or retained on the colony. Whether released as free medusae or retained as attached gonophores, they produce gametes for the sexual phase of the hydrozoan life cycle. The living tissue (coenosarc) of the gonozooid is called the **blastostyle**; the gonophores arise from this tissue. When a **gonotheca** surrounds the blastostyle, the zooid is called a **gonangium**.

The most dramatic examples of polymorphism among polyps are seen in the hydrozoan order Siphonophora and the anthozoan order Pennatulacea. Siphonophores (Figures 7.1N, 7.8F,H,I, and 7.9) are hydrozoan colonies composed of both polypoid and medusoid individuals, with as many as a thousand zooids in a single colony. This large order includes a great variety of unusual and poorly understood species, including the famous Portuguese man-of-war, *Physalia* (Figure 7.8F). The gastrozooids of siphonophores are actually highly modified polyps with a large mouth and one long, hollow feeding tentacle that bears many cnidae (Figure 7.9A). This feeding tentacle reaches lengths of 13 m in the Atlantic species *Physalia physalis*. The nonfeeding dactylozooids also bear one long (unbranched) tentacle (Figure 7.9B). The gonozooids (Figure 7.9C) are usually branched; they produce sessile gonophores that are never released as free medusae.

Siphonophores use one or more swimming bells (**nectophores**) or a gas-filled float (a **pneumatophore**), or both, to help maintain their position in the water. Nectophores are true medusoid individuals with many of the structures common to free-swimming medusae, although each nectophore has lost its mouth, tentacles, and sense organs. The pneumatophore, once also thought to be a modified medusa, is now known to be derived directly from the larval stage and may represent a highly modified polyp. Pneumatophores are double-walled chambers lined with chitin. Each float houses a gas gland, which consists of a mitochondria-laden glandular epithelium lining a chamber. The gland secretes a gas usually similar to air in composition, although in *Physalia* it apparently includes a surprisingly high proportion of carbon monoxide. Many siphonophores have mechanisms by which they regulate gas in their floats to keep the colony at a particular depth, much like the swim bladders of fishes.

Siphonophores were formerly classified into three suborders on the basis of colony structure: the Calycophorae included colonies with swimming bells but no float; Physonectae included those with a small float

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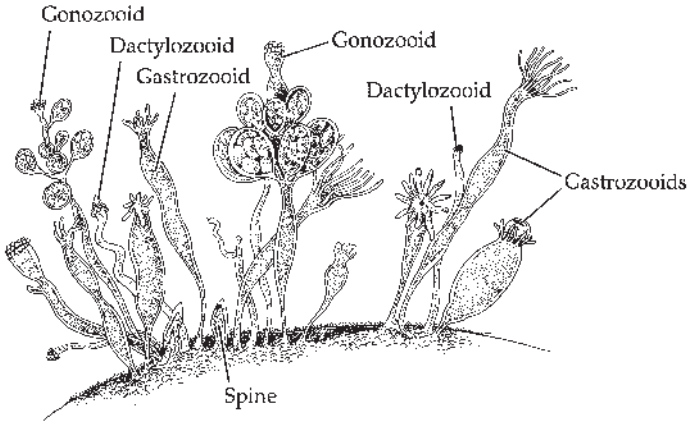

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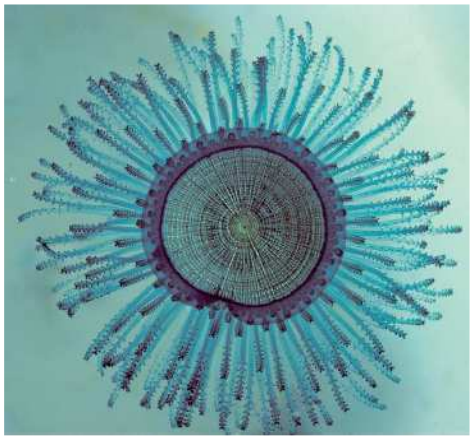

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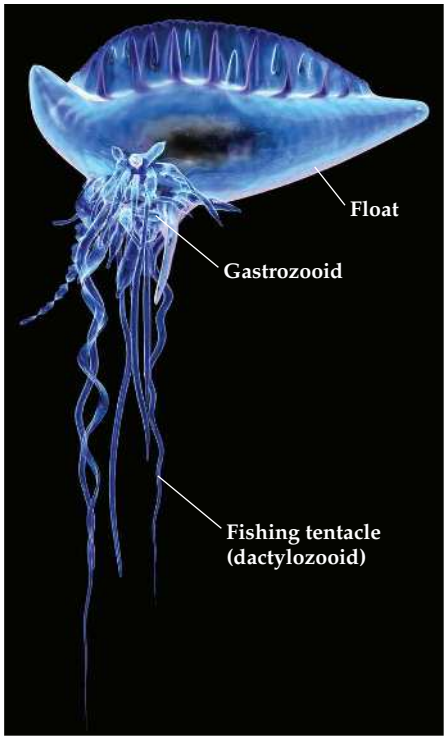

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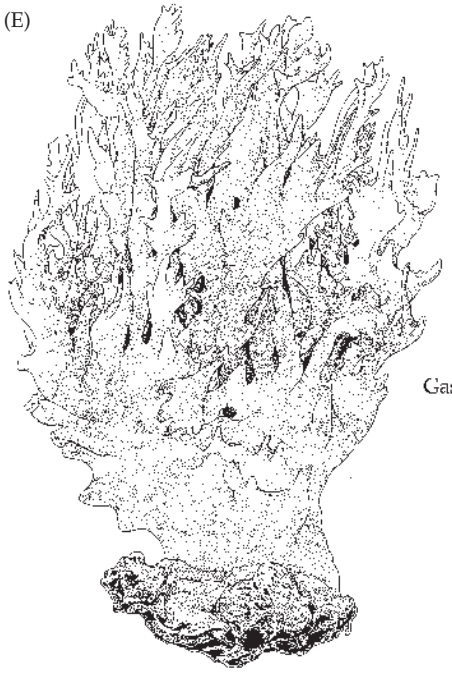

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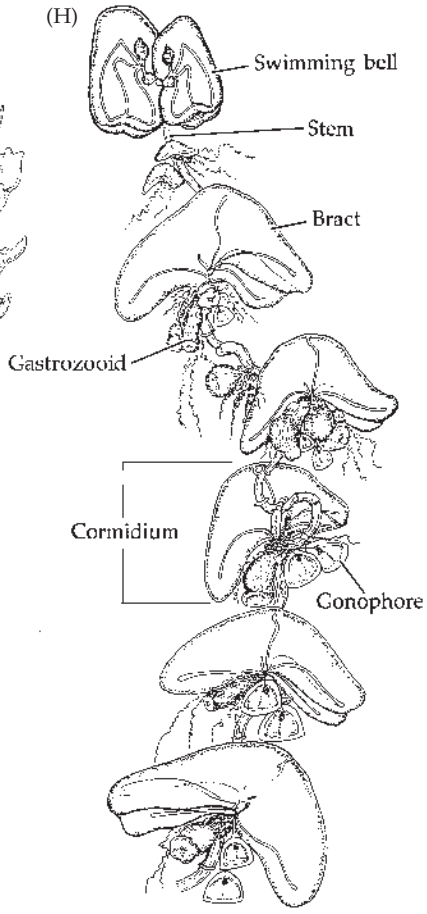

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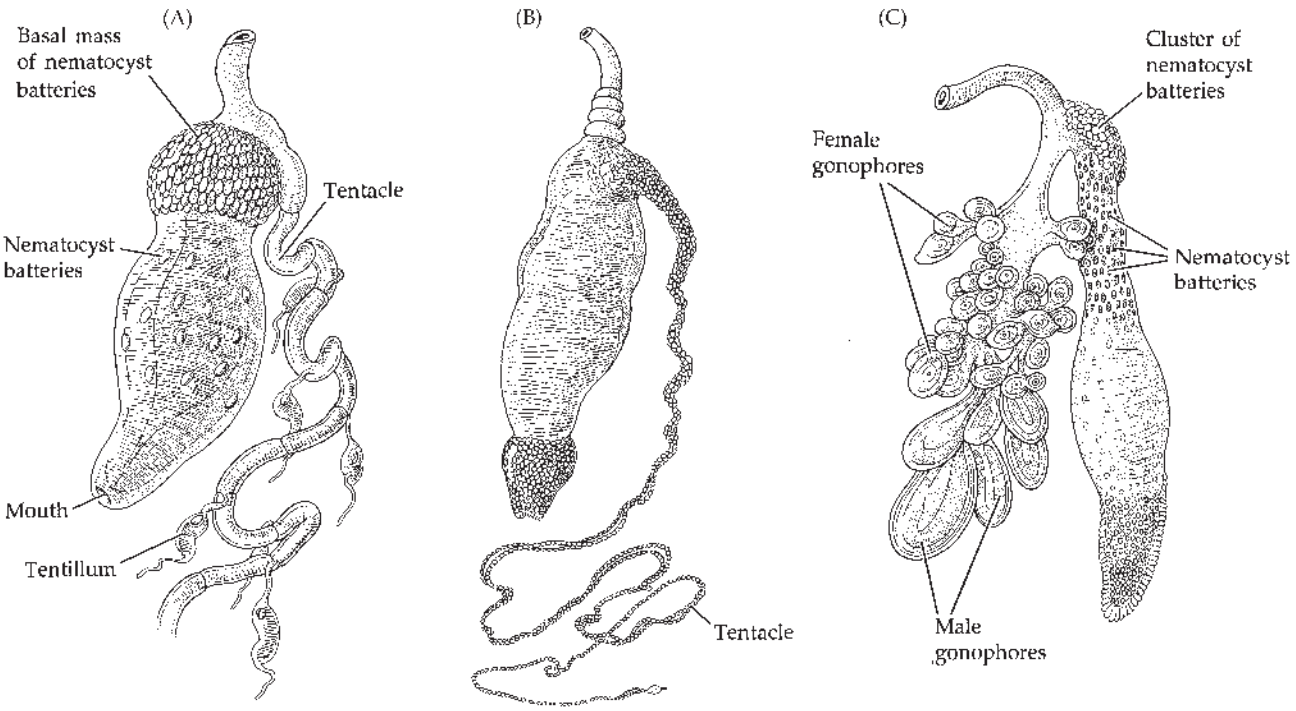

FIGURE 7.9 Siphonophore zooids. (A) A gastrozooid. (B) A dactylozooid. (C) A gonozooid.

and a long train of swimming bells; and Cystonecta had a large float and no bell. However, recent molecular phylogenetic evidence suggests that Cystonecta is the sister group to other siphonophores, with the monophyletic Calyphora nested within a paraphyletic Physonectae, both grouped for now within the suborder Codonophora (see Taxonomic History and Classification section). Calycophorans have a long tubular stem extending from the swimming bell, from which various types of zooids bud in groups called **cormidia** (Figure 7.8H). Each cormidium acts as a colony within a colony, and it is usually composed of a shieldlike bract, a gastrozooid, and one or more gonophores that may function as swimming bells. The cormidia commonly break loose from the parent colony to live an independent existence, at which time they are termed **eudoxids**. The members of the former physonectans have an apical float with a long stem bearing a series of nectophores followed by a long train of cormidia, thus a plesiomorphic condition within Codonophora. The cystonectans, including *Physalia*, usually have a large pneumatophore with a prominent budding zone at its base, which produces the various polyps and medusoids (Figure 7.8F).

Within the hydrozoan suborder Capitata, a group formerly known as the "chondrophora" is composed of colorful oceanic organisms that drift about on the sea surface in enormous flotillas, occasionally washing ashore to coat the beach with their bluish-purple bodies (Figures 7.1M and 7.10). Although they superficially resemble some siphonophores, current opinion holds these animals to be large, solitary, athecate hydranth polyps, floating upside down instead of sitting on a stalk attached to the bottom. The aberrant medusae of "chondrophorans" are short-lived and do not possess a functional mouth or gut, probably relying instead on their symbiotic zooxanthellae for nutrition. The aboral sail in *Velella* (the "by-the-wind-sailor") has no counterpart in sessile hydroids. In its ability to sail at an angle to the wind, *Velella* resembles the siphonophore *Physalia*—a similarity attributed to convergent evolution. Figure 7.10 compares a chondrophoran and a sessile hydroid, such as *Tubularia* or *Corymorpha*.

The pennatulaceans are the sea pens and sea pansies, and these are the most complex and polymorphic members of the class Anthozoa (Figures 7.1C,E and 7.11D). The colony is built around a main supportive stem, which is actually the primary polyp and buds lateral polyps in a regular fashion. The base of the primary polyp (the **stalk** or **peduncle**) is anchored in sediment, but the upper, exposed portion (the **rachis**) produces polyps in whorls or rows or sometimes united in crescent-shaped "leaves." Often these polyps are of two distinct types. **Autozooids** bear tentacles and function in feeding; **siphonozooids** are small, have reduced tentacles, and serve to create water currents through the colony. In sea pens the rachis is elongated and cylindrical; in sea pansies it is flattened and shaped like a large leaf (Figure 7.1E). In the odd deep-sea genus *Umbellula*, (Figure 7.1F) the secondary polyps radiate outward to give the colony the appearance of a pinwheel set on the end of a narrow stalk that can grow taller than a person. The first deep benthic photos of *Umbellula* had biologists scratching their heads for years, wondering to which phylum this preposterous creature might belong.

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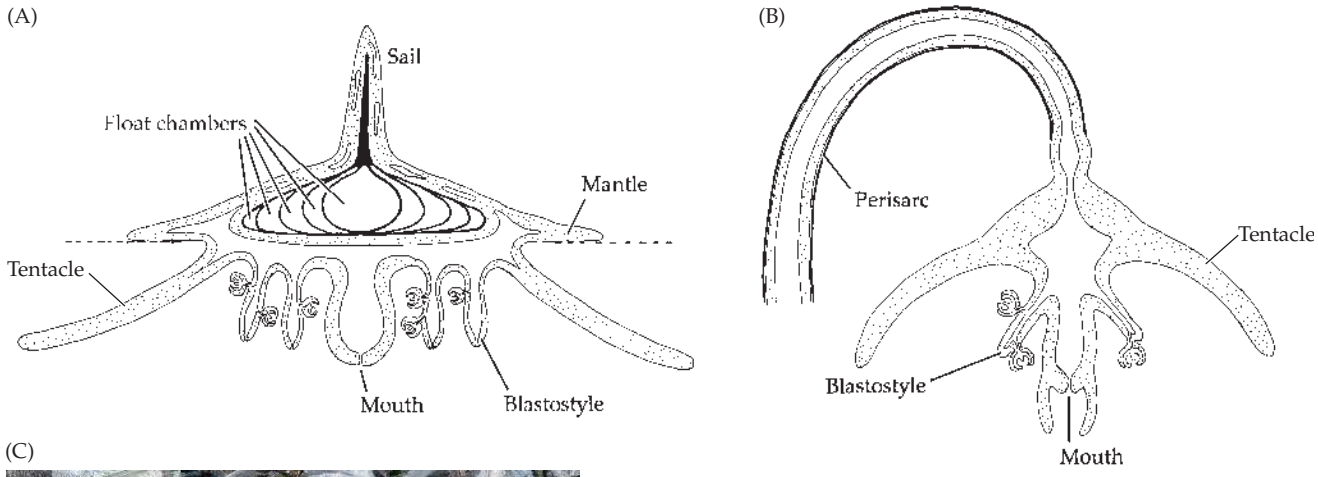

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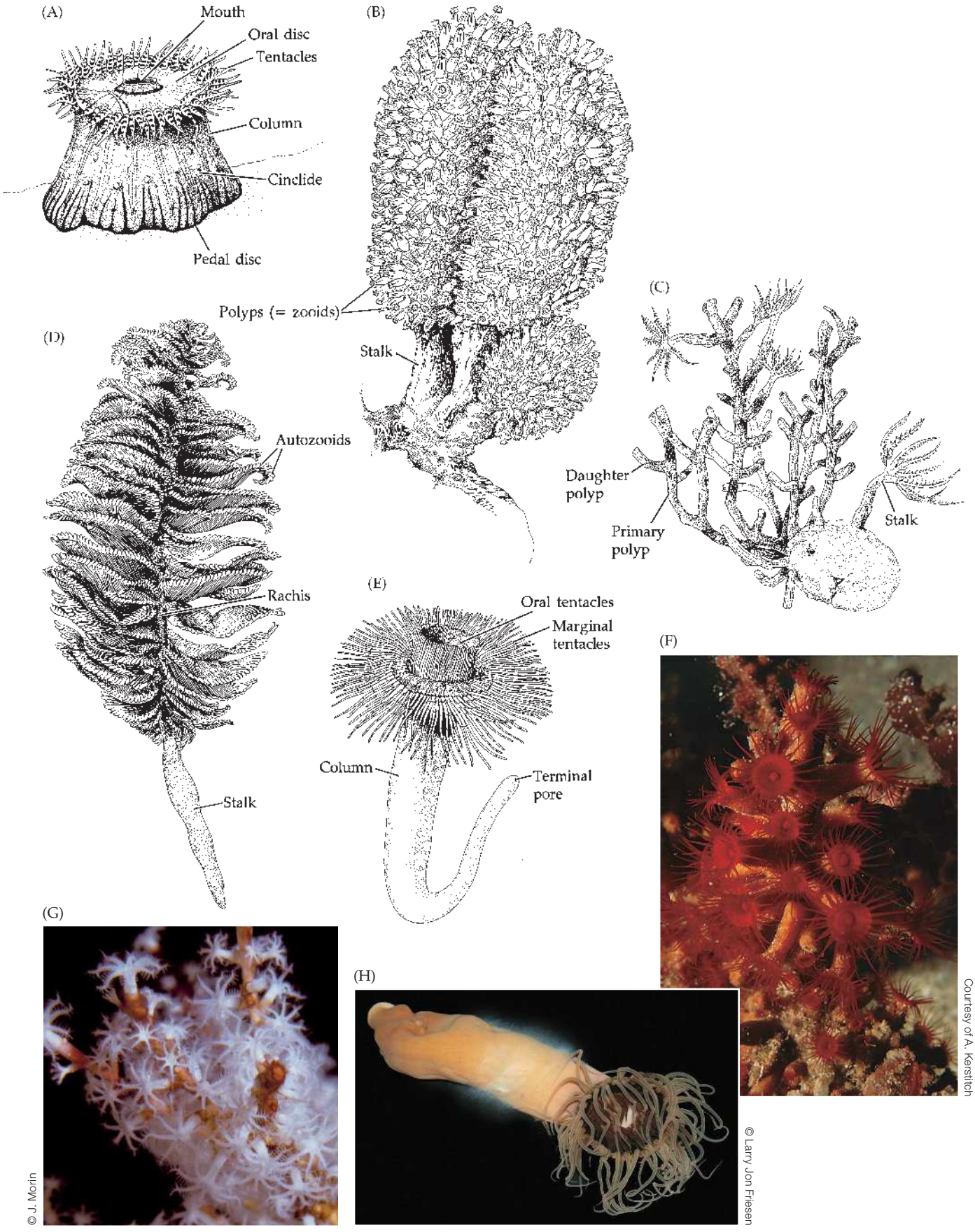
FIGURE 7.10 *Velella.* (A) A capitate hydrozoan such as *Velella* compared with (B) a sessile tubularian hydranth, in support of the view that "chondrophorans" are highly specialized, solitary tubularian zooids. (C) *Velella* skeletons in beach wrack, coast of Washington State.

Gorgonians are also colonial anthozoans (Figures 7.1D and 7.12). Some grow in bushy shapes, whereas others are planar; size and shape of the colony are often mediated by the hydrodynamics of prevailing surge and currents. Where prevailing currents are more or less in one plane (although they may move in two directions back and forth), the branches of the colony tend to grow largely in one plane also—perpendicular to the flow. In regions of mixed currents, the same species tends to grow in two planes.

The apparent polyps of *Polypodium hydriforme* (the only species in the bizarre class Polypodiozoa, of the subphylum Endocnidozoa) exist intracellularly within the ova of their fish hosts as an inverted stolon whose digestive surface faces outward. Prior to host spawning when ova are provisioned with yolk, *Polypodium* everts to assume normal cell layer position, filling its gastric cavity with host yolk and revealing tentacles distributed along the stolon's length.

The medusoid form Free medusae occur only in the subphylum Medusozoa. Although variation in form exists, medusae are far less diverse than polyps, and it is much easier to generalize about their anatomy. (After reading about the amazing variation in polypoid colonies, you're probably happy to hear this!) The relative uniformity of medusae may be largely a result of their usually similar lifestyles in open water and of their inability (except among hydrozoans) to form colonies by asexual reproduction. Sessile benthic medusae exist, but they are relatively rare (Figure 7.1G). Despite their simplicity relative to polypoid forms, medusae do vary considerably in size, ranging from 2.0 mm diameter hydromedusae to 2.0 m scyphomedusae, and depending on their habitat can exhibit particular morphological specializations associated with movement in a fluid medium. In many medusae the radial canals open near the ring canal onto the subumbrellar surface by separate pores. These are thought to be "excretory pores" for the ejection of wastes and indigestible materials that have been seen passing through them. While polyps often represent the vegetative stage of development among cnidarians, most medusae are the sexual form.

Even though the body walls of medusae and polyps are similar and both adhere to the general cnidarian body plan outlined earlier, their gross morphologies are adapted to their very different lifestyles. Medusae are bell or umbrella shaped and are usually imbued with a thick, jellylike mesogleal layer (hence the name "jellyfish" or simply "jellies"). The convex upper (aboral) surface is called the **exumbrella**; the concave lower (oral) surface is the **subumbrella**. The mouth is located in the center of the subumbrella, often suspended on a pendant, tubular extension called the **manubrium**,



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◀ **FIGURE 7.11 Anthozoans.** (A) A sea anemone, *Actinia* (Actiniaria). (B) A soft coral, *Alcyonium* (Alcyonacea). (C) The octocoral *Telesto* (Alcyonacea). (D) The sea pen *Pennatula* (Pennatulacea). (E) A ceriantharian anemone removed from its tube (Ceriantharia). (F) The cup coral *Phyllangia (Scleractinia)*. (G) A soft coral (Alcyonacea). (H) A burrowing anemone, *Pachycerianthus torreyi* (Ceriantharia), which lives in bays and lagoons on the west coast of North America. Note the double circle of distinct tentacles and the lack of an attaching basal disc (instead the rounded physa). Ceriantharians build tubes in soft sediment, made of fine sediment particles, specialized cnidae (ptychocysts), and mucus.

which is almost always present on hydromedusae (Figure 7.13) but usually reduced or absent in scyphomedusae (Figure 7.14).

The coelenteron or gastrovascular cavity occupies the central region of the umbrella and extends radially in the body via **radial canals**. In most hydromedusae (medusae of the class Hydrozoa), a marginal ring canal within the rim of the bell connects the ends of the radial canals. The presence of four radial canals and of tentacles in multiples of four (in hydromedusae) and the division of the stomach by mesenteries into four **gastric pouches** (in scyphomedusae) give most jellyfish a quadriradial (= tetramerous) symmetry (Figure 7.3A). Most hydromedusae have

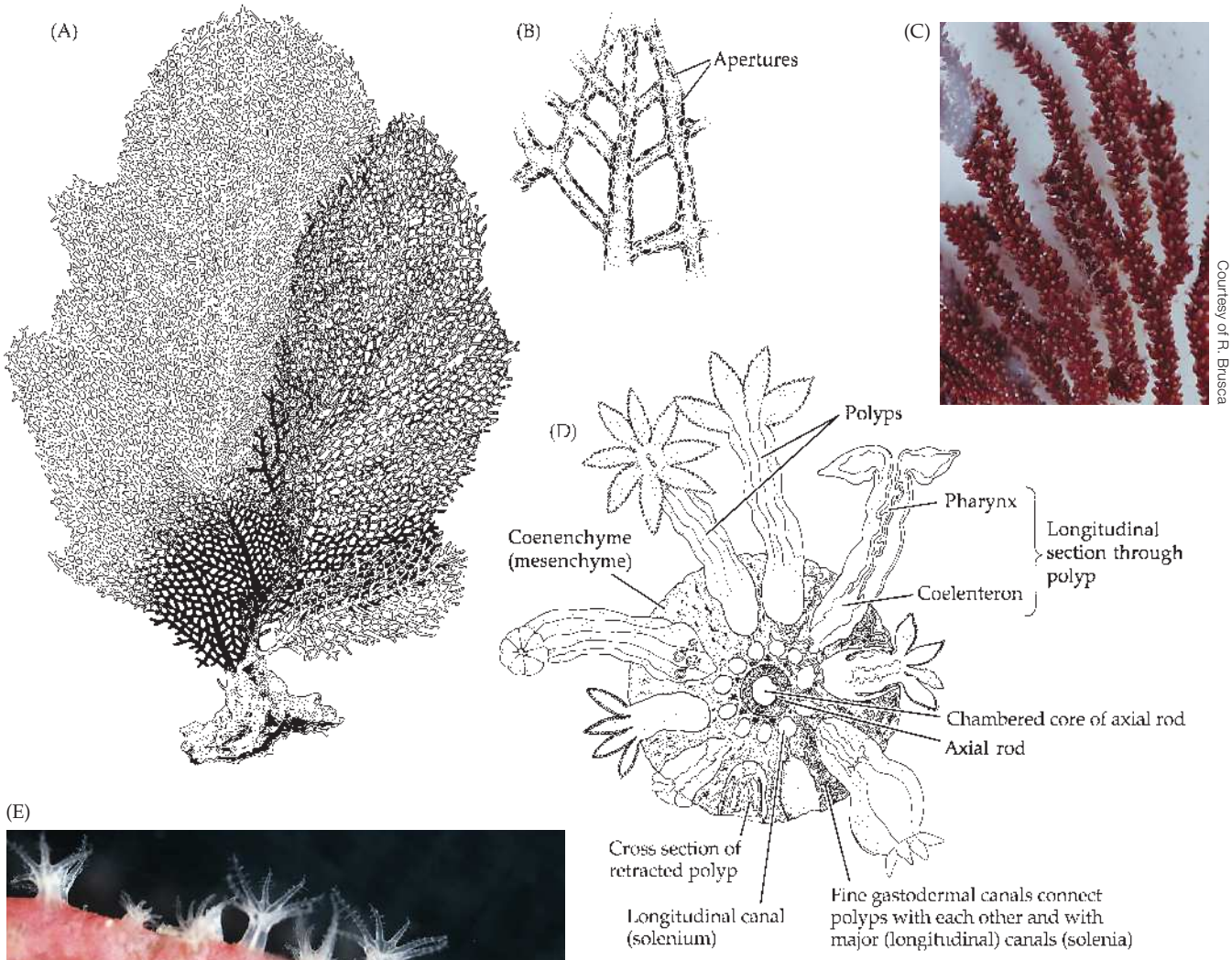

FIGURE 7.12 Gorgonians (class Anthozoa, subclass Octocorallia, order Alcyonacea). (A) The sea fan *Gorgonia* has lacelike branches. (B) Apertures of retracted polyps are visible on the branches of *Gorgonia*. (C) The Pacific gorgonian, *Muricea californica*, releasing round white eggs from reproductive polyps. (D) A branch of the sea fan *Pseudoplexaura* (cross section). (E) Polyps of *Psammogorgia*.

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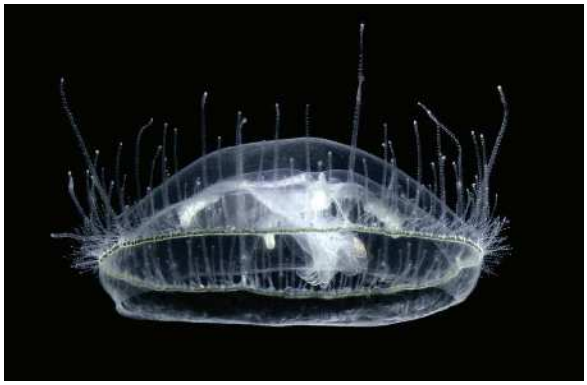

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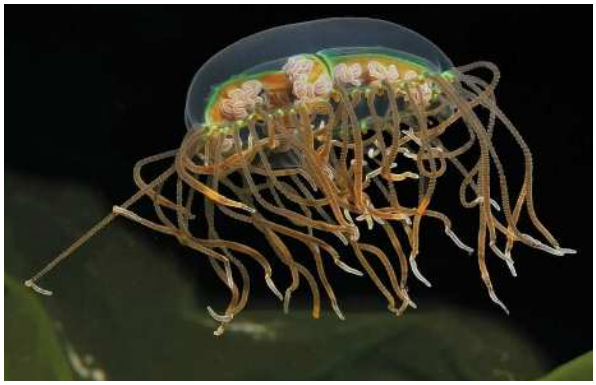

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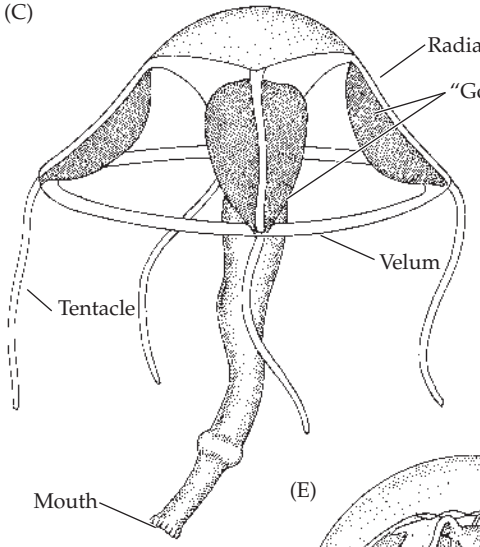

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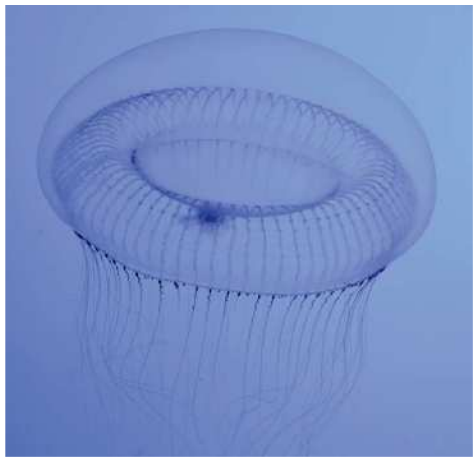

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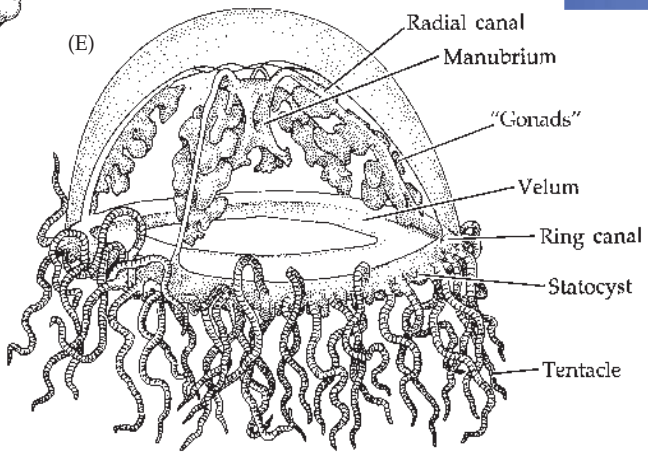

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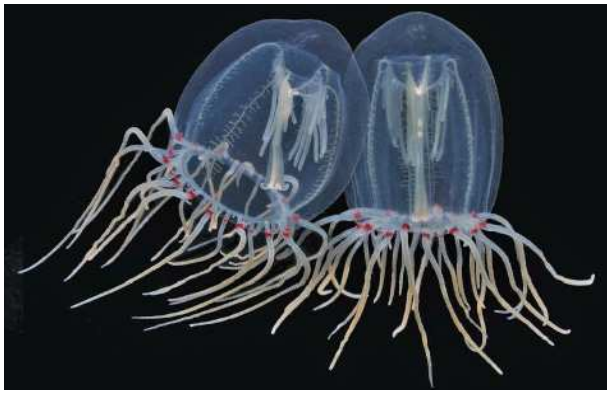

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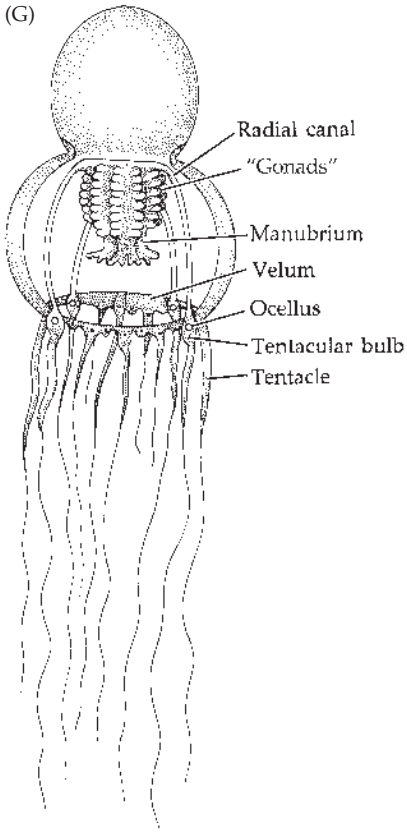

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◀ **FIGURE 7.13 Hydrozoan medusae.** (A–C) Limnomedusae (subclass Trachylina). (A) a freshwater limnomedusa, *Craspedacusta sowerbii*. (B) A temperate coastal species, *Gonionemus vertens*. Sometimes called "stinging jellies," most species in this genus have been shown to have a potent sting. (C) *Liriope tetraphylla*. (D,E) Leptomedusae (subclass Hydroidolina). (D) *Aequorea victoria*. (E) Anatomy of a typical leptomedusan. (F,G) Anthomedusae (subclass Hydroidolina). (F) Two individuals of *Polyorchis* sp. (G) Anatomy of a typical anthomedusan.

a thin circular flap of tissue, the **velum**, within the margin of the bell (Figure 7.13). Such medusae are termed **craspedote**. Those lacking a velum, such as scyphomedusae, are said to be **acraspedote** (Figures 7.14 and 7.15). The medusae of cubozoans possess an independently evolved structure, the **velarium** (Figure 7.15A), which is structurally different but functionally similar to the hydromedusan velum. As in polyps, the external surfaces of medusae are covered with epidermis, and the internal surfaces (coelenteron and canals) are lined with gastrodermis. The bulky, gelatinous middle layer is either a largely acellular mesoglea or a partly cellular mesenchyme.

Although scyphozoan genera are morphologically similar, diversity may be much greater than previously suspected. For example, molecular evidence suggests that the moon jellyfish *Aurelia aurita*, a cosmopolitan semaeostome species often used in invertebrate zoology laboratories to illustrate medusoid structure and the alternation of generations in the life cycle of cnidarians, may consist of seven or more distinct species. While morphologically indistinguishable (so far), these genetically distinct populations may have diverged as early as the Late Cretaceous (> 65 Ma).

Support

Cnidarians employ a wide range of support mechanisms. Polyps rely substantially on the hydrostatic qualities of the water-filled coelenteron, which is constrained by circular and longitudinal muscles of the body wall. With few exceptions, polyps have smooth muscle, but medusae have both smooth and striated (though mononuclear) muscles in the umbrella. However, the muscles of cnidarians lack crucial components of bilaterian striated muscles, such as genes that code

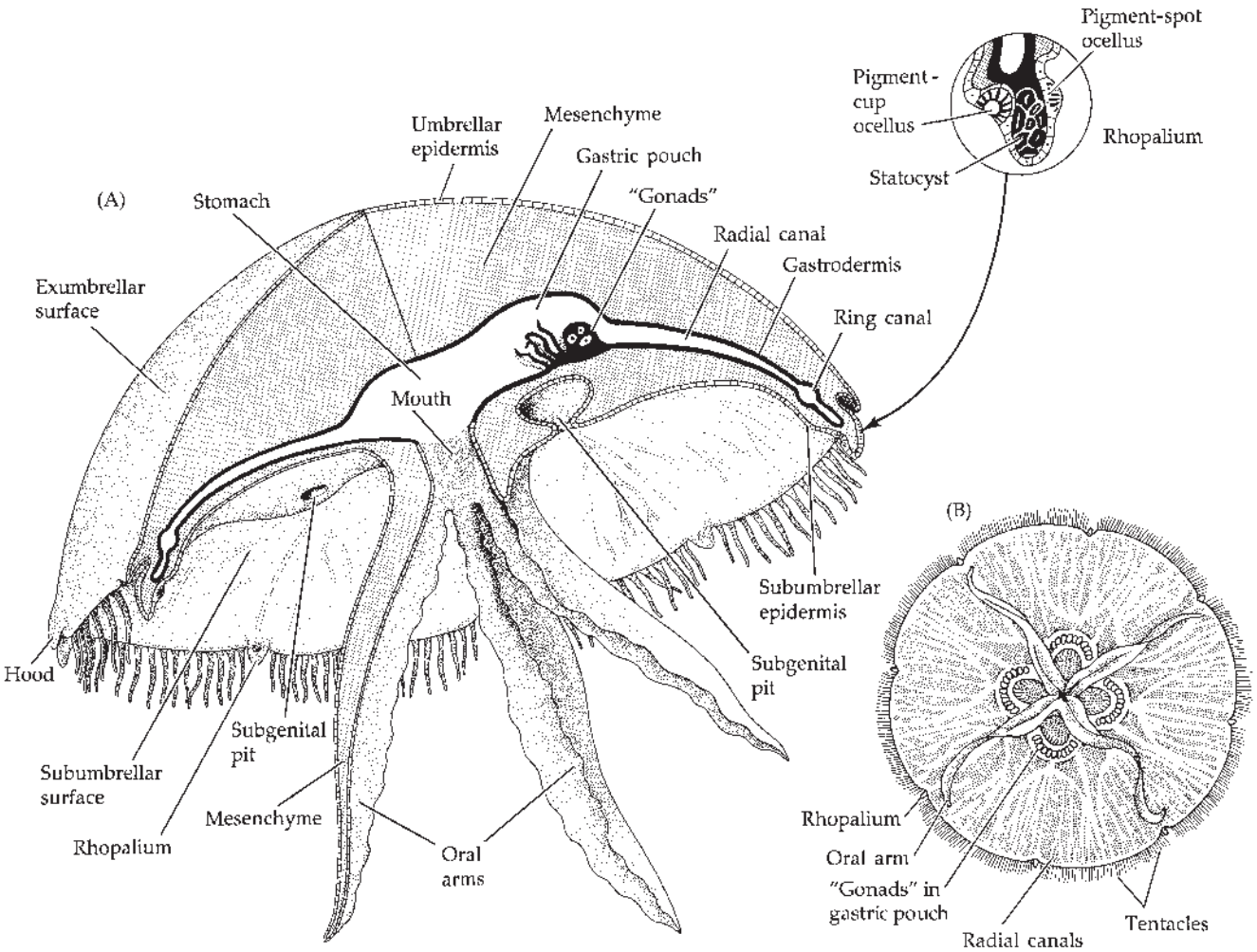

FIGURE 7.14 A typical scyphozoan medusa. (A) Cutaway side view. (B) Oral view.

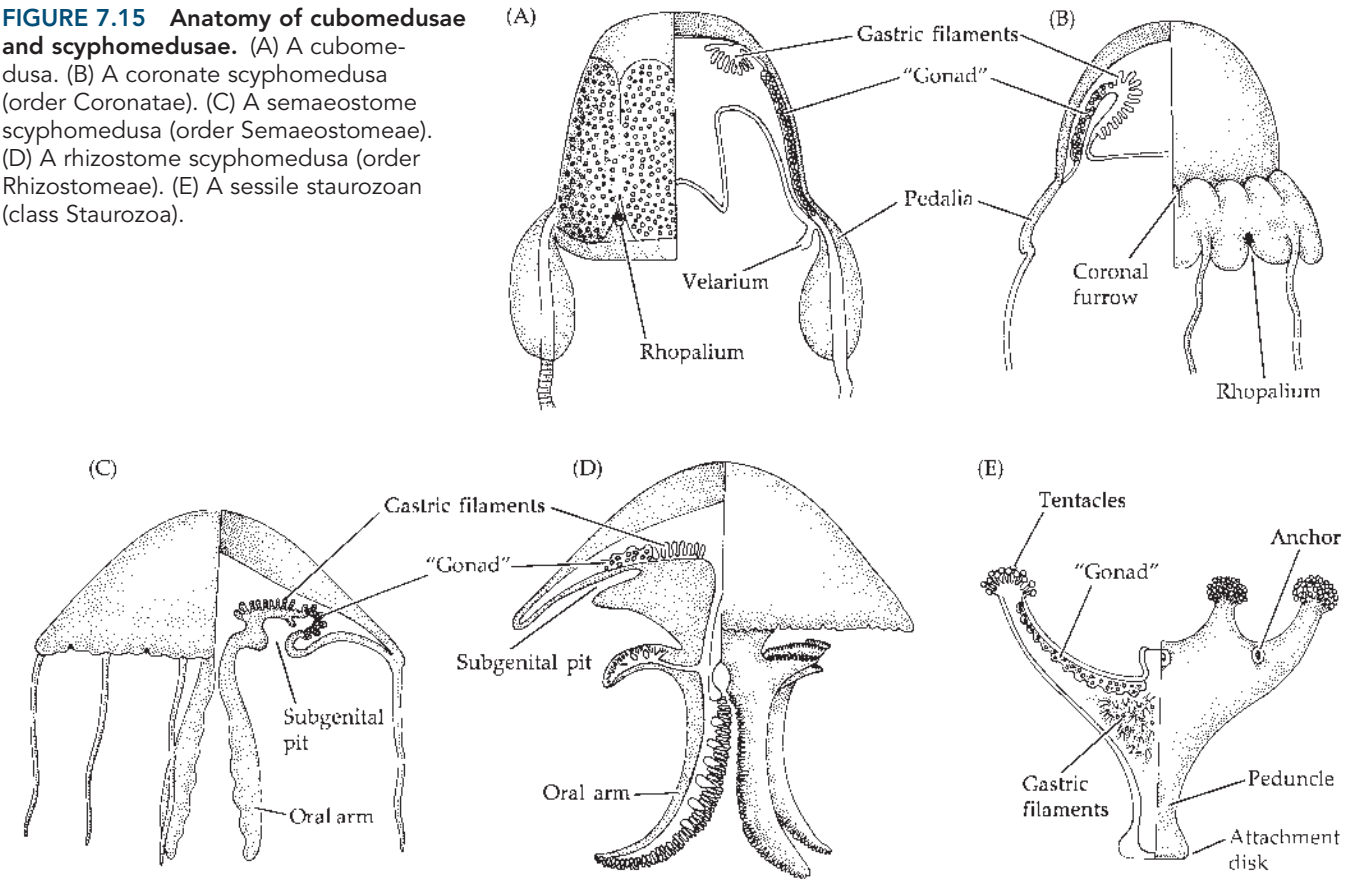

FIGURE 7.15 Anatomy of cubomedusae and scyphomedusae. (A) A cubomedusa. (B) A coronate scyphomedusa (order Coronatae). (C) A semaeostome scyphomedusa (order Semaeostomeae). (D) A rhizostome scyphomedusa (order Rhizostomeae). (E) A sessile staurozoan (class Staurozoa).

for the muscle proteins titin (a.k.a. connectin) and the troponin complex. In addition, the mesenchyme may be stiffened with fibers, particularly in the anthozoans. Colonial anthozoans may incorporate bits of sediment and shell fragments onto the column wall for further support. Many colonial hydrozoans produce a flexible, horny perisarc, composed largely of chitin secreted by the epidermis. In medusae, the principal support mechanism is the middle layer, which ranges from a fairly thin and flexible mesoglea to an extremely thick and stiffened fibrous mesenchyme, which may be almost cartilaginous in consistency. Even the small, benthic polyp phase of medusozoans typically has a thin, flexible, chitin-based covering secreted by the epidermis and similar to that seen in anthozoans.

In addition to these soft or flexible support structures, there is an impressive array of hard skeletal structures of three fundamental types: horny or woodlike axial skeletal structures, calcareous sclerites, and massive calcareous frameworks. Horny axial skeletons occur in several groups of colonial anthozoans such as gorgonians, sea pens, and antipatharian corals (Figures 7.11 and 7.12). Amebocytes in the coenenchyme secrete a flexible or stiff internal **axial rod** as a supportive base embedded in the coenenchymal mass. Axial rods are protein-mucopolysaccharide complexes (called **gorgonin** for "gorgonian" corals in the octocoral order Alcyonacea). In the antipatharians (black corals), the axial skeleton is so hard and dense that it is ground and polished to make jewelry, leading to a serious overharvesting of these animals around the world.

In most octocorals, mesenchymal cells called **scleroblasts** secrete calcareous sclerites of various shapes and colors (Figure 7.16C). It is usually these sclerites that give soft corals and gorgonians their characteristic color and texture. In many species, the sclerites become quite dense and may even fuse to form a more-or-less solid calcareous framework. The precious red corals in the genus *Corallium* are actually gorgonians with fused red coenenchymal sclerites. In the stoloniferan organ-pipe corals (*Tubipora*), the sclerites of the body walls of the individual polyps are fused into rigid tubes. Invertebrate calcium carbonate skeletons do not usually have collagen incorporated into their framework, as occurs in vertebrates. However, in at least some gorgonians (e.g., *Leptogorgia*) the calcareous spicules do include a collagen component.

Massive calcareous skeletons are found in only certain groups of Anthozoa and Hydrozoa. The best known are the stony anthozoan corals (order Scleractinia), in which epidermal cells on the lower half of the column secrete a calcium carbonate skeleton (Figure 7.17) through a complex biologically controlled process. The skeleton is covered by the thin layer of living epidermis that secretes it, and thus it might technically be considered an internal skeleton. However, because the stony coral colony generally sits atop a large nonliving calcareous framework, most biologists speak of the skeleton as being external.

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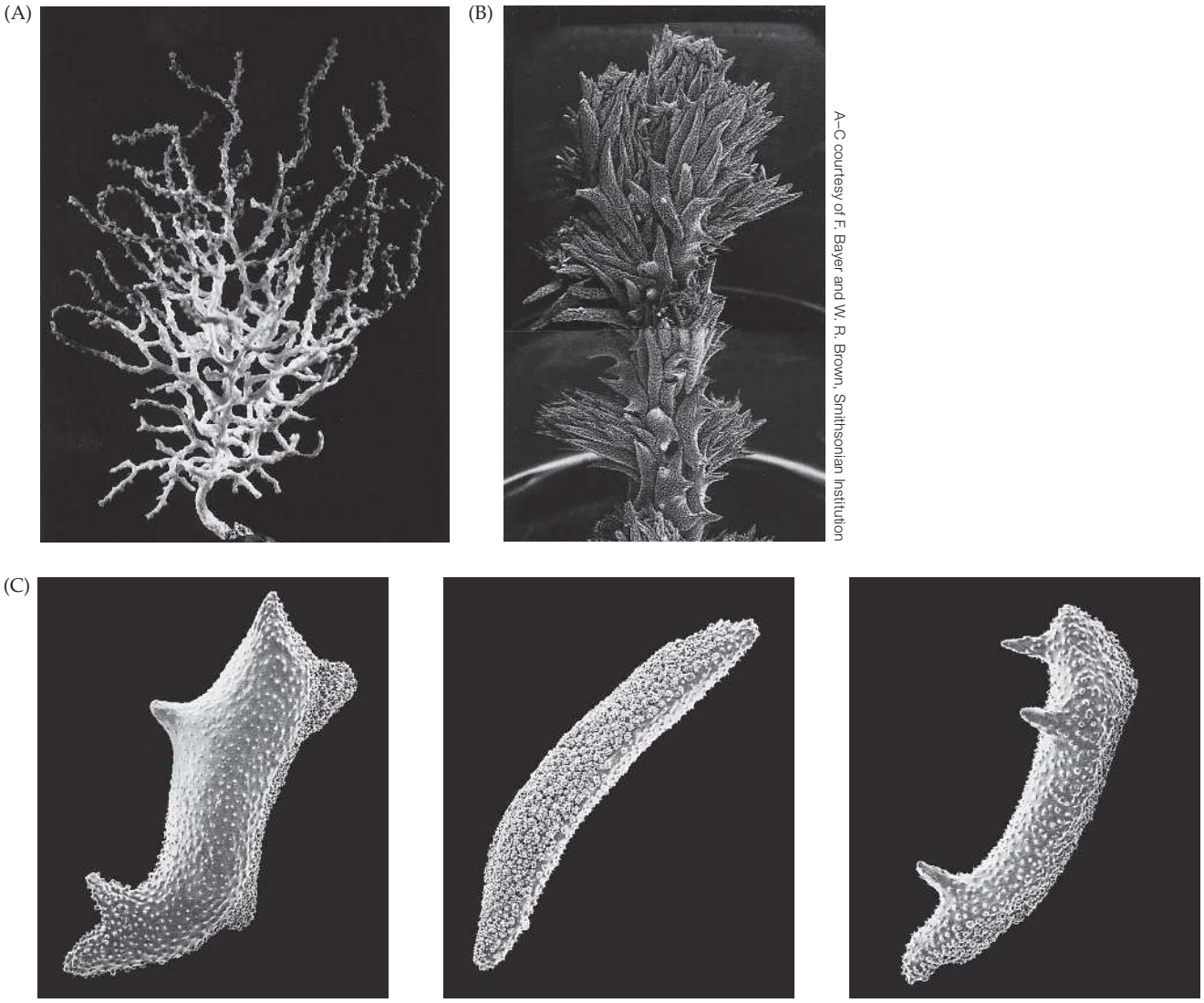

FIGURE 7.16 The skeleton of gorgonians, illustrated at successively greater magnification of the gorgonian *Muricea fruticosa*. (A) A complete colony. (B) Colony branches bear whorls of polyps. (C) Sclerites from the tissues of a single polyp.

The entire colony of a scleractinian coral is called a **corallae**, and its skeleton is the **corallum**, regardless of whether the animal is solitary or colonial; the skeleton of a single polyp, however, is called a **corallite**. The outer wall of the corallite is the **theca**; the floor is the **basal plate** (Figure 7.17). Rising from the center of the basal plate is often a supportive skeletal process called the **columella** (or pedicel). The basal plate and inner thecal walls give rise to numerous radially arranged calcareous partitions, the **septa**, which project inward and support the mesenteries of the polyp. Polyps occupy only the uppermost surface of the corallum. Skeletal thickness increases as polyps grow, and the bottoms of the corallites are sealed off by transverse calcareous partitions called **tabulae**, each of which

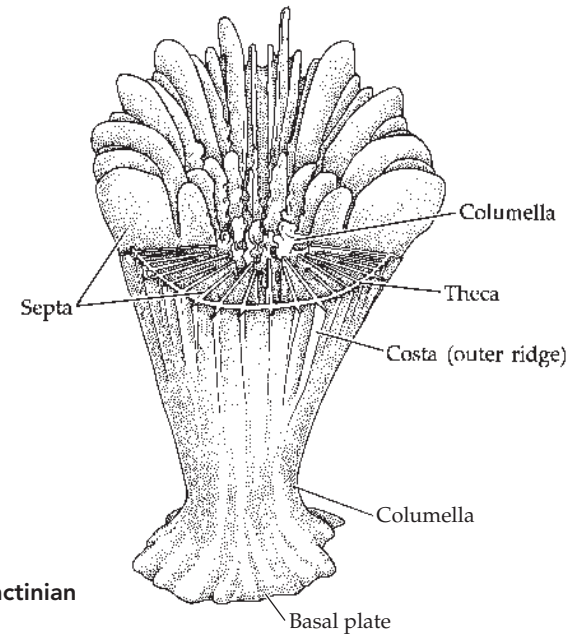

FIGURE 7.17 The corallite of a solitary scleractinian coral illustrating morphological features.

becomes the basal support of a new polyp. The corallum can assume a great variety of shapes and sizes, from simple cup-shaped structures in solitary corals to large branching or encrusting forms in colonial species.

Members of the hydrozoan families Milleporidae (fire corals) and Stylasteridae (stylasterids) also produce calcareous exoskeletons, and they are often referred to as the hydrocorals. Like stony corals (Scleractinia), milleporid colonies may assume a variety of shapes, from erect branching forms to encrustations. The milleporid exoskeleton, termed a **coenosteum**, is perforated by pores of two sizes that accommodate two kinds of polyps. The gastrozooids live in large holes, or **gastropores**, and are surrounded by a circle of smaller **dactylopores**, which house the dactylozooids. Canals lead downward from the pores into the coenosteum and are closed off below by transverse calcareous tabulae. As growth proceeds and the colony thickens, new tabulae are formed, keeping the polyp pores at a more or less fixed depth. Hydrocoral colonies thus differ from scleractinian colonies in having the skeleton penetrated by living tissue. The stylasterid skeleton is similar to the milleporid skeleton, but the margins of the gastropores often bear notches that serve as dactylopores, and the gastrozooids and dactylozooids are supported by calcareous, spine-like **gastrostyles** and low ridges called **dactylostyles**, respectively (Figure 7.18). Stylasterid gonophores arise in chambers called **ampullae**, which connect to the feeding zooids through the coenosteum. In hydrocorals such as *Millepora*, ampullae open briefly to release large numbers of tiny medusae, which for each **coralla** (colony) contain either eggs or sperm, as milleporids are gonochoristic.

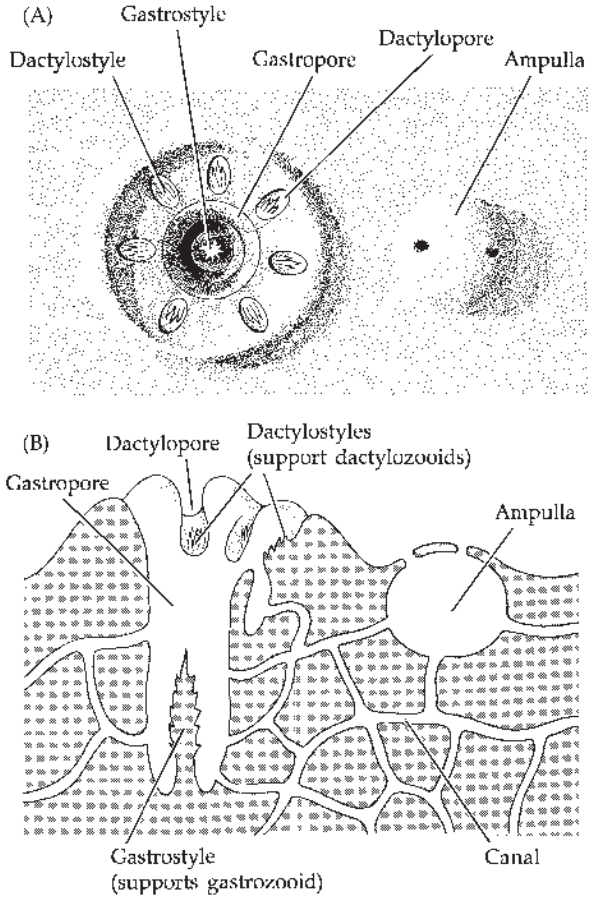

FIGURE 7.18 Hydrozoan skeletons. The stylasterid hydrocoral *Stylaster* has a calcareous skeleton. Plane view, from above (A) and cross section through the skeleton (B).

The calcium carbonate skeletons of cnidarians make them particularly vulnerable to ocean acidification—an outcome of anthropogenic carbon emissions and resulting global warming. Increased atmospheric carbon leads to more CO_2 dissolving into seawater (now estimated to occur at a rate of 1 million tons per hour), a reaction that accelerates with increasing temperature. More dissolved CO_2 reduces the pH of the ocean water, which tends to dissolve and thus destroy the primary building material of coral skeletons, calcium carbonate. Whereas calcification rates on the Great Barrier Reef increased 5.4% between 1900 and 1970, they dropped 14.2% between 1990 and 2005. The shells of echinoderms, molluscs, crustaceans, certain protists, and many other marine species are at similar and alarming risk.

Movement

The contractile elements of cnidarians are derived from their myoepithelial cells (Figure 7.19). In spite of the epithelial origin of these elements, for convenience we use the terms "muscles" and "musculature" for the sets of longitudinal and circular fibrils. In polyps, these two muscle systems work in conjunction with the gastrovascular cavity as an efficient hydrostatic skeleton, as well as facilitating body movements. However, unlike the fixed-volume hydrostatic skeletons of many animals (e.g., many worms), water can enter and leave the coelenteron of cnidarians, adding to its versatility as a support device. Polyp body musculature is most highly specialized and well developed in the anthozoans, particularly the sea anemones, and many muscles lie in the mesenchyme. In anemones, the muscles of the column wall are largely gastrodermal, although epitheliomuscular cells occur in the tentacles and oral disc. Bundles of longitudinal fibers lie along the sides of the mesenteries and act as retractor muscles for shortening the column (Figure 7.20). Circular muscles derived from the gastrodermis of the column wall are also well developed. In most anemones, the circular muscles form a distinct sphincter at the junction of the column and the oral disc. Circular fibers also occur in the tentacles and the oral disc, and circular muscles surrounding the mouth can close it completely. When an anemone contracts, the upper rim of the column is pulled over to cover the oral disc. In many sea anemones, a circular fold—the **collar**, or **parapet**—occurs near

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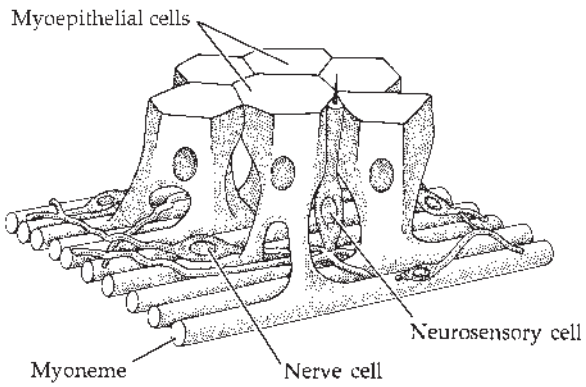

FIGURE 7.19 **Myoepithelial cells and the nerve net of cnidarian epithelium.**

the sphincter to further cover and protect the delicate oral surface upon contraction.

Polyps are sedentary or sessile. Their movements consist mainly of food-capturing actions and the withdrawal of the upper portion of the polyp during body contractions. These activities are accomplished primarily by the epidermal muscles of the tentacles and oral disc and by the strong gastrodermal muscles of the column. Circular muscles work in conjunction with the hydrostatic skeleton to distend the tentacles and body.

A variety of locomotor methods have evolved among polyps (Figure 7.21). Most can creep about slowly by using their pedal disc musculature. In some solitary hydrozoan polyps (e.g., *Hydra*), the column can bend far enough to allow the tentacles to contact and temporarily adhere to the substratum, whereupon the pedal disc releases its hold and the animal somersaults or moves like an inchworm. Simple polyps like the hydrozoan *Hydra* transfer fluid within their gastrovascular cavity using contractions of the peduncle; these contractions are biochemically mediated by RFamides, chemicals that induce cardiac contraction in higher metazoans, suggesting that muscular contractions in these distantly related taxa might share neurological similarities. A few sea anemones can detach from the substratum and actually swim away by "rapid" flexing or bending of the column (e.g., *Actinostola*, *Stomphia* [Figure 7.21E]); others swim by thrashing the tentacles (e.g., *Boloceroides*). These swimming activities are temporary behaviors, generally elicited by the approach or contact of a predator. In a few species of sea anemones, the basal disc may detach and secrete a gas bubble, permitting the polyp to float away to a new location.

Many species of small anthozoans can temporarily float hanging upside down on the sea surface by using water surface-tension forces (e.g., *Epiactis*, *Diadumene*). Sea anemones of one family (Minyadidae) are wholly pelagic and float upside down in the sea by means of a gas bubble enclosed within the folded pedal disc. *Hydra* also is known to float upside down by means of a mucus-coated gas bubble on the bottom of its pedal disc. One of the oddest forms of polyp locomotion is that of the sea anemone *Liponema brevicorne* of the Bering Sea, which is capable of drawing itself into a tight ball that can be rolled around the seafloor by the bottom currents (Figure 7.21D). Even colonial sea pansies (Pennatulacea) are motile, in that they can use their muscular peduncle to move to different depths on the seafloor.

Most ceriantharian anemones are burrowing, tube-building organisms (Figure 7.11E). They differ from the sea anemones (Actiniaria) in several important ways. They have no sphincter muscle, and their weak longitudinal gastrodermal muscles do not form distinct retractors in the mesenteries. As a result, cerianthariens cannot retract the oral disc and tentacles as they withdraw into their tubes. In contrast to other anemones, however, they possess a complete layer of longitudinal epidermal muscles in the column, which allows a very rapid withdrawal response. The mere shadow of a passing hand will cause a ceriantharian to rapidly pull itself deep into its long, buried tube.

In medusae, epidermal and subepidermal musculatures predominate, and the gastrodermal muscles that are so important in polyps are reduced or lacking. The epidermal musculature is best developed around the bell margin and over the subumbrellar

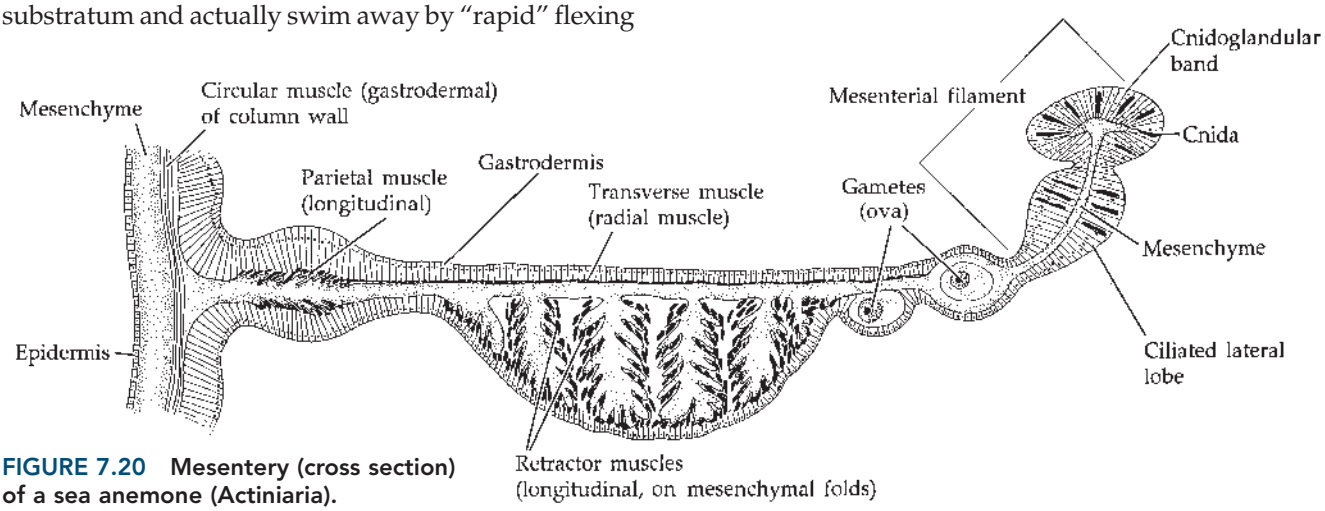

FIGURE 7.20 **Mesentery (cross section) of a sea anemone (Actiniaria).**

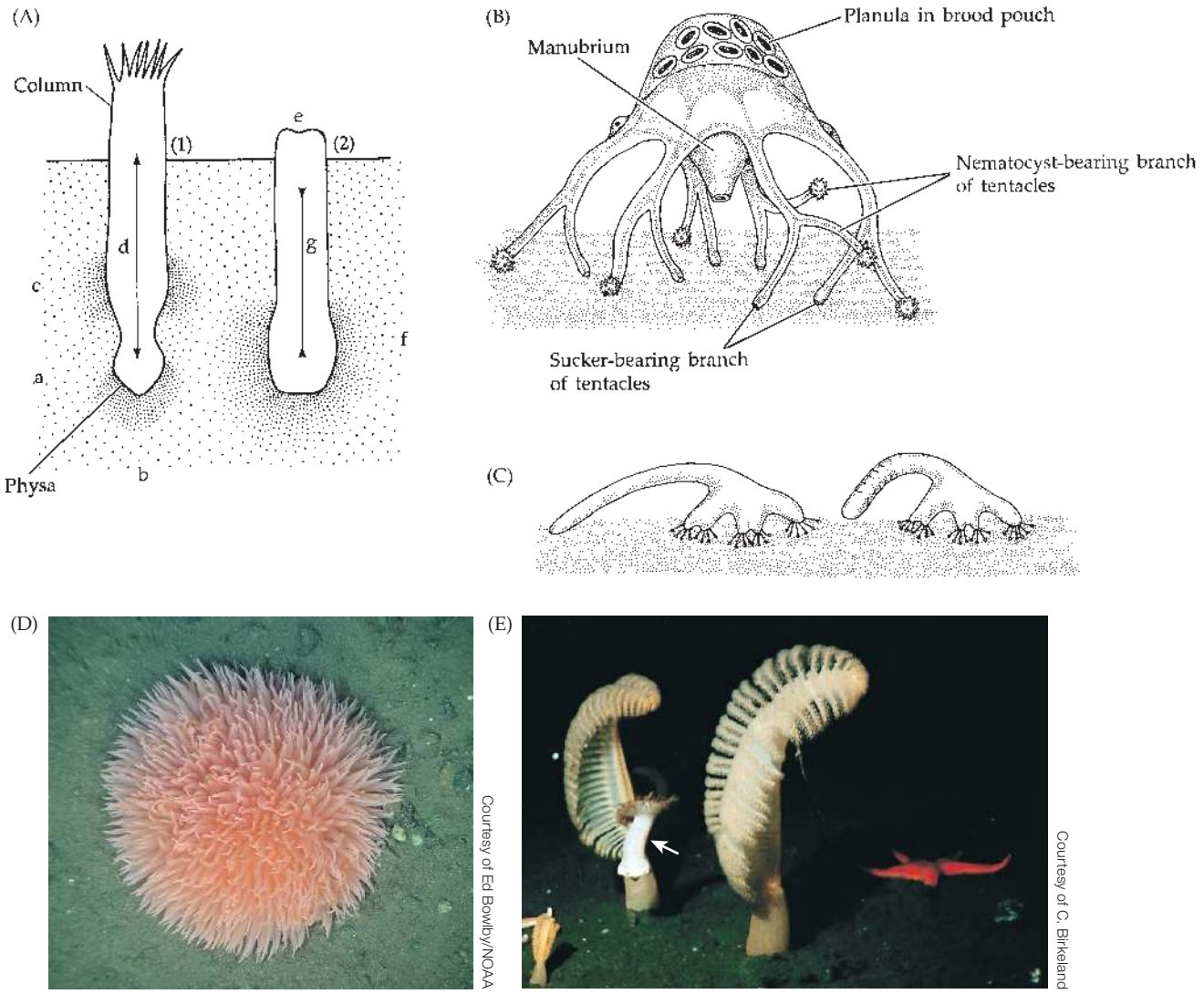

FIGURE 7.21 Benthic locomotion in some cnidarians. (A) A sea anemone burrowing: (1) eversion of the physa with displacement of sand (a) and further penetration (b) into substratum; the anemone is held by a column anchor (c) as extension (d) follows retraction in (2); with the tentacles folded inward (e), the physa is swollen to form an anchor (f), which allows retractor muscles (g) to pull the anemone into the sand. (B) The hydromedusan *Eleutheria*, which creeps about on its tentacles. (C) The staurozoan *Lucernaria*, which also creeps about on its tentacles. (D) *Liponema brevicorne*, a sea anemone that folds itself into a "ball" and rolls about on the seafloor with the bottom currents. (E) The sea anemone *Stomphia* (white arrow) swimming off the substratum by undulatory back-and-forth contractions of the column—an escape response to the predatory sea star *Gephyreaster swifti*, visible in this photo (Puget Sound, Washington).

surface. Here the muscle fibers usually form circular sheets called **coronal muscles** that are partly embedded in the mesenchyme or mesoglea. Contractions of the coronal muscles produce rhythmic pulsations of the bell, driving water out from beneath the subumbrella and moving the animal by jet propulsion. The restriction of striated myofibrils to epithelial cells appears to constrain the force with which bell musculature may contract, favoring either small solitary or prolate (streamlined) bells that move by jet propulsion (e.g., Anthoathecata, Trachymedusae, Siphonophora, Cubozoa) or larger, oblate (flattened) bells that move by more gentle contractions of the bell margin, sometimes called "rowing" (e.g., Leptothecata, Narcomedusae, scyphozoan medusae). In addition to this "pushing water" movement by medusae, there is evidence that bell contractions also generate low-pressure areas on the exumbrellar surface that help "pull" the animal forward through the water.

The stiffened cellular collenchyme of scyphomedusae and cubomedusae includes elastic fibers that provide the antagonistic force to restore the bell shape between contractions. Many medusae also possess radial muscles that aid in opening the bell between pulses. In craspedote forms, the velum serves to reduce the size of the subumbrellar aperture, thus increasing the force of the water jet (Figure 7.13). The velarium of the fast-swimming cubomedusae has

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the same effect (Figure 7.15A), and the evolutionary forces that produced these two convergent features were probably similar.

Most medusae spend their time swimming upward in the water column, then sinking slowly down to capture prey by chance encounter, thereafter to pulsate upward once again. Some medusae have the ability to change direction as they swim, however, and many are strongly attracted to light (especially those species that harbor symbiotic zooxanthellae). The medusoid form also appears to correlate with feeding mode. Jet propulsion is associated with ambush foraging by medusae that lie motionless, waiting for motile prey to swim into their tentacles before rapidly consuming the ensnared prey, whereas "rowing" propulsion is associated with cruising foraging by medusae that swim continuously with tentacles extended to capture slow-moving or floating prey. At least some medusae house their zooxanthellae in small pockets that remain contracted at night but expand during the day, exposing the algae to light.

Medusae can be abundant in certain localities. Some, such as the moon jelly *Aurelia* (Figure 7.22), are known to aggregate at temperature or salinity discontinuity layers in the sea, where they feed on small zooplankters, which also concentrate at these boundaries. Large flotillas of scyphomedusae are sometimes seen at sea (e.g., *Phacellophora* in the eastern Pacific). A few unusual groups of medusae are benthic. Some hydromedusae (e.g., *Eleutheria*, *Gonionemus*) crawl about on algae or sea grasses by adhesive discs on their tentacles (Figure 7.21B). Members of the class Staurozoa (e.g., *Haliclystus*) develop directly from the stauropolyp stage and affix to algae and other substrata by an aboral adhesive disc (Figure 7.1F). Aggregations are common in scypho- and cubomedusae, possibly to enhance feeding or defense. Almost all cubomedusae are tropical to subtropical in their range, but a large temperate species (*Carybdea branchi*) occurs on the Skeleton Coast of southwestern Africa, where it can occur in dense "clouds" of an acre or more across.

Cnidae

Before considering feeding and other aspects of cnidarian biology, it is necessary to present some information on the structure and function of cnidae. **Cnidae** (sing. cnida), often casually referred to collectively as "nematocysts" in older works, are unique to the phylum Cnidaria. They have a variety of functions, including prey capture, defense, locomotion, and attachment. They are produced inside cells called **cnidoblasts**, which develop from interstitial cells (also called I-cells), a type of proliferative cell in the epidermis and, in many groups, also in the gastrodermis. Once the cnida is fully formed, the cell is properly called a **cnidocyte**. During formation of a cnida, the cnidoblast produces a large internal vacuole in which a complex but poorly understood intracellular reorganization takes place. Cnidae may be complex secretory products of the Golgi apparatus of the cnidoblast.

Cnidae are among the largest and most complex intracellular structures known. When fully formed, they are cigar- or flask-shaped capsules, 5–100 μm or more long, with thin walls composed of a collagen-like protein. One end of the capsule is turned inward as a long, hollow, coiled, eversible tubule (Figure 7.23). The outer capsule wall consists of globular proteins of uncertain function. The inner wall is composed of bundles of collagen-like fibrils having a spacing of 50–100 nm, with cross striations every 32 nm (in the nematocysts of *Hydra*). The distinct pattern of minicollagen fibers provides the tensile strength necessary to withstand the high pressure in the capsule. The entire structure is anchored to adjacent epithelial cells (supporting cells) or to the underlying mesenchyme.

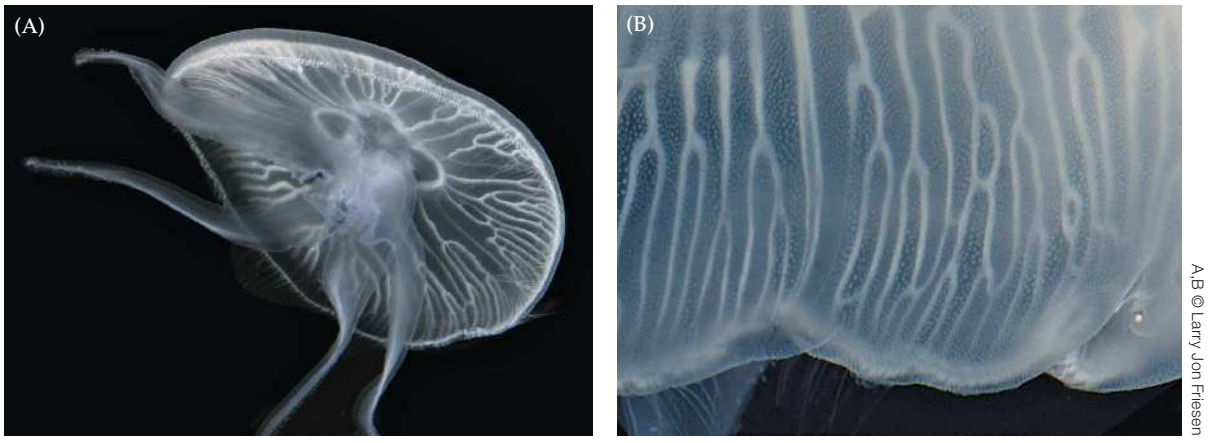

FIGURE 7.22 The semaeostoman medusa *Aurelia* (moon jellies) often form large swarms. (A) *Aurelia aurita*; notice elongated oral arms. (B) *Aurelia* radial canals and rhopalium.

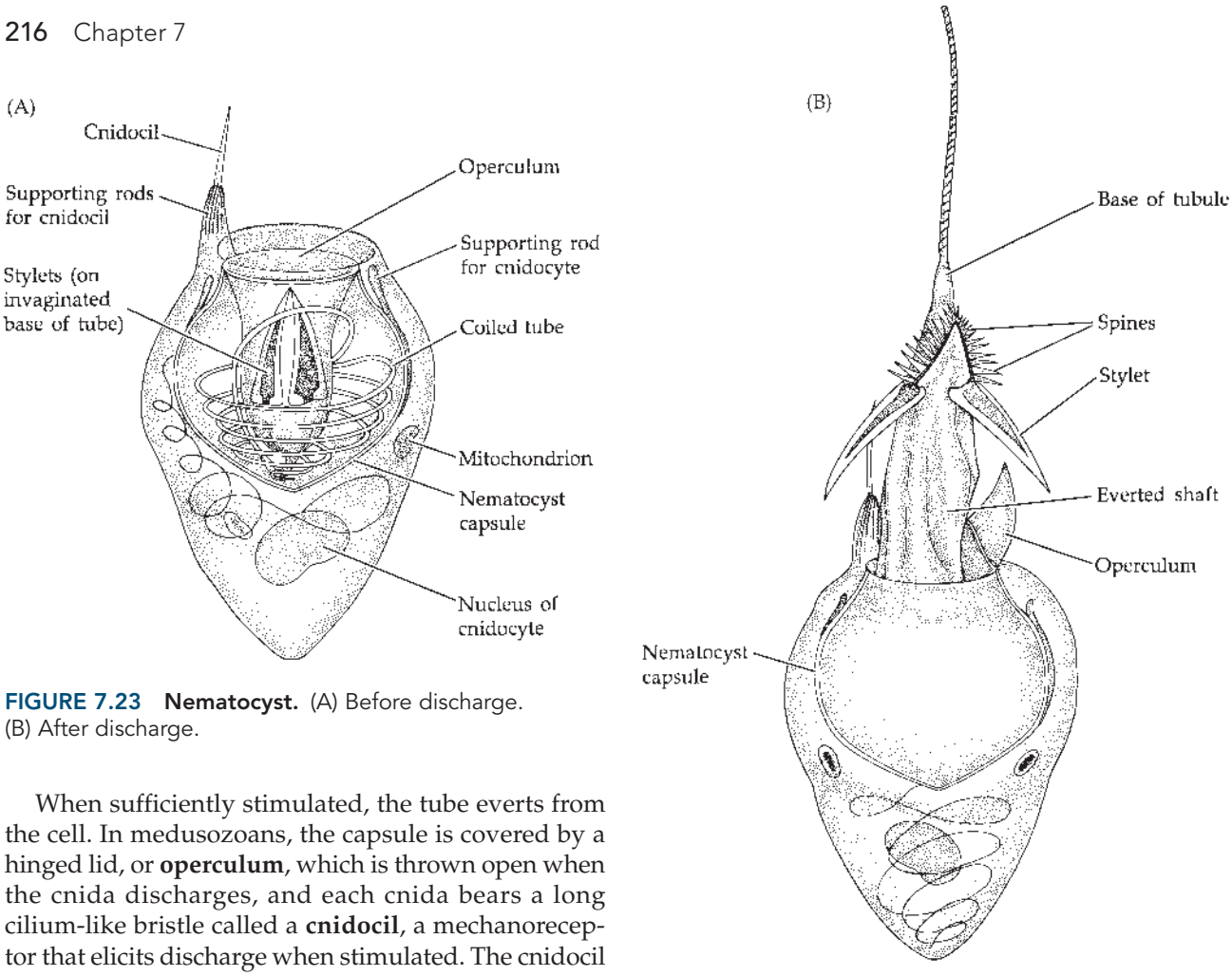

FIGURE 7.23 Nematocyst. (A) Before discharge. (B) After discharge.

When sufficiently stimulated, the tube everts from the cell. In medusozoans, the capsule is covered by a hinged lid, or **operculum**, which is thrown open when the cnida discharges, and each cnida bears a long cilium-like bristle called a **cnidocil**, a mechanoreceptor that elicits discharge when stimulated. The cnidocil responds to specific waterborne vibration frequencies. Anthozoan cnidae lack a cnidocil and have a tripartite apical flap instead of an operculum (anthozoan cnidae are only spirocysts and ptychocysts). Cnidocytes are most abundant in the epidermis of the oral region and the tentacles, where they often occur in clusters of wartlike structures called **nematocyst batteries**.

About 30 kinds of cnidae have been described, and 2–6 types usually occur in any given species (Figures 7.24 and 7.25). Combinations of cnida types, called **cnidomes**, occur in recognizable taxonomic patterns within Cnidaria, and these have had limited resolution in the phylogenetic patterns in the phylum. However, cnidae more or less sort out as three basic types. True **nematocysts** have double-walled capsules containing a toxic mixture of phenols and proteins. The tubule of most types is armed with spines or barbs that aid in penetration of and anchorage in the victim's flesh. The toxin is injected into the victim through a terminal pore in the thread or is carried into the wound on the tubule surface. **Spirocysts** have single-walled capsules containing mucoprotein or glycoprotein. Their adhesive tubules wrap around and stick to the victim rather than penetrating it. The capsule tubules of spirocysts never have an apical pore. Nematocysts occur in members of all cnidarian classes except within the Myxozoa; spirocysts occur only in the Hexacorallia. The third kind of cnidae, the **ptychocyst**, differs morphologically and functionally from both nematocysts and spirocysts. The capsule tubule of a ptychocyst lacks spines and an apical pore and is strictly adhesive in nature. In addition, the tubule is folded into pleats rather than coiled within the capsule. Ptychocysts occur only in the cerianthariens and function in forming the unique tube in which these animals reside.

The **polar capsules** of myxozoans are now widely viewed as homologous with other cnidarian cnidae, although they are simpler in form. Polar capsules are found in both myxosporean and actinosporean life stages of myxozoans. The capsules consist of a thick capsular wall; an eversible hollow filament that is spiraled along its length, may vary in length (up to ten times the length of the capsule), and is contiguous with the capsule; and a stopperlike structure that covers the inverted filament at its base. A variety of substances have been explored as possible inducers of polar filament extrusion, and like cnidae, polar capsules appear to be sensitive to pressure and extreme pH and K^+ concentrations. However, no consistent physical or chemical cue responsible for extrusion appears to exist across most taxa.

Cnidae have usually been viewed as independent effectors, and, indeed, they often discharge upon direct stimulation. However, experimental evidence suggests that the animals do have at least

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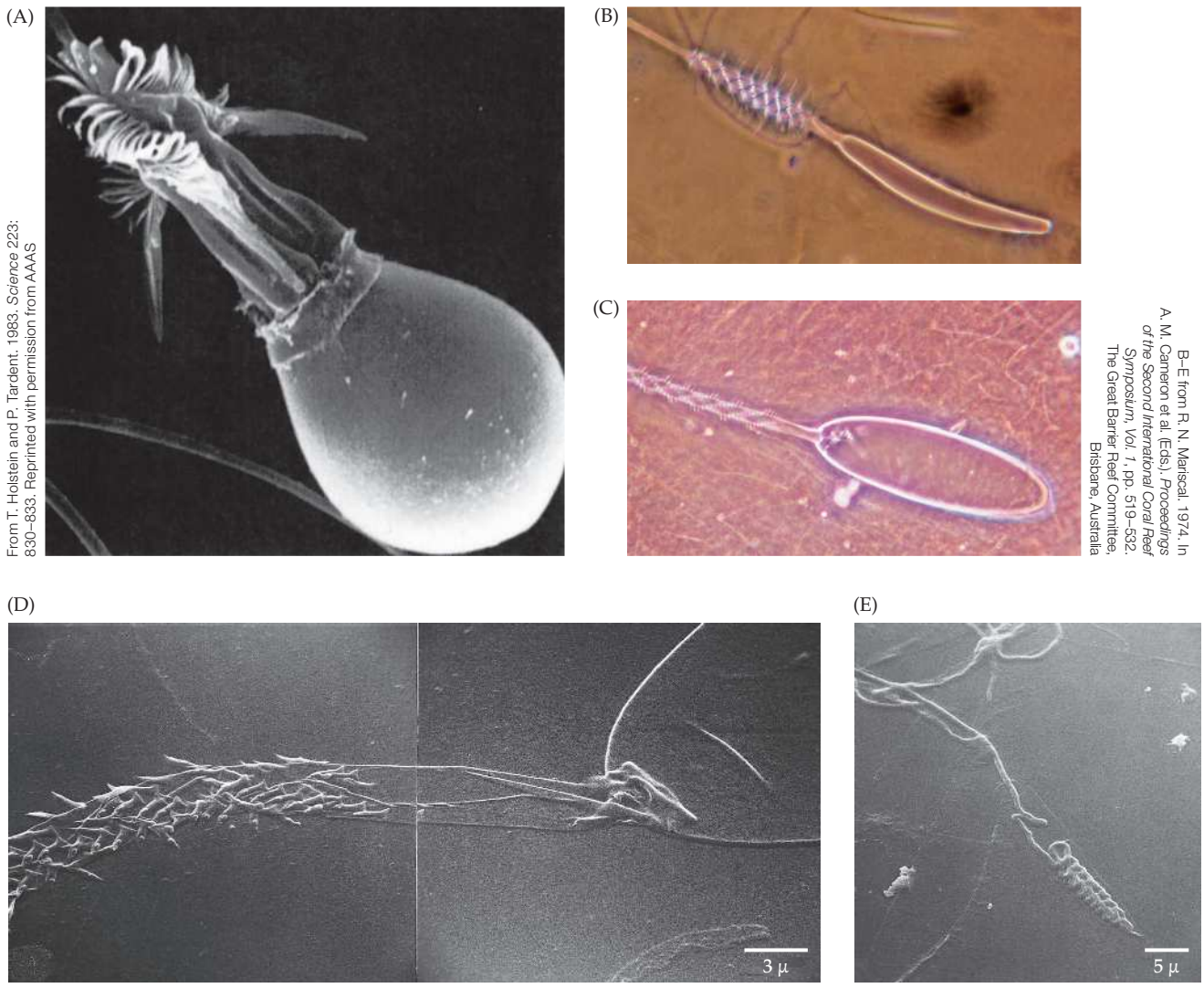

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B–E from R. N. Mariscal. 1974. In A. M. Cameron et al. (Eds.), *Proceedings of the Second International Coral Reef Symposium, Vol. 1*, pp. 519–532. The Great Barrier Reef Committee, Brisbane, Australia

FIGURE 7.24 Discharged nematocysts. (A) The base of a discharged nematocyst from the hydrozoan *Hydra* (SEM). (B) A nematocyst of the anthozoan *Corynactis californica* (Corallimorpharia). The nematocyst has been "stopped" when partially everted (light micrograph). (C) A fully everted nematocyst of *C. californica* (light micrograph). (D) A fully everted nematocyst of *C. californica* (SEM of the base of the everted thread and the tip of the capsule). (E) Everting nematocyst of the anthozoan coral *Balanophyllia elegans*.

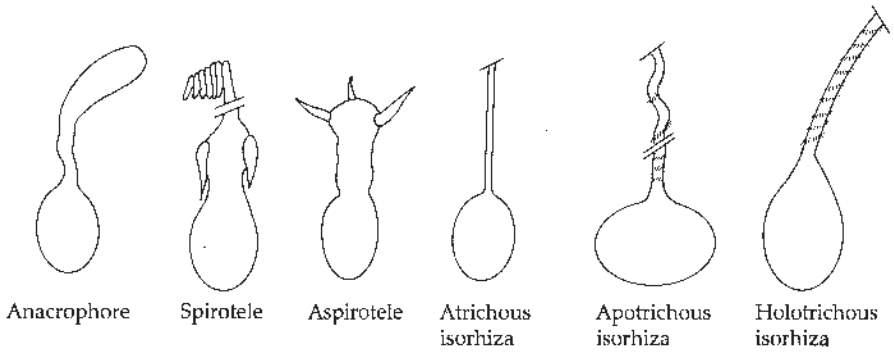

FIGURE 7.25 Some types of cnidae and their specialized nomenclature.

some control of the action of their cnidae. For example, starved anemones seem to have a lower firing threshold than satiated animals. It has also been demonstrated that stimulating discharge of cnidae in one area of the body results in discharge in surrounding areas. Still, chemical and/or mechanical stimuli, initially perceived by the cnidocil or a similar structure, cause most cnidae to fire. Cnidarians are known to discharge their cnidae in the presence of various sugars and low-molecular-weight amino compounds.

The rapid protrusion of the tubule from a cnida is called **exocytosis**, and an individual cnida can be fired only once. Three hypotheses have been proposed to explain the mechanism of firing: (1) the discharge is the result of increased hydrostatic pressure caused by a rapid influx of water (the osmotic hypothesis); (2) intrinsic tension forces generated during cnidogenesis are released at discharge (the tension hypothesis); and (3) contractile units enveloping the cnida cause the discharge by "squeezing" the capsule (the contractile hypothesis). Because of the small size of cnidae and the extreme speed of the exocytosis process, these hypotheses have been difficult to test. Recent work using ultra-high-speed microcinematography suggests that both the osmotic and tension models may be at work and that capsules have very high internal pressures. The coiled capsular tubule is forcibly everted and thrown out of the bursting cell to penetrate or wrap around a portion of the unwary victim. It takes only a few milliseconds for the cnida to fire, and the everting tubule may reach a velocity of 2 m/sec—an acceleration force of about 40,000 g—making it one of the fastest cellular processes in nature. The firing mechanism of hydrozoan cnidae is thwarted by certain nudibranch gastropods that, in order to feed upon and capture intact cnidae from their prey, release copious amounts of mucus to entangle and envelop hydroid tentacles containing still-intact cnidae.

Most nematocysts contain several different toxins that vary in activity and strength, but as a class of chemicals they are all potent, complex, biological poisons capable of subduing large, active prey, including fish. Most appear to be neurotoxins. The toxins of some cnidarians are powerful enough to affect humans (e.g., those of cubozoans; some jellyfish; certain colonial hydroids, such as *Macrorhynchia*; medusae of some *Gonionemus* species; many hydrocorals, such as *Millepora*; and many siphonophores, such as *Physalia*). The toxins of most scyphozoans are not strong enough to create problems for most people, unless they have an allergic reaction; even the effects of *Physalia* stings typically disappear within a few hours. However, toxins of most cubomedusans (box jellies) are another story altogether; they kill dozens of people annually (mostly in the west Pacific), and their venom is estimated to be as potent as cobra venom. In tropical Australia, twice as many people die annually from box jellies as from sharks. Stings by *Chironex* (the "sea wasp") usually result in severe pain at least, and they cause fatal respiratory or cardiac failure at worst. If you want to swim in an area known to be frequented by dangerous jellies, you can always do what lifeguards in northern Australia do—don a pair of pantyhose (not fishnet!), which seem to offer some protection.

Most cubozoan victims die from cardiac arrest within minutes. Surprisingly the exact nature of cnidarian nematocyst toxins is still debated. One hypothesis holds that the venom contains proteins called porins, which puncture red blood cells and release potassium, disrupting the electrical rhythm that keeps the heart beating. High levels of potassium in the blood, or hyperkalemia, is well known to cause cardiac arrest. Another hypothesis suggests certain compounds in the venom are ion channel blockers, molecules that disrupt movement of ions in and out of cells. The blockage shuts down nerve and muscles cells, including those that keep the heart pumping. One recently developed commercial antidote contains copper gluconate; when applied to the sting, it is said, it inhibits the injected venom.

Feeding and Digestion

All cnidarians are carnivores (or parasites), and the gastrodermis of the gut of the various species produces a spectrum of enzymes that hydrolyze carbohydrates, proteins, and lipids (Figure 7.4). Typically, nematocyst-laden feeding tentacles capture animal prey and carry it to the mouth region, where it is ingested whole (Figure 7.26). Digestion is initially extracellular in the coelenteron. In many groups, gastrodermal cilia (or flagella) aid in mixing of the gut contents. In the absence of a true circulatory system, the gastrovascular cavity distributes the partially digested material. The larger the cnidarian, the more extensively branched or partitioned is its coelenteron. The product of this preliminary breakdown is a soupy broth, from which polypeptides, fats, and carbohydrates are taken into the nutritive-muscular cells by phagocytosis and pinocytosis. Digestion is completed intracellularly within food vacuoles. Undigested wastes in the coelenteron are expelled through the mouth. In cubozoans, and at least some hydrozoans, ciliary movement of material in the coelenteron is enhanced by peristaltic movements.

In anthozoans, the free edges of most of the gastrovascular mesenteries are thickened to form three-lobed mesenterial filaments (Figures 7.6 and 7.20). The lateral lobes are ciliated and aid in circulating the digestive juices in the coelenteron. The middle lobe, called the **cnidoglandular band**, bears cnidae and gland cells. In some sea anemones (e.g., *Aiptasia*, *Anthothoe*, *Calliactis*, *Cylista*, *Diadumene*, *Metridium*), the cnidoglandular band continues beyond the base of the pharynx as a free thread called an acontium, which floats about in the coelenteron. The cnida-bearing acontia not only

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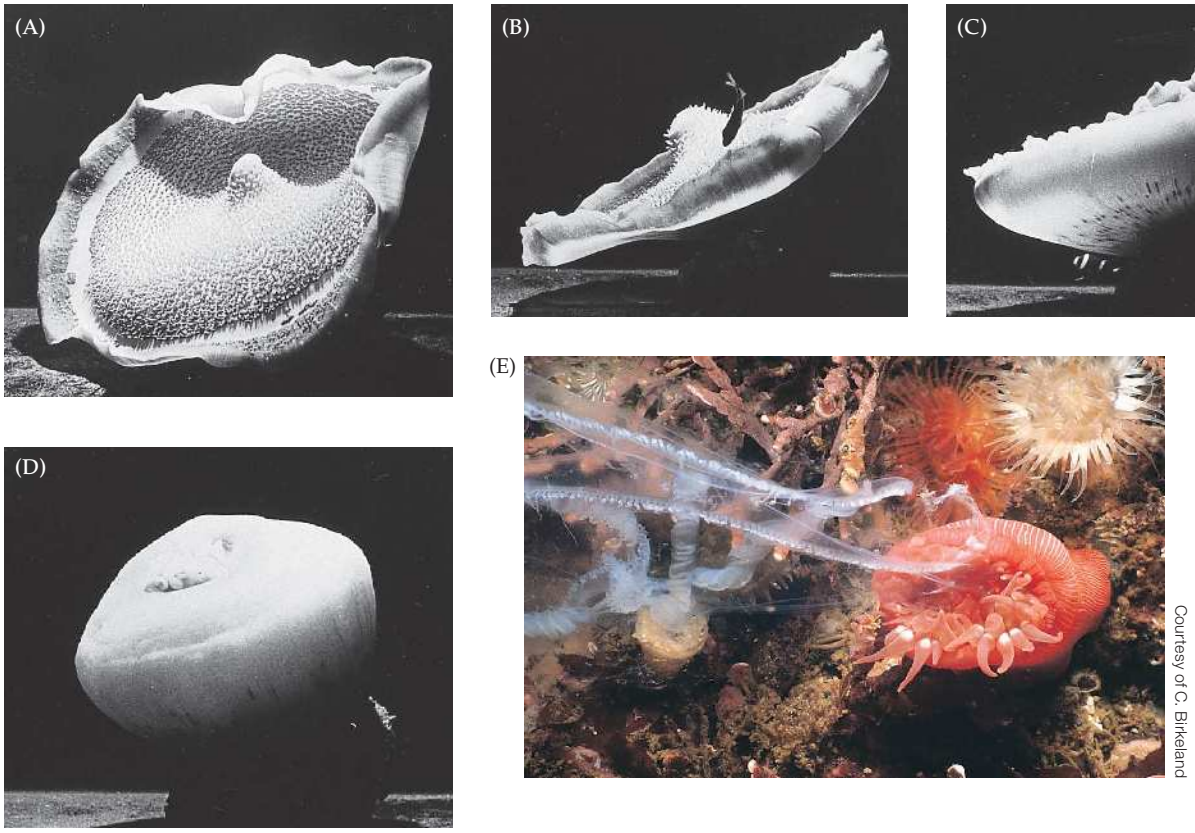

FIGURE 7.26 Feeding anemones. (A–D) Feeding sequence in the tropical sea anemone *Amplexidiscus fenestrafer*. (A) An expanded oral disc has a tentacle-free area near the periphery, and an oral cone. (B) An expanded disc (side view). (C) Closure one-third complete, 1 second after stimulation of the oral disc. (D) Complete closure, 3 seconds after stimulation. (E) The temperate sea anemone *Epiactis prolifera* capturing a jellyfish (*Aequorea*?).

subdue live prey within the coelenteron, but may be shot out through the mouth or through pores in the body wall (called **cinclides**) when the animal contracts violently; when this occurs, the acontia presumably play a defensive role.

Prey type appears to influence medusoid form. Most oblate medusae feed on small ciliated or soft-bodied prey, following their quarry by continuous rowing (using their large flat bell), and then using nematocysts on the tentacles, the oral arms, or both to capture their victims. *Pelagia noctiluca*, an open-sea diurnal migrator, follows the other migrating macrozooplankton upon which it feeds, uses its marginal tentacles to paralyze and capture moving prey, then transports them to the oral arms dangling from the center of the subumbrella. The oral arms transport the prey to the mouth. Motionless prey are also captured by the oral arms directly through chance contact. Most prolate medusae feed on actively swimming prey. These species often retract their tentacles while swimming, to reduce drag. Cubomedusae such as *Chironex* spp. feed actively on fish and can swim in bursts of up to 5 feet/sec. Because of their higher metabolic demands, unlike other Medusozoa, they move semidigested food from their central gastrovascular cavity to canals lining the interior walls of each tentacle for absorption. Some cubomedusae catch and ingest fish and prawns matching their own diameter, and a large *Chironex* can eat fish 20–50 cm in length! Some cubomedusae are less active hunter-predators and feed primarily by passive hunting (e.g., *Tripedalia cystophora*, and perhaps also *Chironex fleckeri* and *Carybdea rastonii*), and in these cases their eyes may be used to position themselves in the right food-rich habitat.

Several groups of cnidarians have adopted feeding methods other than the direct use of nematocyst-laden tentacles. One group of large tropical anemones in the order Corallimorpharia (e.g., *Amplexidiscus*) lacks nematocysts on the external surfaces of most tentacles. These remarkable anemones capture prey directly with the oral disc, which can envelop crustaceans and small fishes, rather like a fisherman's cast net (Figure 7.26A–D).

In addition to tentacular feeding on small plankters, many corals are capable of mucous-net suspension feeding, which is accomplished by spreading thin mucous strands or sheets over the colony surface and collecting organic particulate matter that rains down from the water. The food-laden mucus is driven by cilia to the mouth. In a few corals (e.g., members of the family Agariciidae), the tentacles are greatly reduced

or absent, and all direct feeding is by the mucous-net suspension method. The amount of mucus produced by corals is so great that it is an important food source for certain fishes and other reef organisms, which feed directly off the coral or recover mucus sloughed into the surrounding seawater. Coral mucus released into the sea contains a variable mixture of macromolecular components (glycoproteins, lipids, and mucopolysaccharides) or a mucous lipoglycoprotein of specific character for a given species. These loose mucous webs, or flocs, are usually enriched by bacterial colonies and entrapped detrital materials, further enhancing their nutritional value.

The role of cnidarians as potentially significant members of food webs depends largely on location and circumstance. It has been estimated that as much as 25% of marine biodiversity is associated with coral reefs. Stony corals obviously hold critical trophic positions in tropical reef environments, as do zoantharians and octocorals in many tropical and subtropical habitats. In many warm and temperate areas sea pens and sea pansies dominate benthic sandy habitats. Large scyphomedusae (e.g., *Aurelia*, *Cyanea, Pelagia*, *Phacellophora*) often occur in great swarms and may consume high numbers of larvae of commercially important fishes, as well as competing with other fishes for food. Swarms of jellyfish may be so dense that they clog and damage fishing nets and power plant intake systems. The first author once witnessed a swarm of *Phacellophora* in the Gulf of California that ran like a broad river from Loreto to La Paz, a distance of about 200 km. Certain scyphozoans (e.g., *Chrysaora*) have undergone population blooms in their native habitats, perhaps due to climate shifts, while other species (e.g., *Phyllorhiza*) have become invasive after transport by ships or in shifting currents. In large numbers jellies significantly influence local fish and plankton populations.

Hydromedusae are often major components of temperate pelagic food webs. Members of several hydrozoan genera also occur in huge congregations in tropical seas, where they are important carnivores in the neustonic food web. Best known among these are the "chondrophorans" *Porpita* (which actively feeds on motile crustaceans, such as copepods) and *Velella* (which feeds on relatively passive prey, such as fish eggs and crustacean larvae), and the siphonophore *Physalia* (which actively catches and consumes fish). Other siphonophores inhabiting deep-sea environments (e.g., *Erenna* sp.) possess bioluminescent and red-fluorescent lures that may be important for capturing fish sensitive to long-wavelength light. Like scyphomedusae, hydromedusae and siphonophores can reach high densities in surface waters and have significant effects on zooplankton and human populations. The Chinese freshwater limnomedusa *Craspedacusta sowerbii* is now established throughout the United States and Europe, where it can undergo "blooms" and impact fisheries. The Portuguese man-of-war, *Physalia* sp., is a known menace for swimmers during summer months in coastal areas throughout the world.

Defense, Interactions, and Symbiosis

There are so many interesting aspects of cnidarian biology that do not fall neatly into our usual coverage of each group that we present this special section. The following discussion also points out the surprising level of sophistication possible at the relatively simple diploblastic, radiate grade of complexity.

In most cnidarians, defense and feeding are intimately related. The tentacles of most anemones and jellyfish usually serve both purposes, and the defense polyps (dactylozooids) of hydroid colonies often aid in feeding. In some cases, however, the two functions are performed by distinctly separate structures (as in most siphonophores).

Some species of acontiate sea anemones (e.g., *Metridium*) bear separate and distinct feeding tentacles and defense tentacles. Whereas the former usually move in concert to capture and handle prey, the defense tentacles move singly, in a so-called searching behavior, in which they extend to three or four times their resting length, gently touch the substratum, retract, and extend again. Defense tentacles are used in aggressive interactions with other sea anemones, either those of a different species or nonclonemates of the same species. The aggressive behavior consists of an initial contact with the opponent followed by autonomous separation of the defense tentacle tip, leaving the tip behind attached to the other sea anemone. Severe necrosis develops at the site of the attached tentacle tip, occasionally leading to death. Defense tentacles develop from feeding tentacles and tend to increase under crowded conditions. The development involves loss of typical feeding tentacle cnidae (largely spirocysts) and acquisition of true nematocysts and gland cells, which dominate in defense tentacles. Similarly, elongated "sweeper tentacles" in many species of corals are used for defense and competition for space, by direct contact or release of toxic exudates.

The **acrorhagi** (= marginal tubercles or bumps) that ring the collar of some sea anemones (e.g., *Anthopleura*) also have a defensive function. These normally inconspicuous vesicles at the base of the tentacles bear nematocysts and usually spirocysts. In *A. elegantissima*, contact of an acrorhagi-bearing sea anemone with nonclonemates or other species causes the acrorhagi in the area of contact to swell and elongate. The expanded acrorhagi are placed on the victim and withdrawn, and the application may be repeated. Pieces of acrorhagial epidermis break off and remain on the victim, resulting in localized necrosis. Interclonal strips of bare rock are maintained by this aggressive behavior (Figure 7.27A). In addition to this behavior, the acrorhagi are exposed as a ring of nematocyst batteries around the top of the constricted column

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FIGURE 7.27 Hexacorallian defense behavior
(A) Defensive acrorhagi (white-tipped tentacles) on two sea anemones (*Anthopleura elegantissima*), engaging in territorial chemical combat. (B) Close-up showing acrorhagi of *Anthopleura* sp. (C) Competition between true corals (Scleractinia) in the Virgin Islands. The coral *Isophyllia sinuosa* is seen extruding its mesenterial filaments and externally digesting the edge of a colony of *Porites astreoides*.

whenever an acrorhagi-bearing sea anemone contracts in response to violent stimulation. Other competitive interactions are known among stony corals (Figure 7.27C).

Octocorals, which lack toxic stinging nematocysts, have been shown to be a rich source of biologically active and structurally unusual compounds that appear to provide protection against predators and may allow them to colonize new habitats by causing tissue necrosis in potential competitors. These compounds include prostaglandins, diterpenoids, and antimicrobials. In contrast to many coastal and reef-dwelling species, octocorals are remarkably free from predation except by the few species that are specialized to use them as food. While sclerites have also been proposed to provide antipredatory benefits, there is little clear evidence that sclerites decrease the nutritional value of octocorals sufficiently to deter predation. Thus, like sponges, octocorals appear to use secondary metabolic compounds as their primary antipredator defense. Chemical defenses may have evolved to compensate for poor regenerative abilities in these slow-growing cnidarians or because their sessile habit makes them especially conspicuous to visual predators.

There are many examples of associations between cnidarians and other organisms, some of which are truly symbiotic, others of which are less intimate. With the exception of myxozoans, few groups of cnidarians are truly parasitic, although several species of hydroids infest marine fishes. The polyps of some of these hydroids lack feeding tentacles and occasionally even lack cnidae. The basal portion of the polyp erodes the fish's epidermis and underlying tissues, and nutrients are absorbed directly from the host. One species invades the ovaries of Russian sturgeons (a caviar feeder!).

However, the Myxozoa, by any standard, are indeed parasitic. This group consists of about 2,200 species of tiny parasites, previously classified among the protists as the phylum Myxozoa. Morphological data, DNA sequence data, and the presence of metazoan Hox genes all provide evidence that these strange creatures are allied with the cnidarians, as a sister group to the Medusozoa (Figure 7.44). The coiled polar filaments housed within polar capsules of myxozoans are now viewed as modified cnidae (Figure 7.28).

Myxozoan cnidarians infect annelids and various poikilothermic vertebrates, especially fishes (Figure 7.29). The life cycle begins when **actinospore** larvae (which may vary in form) are released from spores, contact the mucous membranes of an appropriate vertebrate host (either by ingestion or contact; Figure 7.29, part 1), and extrude their **polar filaments** to release sporoplasm into the host cells. Presporogonic development occurs within these cells, producing infective cell-doublets, which rupture host cells and disperse to infect other cells (Figure 7.29, part 2). Infection can spread to other tissues, particularly neural tissue, and can cause disruption of host tissue structure (e.g., a blackened tail in infected trout) or behavior.

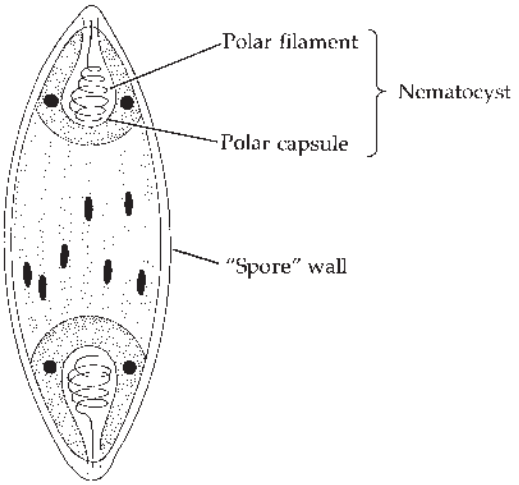

FIGURE 7.28 Previously considered to be protists, myxozoans are now viewed as highly specialized, parasitic cnidarians.

Sporulation often occurs in particular tissues (e.g., cartilage in *Myxobolus cerebralis*), where a multinucleated **plasmodium** develops and produces sporoblasts with variable numbers of internal spores, depending on the species (Figure 7.29, part 3).

Within plasmodia, valvogenic cells produce **spore valves**, which enclose capsulogenic cells that become polar capsules as well as sporoplasm. When complete, this process generates **myxospores** that are released by the vertebrate host and are infective to annelids (Figure 7.29, part 4). Polar filaments facilitate cell penetration of gut cells where multinucleate cells form by a process often called **schizogony** (although this is probably not the same process seen in sporozoan protists; Figure 7.29, parts 5 and 6). These cells then produce numerous uninucleate cells that may either generate other plasmodia or fuse with other cells to become binucleate within the worm gut. Binucleate cells differentiate into multinucleate cells with α or β nuclei that develop into complementary gametes by the end of gametogony, which fuse to produce **pansporocysts** containing zygotes (Figure 7.29, parts 7–9). Zygotes differentiate into infective actinosporean spores that are released in worm feces or remain within the worm's body. Infection of the vertebrate host occurs when spores containing worm feces contact mucous membranes or when spore-bearing worms are ingested (Figure 7.29, part 10).

Most myxozoan species appear to include both a vertebrate and an invertebrate host in their life cycle. *Myxobolus cerebralis*, a parasite of freshwater fishes (especially trout, Figure 7.1O), devours the host's cartilage, leaving the fish deformed. Inflammation resulting from the infection puts pressure on nerves and disrupts balance, causing the fish to swim in circles—a condition known as whirling disease. When an infected fish dies, *M. cerebralis* spores are released from the decaying carcass and may survive for up to 30 years in sediment. Eventually, the spores are consumed by *Tubifex* worms (oligochaete annelids). They reside in this intermediate host until eaten by a new host fish.

Mutualism is common among cnidarians. Many species of hydroids live on the shells of various molluscs, hermit crabs, and other crustaceans. The hydroid gets a free ride, and the host perhaps gains some protection and camouflage. Many members of the leptomedusan family Eirenidae (e.g., *Eugymnanthea*) occupy the mantle cavities of bivalves, where they protect their hosts against trematode parasites by consuming the infective sporocysts. Hydroids of the genus *Zanclea* are epifaunal on bryozoans, where they sting and discourage smaller predators and adjacent competitors, helping the bryozoans to survive and overgrow competing species. The bryozoan lends protection to the hydroid with its coarse skeleton, and the mutualism seems to allow both taxa to cover a larger area than either could individually. The bizarre, aberrant hydroid *Proboscidactyla* lives on the rim of polychaete worm tubes (Figure 7.8A) and dines on food particles dislodged by the host's activities. Another filiferan, *Brinckmannia hexactinellidophila*, lives within the tissues of Arctic glass sponges.

Some sea anemones attach to snail shells inhabited by hermit crabs. These partnerships are mutualistic; the sea anemone gains motility and food scraps while protecting the hermit crab from predators. The most extreme case of this mutualism might be that of the cloak anemones (e.g., *Adamsia*, *Stylobates*), which wrap themselves around a hermit crab's gastropod shell and grow as the crab does (Figure 7.30). Initially, the anemone's pedal disc secretes a chitinous cuticle over the small gastropod shell occupied by the hermit. Such fortunate crabs need not seek new, larger shells as they grow, for the cloak anemone simply grows and provides the hermit with a living protective cnidarian "shell," often dissolving the original gastropod shell over time. As if it were itself a gastropod, the sea anemone grows to produce a flexible coiled house called a **carcinoecium**. In fact, these odd anemone "shells" were initially described and classified as flexible gastropod shells. A similar relationship exists between some hermit crabs of the genus *Parapagurus* and certain species of *Epizoanthus*. The hydroid *Janaria mirabilis* secretes a "long-spined" shell-like casing that is inhabited by hermit crabs, and in an extraordinary case of evolutionary convergence, so does the bryozoan *Hippoporidra calcarea* (Figure 7.31).

So effective are cnidae that many groups of animals have figured out ways to capture or otherwise utilize these structures for their own defense, a phenomenon known as kleptocnidism. Kleptocnidism is best known among nudibranchs, but it has evolved between 10 and 18 times in members of the phyla Ctenophora, Porifera, Platyhelminthes, and Mollusca, as well as in the Acoelomorpha. Several aeolid sea slugs consume cnidarian prey, ingesting and then storing the unfired nematocysts in fingerlike processes on their dorsal surfaces, where they use them for their own defense. The ctenophore *Haeckelia rubra* feeds on certain hydromedusae

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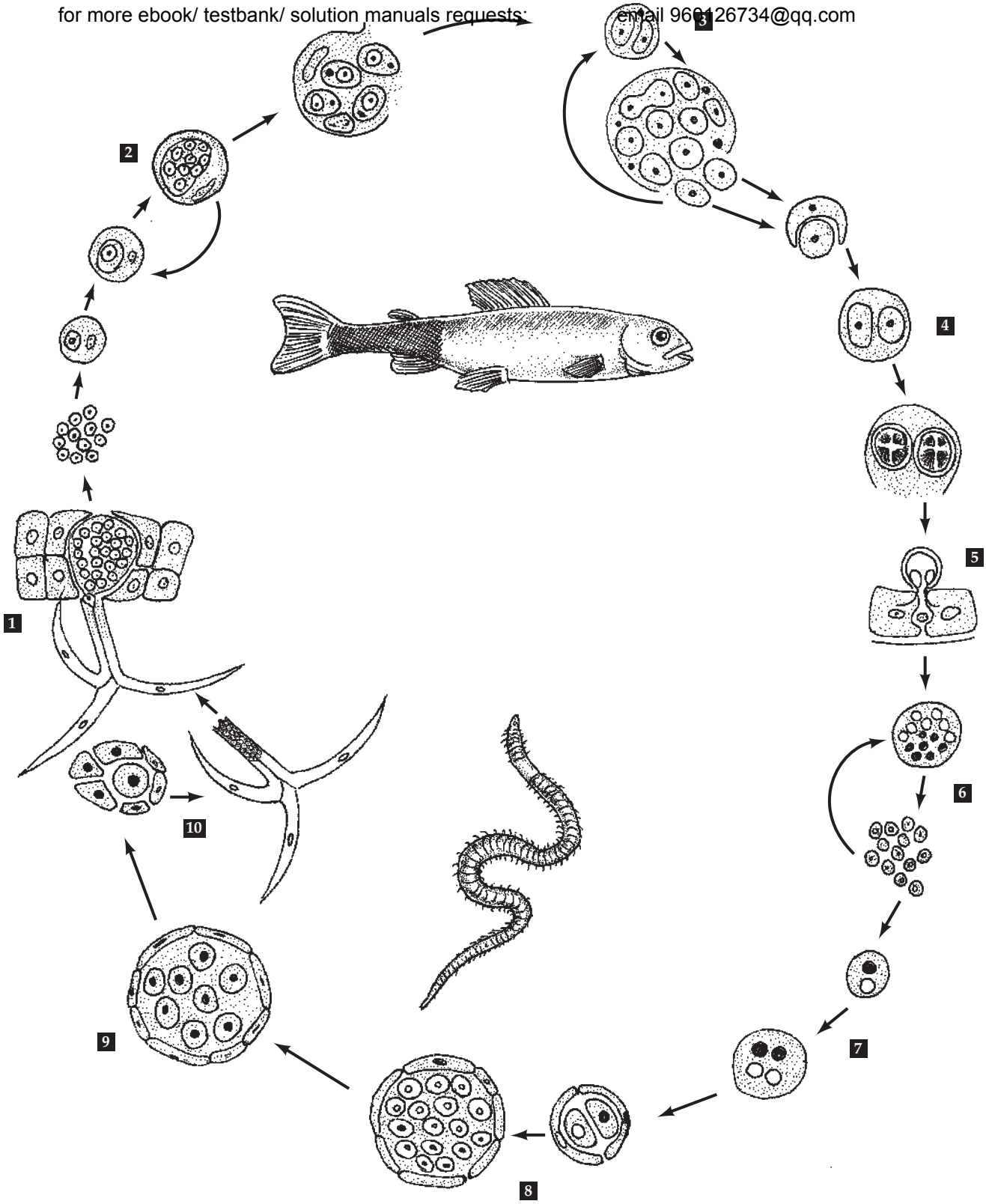
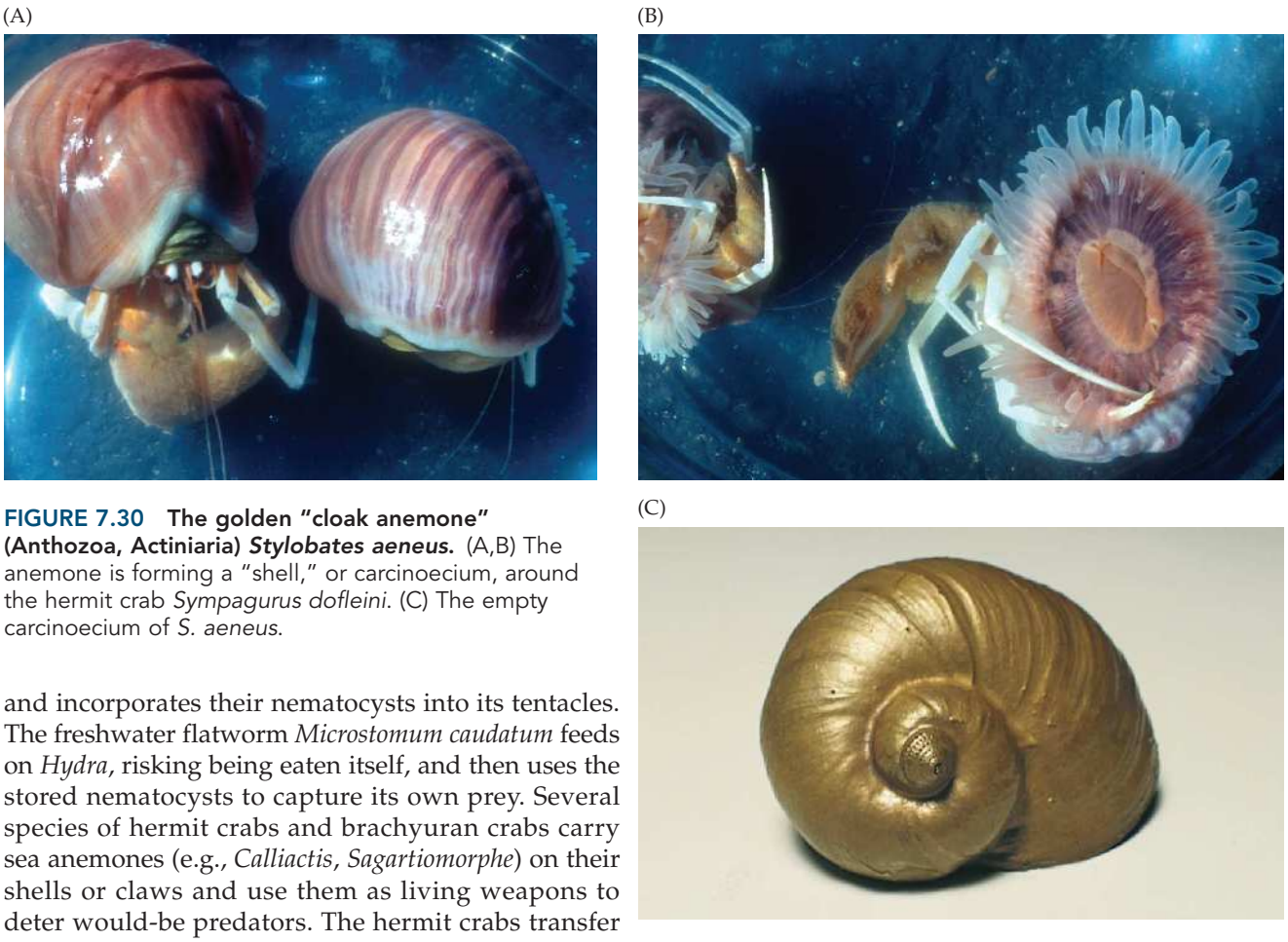


FIGURE 7.29 The life cycle of *Myxobolus cerebralis*. (1) Actinospore stage attaches to fish mucous membranes, extrudes polar filaments, and releases sporoplasm into host cells. (2) Presporogonic development occurs within host cells, producing infective cell-doublets, which rupture and infect other host cells; spreading infection disrupts host tissue, causing a blackened tail in trout. (3) Sporulation and multinucleated plasmodia develop in particular tissues (e.g., cartilage in *M. cerebralis*), further spreading infection. (4) Within plasmodia, sporoblasts form internal myxospores that are (5) released by the vertebrate host and ingested by annelids; polar filaments facilitate penetration of gut cells. (6) Multinucleate cells form, which infect other cells and generate plasmodia or (7) fuse with other cells to become binucleate cells, then differentiate into multinucleate cells with α or β nuclei and (8) become complementary gametes. (9) Gametes fuse to produce pansporocysts containing eight zygotes. (10) Zygotes differentiate into infective actinospores that are released in worm feces or remain within the worm's body; other fish are infected by contact with worm feces or by eating spore-bearing worms.

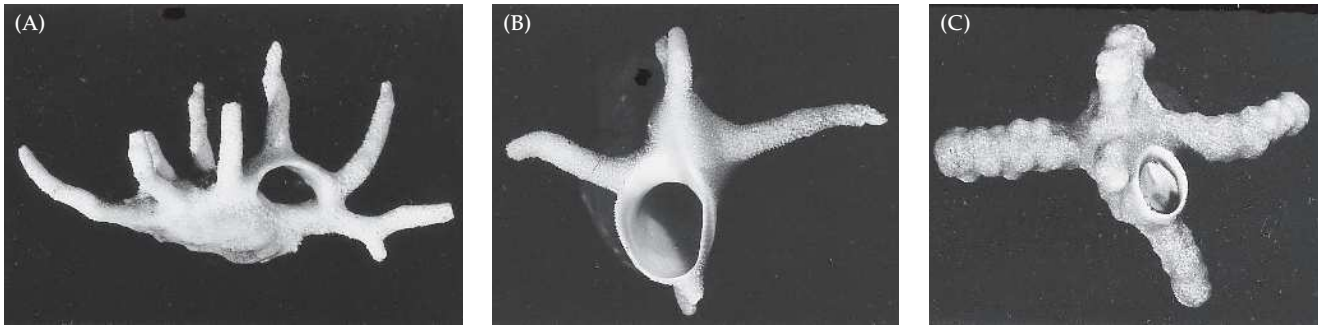


A–C courtesy of D. Fautin

FIGURE 7.30 The golden "cloak anemone" (Anthozoa, Actiniaria) *Stylobates aeneus*. (A,B) The anemone is forming a "shell," or carcinoecium, around the hermit crab *Sympagurus dofleini*. (C) The empty carcinoecium of *S. aeneus*.

and incorporates their nematocysts into its tentacles. The freshwater flatworm *Microstomum caudatum* feeds on *Hydra*, risking being eaten itself, and then uses the stored nematocysts to capture its own prey. Several species of hermit crabs and brachyuran crabs carry sea anemones (e.g., *Calliactis*, *Sagartiomorphe*) on their shells or claws and use them as living weapons to deter would-be predators. The hermit crabs transfer their anemone partners to new shells, or the anemones move on their own, when the hermits take new shells. Some hermit crabs of the genus *Pagurus* often have their shells covered by a mat of symbiotic colonial hydroids (e.g., *Hydractinia*, *Podocoryne*). The presence of the hydroid coat deters more-aggressive hermits (e.g., *Clibanarius*) from commandeering the pagurid's shell.

Several cases of fish-cnidarian symbiosis have been documented. The well-known association of anemone fishes (clown fishes) and their host sea anemones serves an obvious protective function for the fish. About a dozen species of sea anemones participate in this interesting relationship. The fish's ability to live among the sea anemone's tentacles is still not fully understood. However, the sea anemone does not voluntarily fail to spend its nematocysts on its fish partner; rather, the fish alters the chemical nature of its own mucous coating, perhaps by accumulating mucus from the sea anemone, thereby masking the normal chemical stimulus to which the anemone's cnidae would respond. *Nomeus gronovii* is a small fish that lives symbiotically among the tentacles of *Physalia* and appears to survive by simply avoiding direct contact with the



A–C from S. D. Cairns and J. L. Barnard. 1984. *Bull South Calif Acad Sci* 83: 1–11

FIGURE 7.31 A case of remarkable evolutionary convergence. (A,B) The hydrozoan colony *Janaria mirabilis* (Athecata) forms a shell-like corallum inhabited by hermit crabs. (C) The bryozoan *Hippoporidra calcarea*, which forms a similar structure, is also inhabited by hermit crabs.

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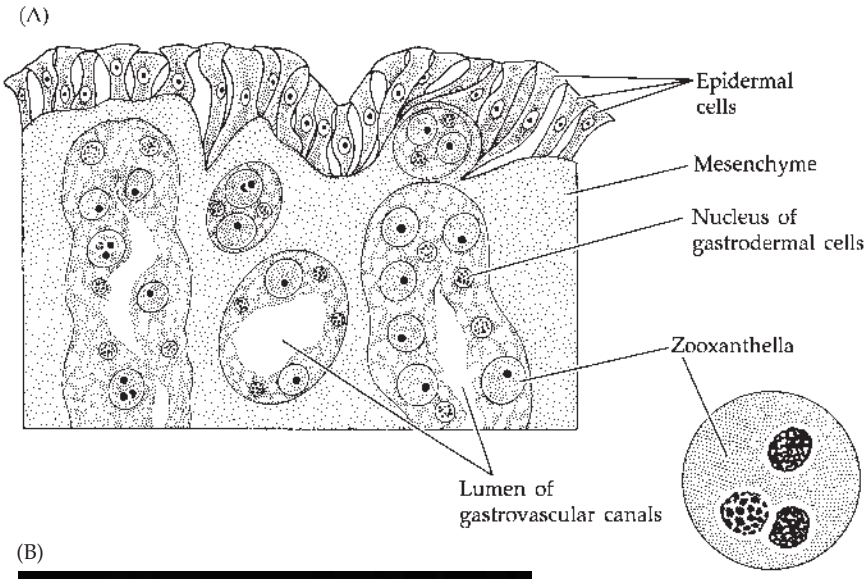

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FIGURE 7.32 Zooxanthellae in cnidarians (A) An octocoral with zooxanthellae distributed throughout the gastrodermis (schematic section). (B) *Mastigias* sp., a rhizostomean medusa, harbors zooxanthellae in its cells.

beast. When stung accidentally, however, it shows a much higher survival rate than do other fishes of the same size. *Nomeus* feeds on prey captured by its host.

A number of associations are known between cnidarians and crustaceans. Nearly all amphipods of the suborder Hyperiidea are symbionts on gelatinous zooplankters, including medusae, and many species of amphipods, crabs, shrimps, and copepods are symbionts with sea anemones (which provide food in the form of uneaten materials and mucus). The nature of many of these associations is unclear, but various species of the amphipods are known to use their hosts as a nursery for the young and perhaps for dispersal. Some actually live among and eat the nematocyst-bearing parts of the host, such as the tentacles or oral arms. Many are commonly found inside the medusa's coelenteron, where they seem unaffected by the host's digestive enzymes. In a relationship similar to that of anemone fish, a few cases of anemone shrimp are known, at least one that is obligate for the shrimp (*Ancylocaris brevicarpalis*).

One of the most noteworthy evolutionary achievements of cnidarians is their close relationship with unicellular photosynthetic partners. The relationship is widespread and occurs in many shallow-water cnidarians. The symbionts of freshwater hydrozoans (e.g., some species of *Hydra*) are single-celled species of green algae (Chlorophyta) called **zoochlorellae**. In marine cnidarians, the protists are unicellular cryptomonads and dinoflagellates called **zooxanthellae**, in several genera (Figure 7.32). In some cases, these algae are capable of living free from their hosts, and perhaps do so normally, but very little is known about their natural history. Dinoflagellates in the family Symbiodiniaceae (e.g., *Symbiodinium*, *Breviolum*) are essential for reef-building (hermatypic) corals, and these symbionts have been shown to transfer photosynthates (glycerol, glucose) directly to their coral hosts. The algae typically reside in the host's gastrodermis or epidermis, although some cnidarians harbor extracellular zooxanthellae in the mesoglea. It is usually the algal symbionts that give cnidarians their green, blue-green, or brownish color, and different strains or species of Symbiodiniaceae can give different colors to individuals of the same coral species. Corals that are reef builders (i.e., **hermatypic corals**), if living in the photic zone, always harbor zooxanthellae (they are "zooxanthellate corals"). Resident populations of zooxanthellae in these corals may reach a density of 30,000 algal cells per cubic millimeter of host tissue (or 1–2 million cells per square centimeter of coral surface). Zooxanthellae also occur in many tropical octocorals, anemones, and zoantharians, as well as in other phyla. Obviously, zooxanthellate corals are restricted to the photic zone in the sea, although many can live at depths that receive 15 to 300 times less photon flux than the surface (in the "twilight" zone, or at "mesophotic" depths). Corals living at greater depths shift their energy budget increasingly toward heterotrophic predation. Many

corals have fluorescent pigments that provide a photobiological system for regulating the light environment of their symbionts, and in excessive sunlight some of these are photoprotective. Some fluorescent pigments (produced by the corals themselves) have been shown to also enhance the resistance to bleaching of corals during periods of heat stress. However, some of the most heavily pigmented (blue) corals have actually shown a greater susceptibility to heat stress, so the protection effect of these fluorescent pigments is variable. Although not common, deep-water, azooxanthellate coral reefs (sometimes called "cold-water coral reefs") also exist, and these depend upon sinking detritus and plankton as a food resource.

Surprisingly, both zoochlorellae and zooxanthellae occur within the tissues and cells of one group of sea anemones, *Anthopleura* of the northeast Pacific coast: *A. elegantissima* and *A. xanthogrammica*. Data suggest that zoochlorellae in these anemones photosynthesize more efficiently and grow faster at lower temperatures and light, whereas zooxanthellae do so under higher temperatures or light regimes. The two anemones are the most abundant rocky intertidal anemones in their range, from Alaska to Baja California, and the distributions of their symbionts have been shown to be (predictably) related to latitude and intertidal position.

Even some scyphozoans harbor large colonies of zooxanthellae in their bodies, and it is now known that these protist colonies produce much of the energy required by their host jellyfish (e.g., *Cassiopea*, *Linuche*, *Mastigias*). Some of this information comes from studies on the scyphomedusa *Mastigias* (Figure 7.32C). These jellyfish live in marine lakes on the islands of Palau, where they may occur in densities exceeding 1,000 per cubic meter. In these lakes, *Mastigias* makes daily vertical migrations between the oxygenated, nutrient-poor upper layers and the anoxic, nutrient-rich lower layers, as well as horizontal migrations to track the movement of the sun across the lake. This behavior appears to be related to the light and nutrient requirements of its symbiotic zooxanthellae. Unlike the zooxanthellae in benthic cnidarians, which tend to reproduce more-or-less evenly over a 24-hour period, the zooxanthellae of *Mastigias* show a distinct reproductive peak during the hours when their host occupies a position in the deeper, nitrogen-rich layers of the lakes. This reproductive peak may be a result of the alga's use of free ammonia as a nutrient source.

Many cnidarians seem to derive only modest nutritional benefit from their algal symbionts, but in many others a significant amount of the hosts' nutritional needs appears to be provided by the algae. In such cases, a large portion of the organic compounds produced by photosynthesis of the symbiont may be passed on to the cnidarian host, probably as glycerol but also as glucose and the amino acid alanine. In return, metabolic wastes produced by the cnidarian provide the symbiotic alga with needed nitrogen and phosphorus. In corals, the symbiosis is thought to be important for rapid growth and for efficient deposition of the calcareous skeleton, and many corals can only form reefs when they maintain a viable dinoflagellate population in their tissues. Different coral species serve as hosts to genetically distinct algal symbiont taxa. Each of these appears to be adapted to its host as well as that host's particular ambient light regime. Although the precise physiological-nutritional link between corals and their zooxanthellae has been elusive, the algae clearly seem to increase the rate of calcium carbonate production. Corals and other cnidarians can be deprived of their algal symbionts by experimentally placing the hosts in dark environments. In such cases the algae may simply die, they may be expelled from the host, or they may (to a limited extent) actually be consumed directly by the host. Because they are dependent on light, zooxanthellate corals can live to depths of only 90 m or so. Most zooxanthellate corals also require warm waters and thus occur almost exclusively in shallow tropical seas (although zooxanthellae occur in some high-latitude anemones). As noted above, deep-water and cold-water corals also exist but tend to be entirely carnivorous. They grow at extremely slow rates and thus tend to produce reefs that have existed for thousands and even millions of years, providing a detailed record of changes in sea temperature. Due to their old age and slow growth rates, these reefs are extremely vulnerable and have recently attracted attention by conservation biologists.

Under stress, such as unusually high temperatures, corals may lose their zooxanthellae—a process known as **coral bleaching**. The long-term impact of coral bleaching, now accelerating throughout the world's tropics, due to a combination of warming seas and changes in oceanic acid-base balance due to increased atmospheric CO_2, is unclear. Certainly it seems detrimental in the short run and often leads to death of entire coral colonies and large fractions of reefs. In addition, anthropogenic pollution such as increases in phosphates, nitrates, and ammonia in the sea is enhancing growth of algae and bacteria that compete with coral. A 2018 study found the median return time between severe bleaching events worldwide to be just six years, and diminishing, suggesting that the interval between events may be too short for full recovery of mature assemblages. Caribbean reefs have been devastated over the last few decades, having lost about 80% of their historical coral cover. Interestingly, a few recent studies have suggested that bleaching might lead to corals acquiring new types of zooxanthellae better adapted to the changing environment. If true, it would remain to be seen whether this symbiont switch could take place quickly enough to keep up with today's rapidly changing ocean chemistry. Evidence that selectivity between symbiotic partners

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may exist could mean slower symbiotic reassociations (i.e., certain combinations of hosts and algae are favored while others are impossible). Additionally, there is tantalizing evidence that corals in some areas are adapting to the warmer sea temperatures. However, current thinking is that they may not be able to adapt fast enough (and the interval between recurrent bouts of coral bleaching may be too short) for full recovery of mature reef coral assemblages.

Loss of zooxanthellae by corals usually results in loss of the ability to secrete the calcium carbonate skeleton. The widespread disappearance of Caribbean corals is now considered responsible for a 32%–72% decrease in reef fish populations, a potentially catastrophic change for coastal communities dependent on fishing. Coral reef biodiversity correlates with reef area, thus the long-term effects of reef loss are likely to be cumulative and difficult to reverse. However, one recent experiment found that colonies of some coral species that lost their calcium carbonate skeleton continued to exist as soft-bodied polyps. These recent discoveries have suggested a possible explanation for the geologically "sudden" appearance of the modern stony corals (Scleractinia) in the Middle Triassic, when geochemically perturbed oceans returned to "normal." Before this time, corals and reefs had disappeared from the fossil record for millions of years, but perhaps they continued to exist as "naked corals" (and thus not contributing to the fossil record).

Circulation, Gas Exchange, Excretion, and Osmoregulation

There is no independent circulatory system in cnidarians. The coelenteron largely serves this role by circulating partly digested nutrients through the interior of the body, absorbing metabolic wastes from the gastrodermis, and eventually expelling waste products of all types through the mouth. But large anemones and large medusae confront a serious surface-area-to-volume ratio dilemma. In such cases, the efficiency of the gastrovascular system as a transport device is enhanced by the presence of mesenteries in anemones and the radially arranged canal system in medusae.

Cnidarians also lack special organs for gas exchange or excretion. The body wall of most polyps either is fairly thin or has a large internal surface area, and the thickness of many medusae is due largely to the gel-like mesoglea or mesenchyme. Thus, diffusion distances are kept to a minimum. Gas exchange occurs across the internal and external body surfaces. Facultative anaerobic respiration occurs in some species, such as anemones that are routinely buried in soft sediments. Nitrogenous wastes are in the form of ammonia, which diffuses through the general body surface to the exterior or into the coelenteron. In freshwater species there is a continual influx of water into the body. Osmotic stress in such cases is relieved by periodic expulsion of fluids from the gastrovascular cavity, which is kept hyposmotic to the tissue fluids.

Nervous System and Sense Organs

Cnidarians (and ctenophores) are among the first metazoans to have evolved a distinct, multicellular, integrated nervous system, which is largely in the form of a nerve net(s), or nerve plexus. Consistent with their radially symmetrical body plan, cnidarians generally have a diffuse, noncentralized nervous system; however, great variation exists. Some degree of centralization (not to be confused with cephalization) has been documented in some species of Anthozoa and Medusozoa. In *Hydra*, for example, there is a series of "functional nerve-net networks," these being anatomically nonoverlapping and associated with specific behaviors. Similarly, in the sea anemone *Nematostella vectensis* the nervous system consists of several distinct neural territories along the oral–aboral axis, including pharyngeal and oral nerve rings, and the larval apical tuft. Nonetheless, the neurosensory cells of cnidarians are the most primitive in the animal kingdom, being naked and largely nonpolar. Usually the neurons are arranged in two reticular arrays, called **nerve nets**, one between the epidermis and the mesenchyme and another between the gastrodermis and the mesenchyme (Figure 7.33). This arrangement of an ectodermal and an endodermal nerve net appears to be unique to Cnidaria. The subgastrodermal net is generally less well developed than the subepidermal net and is absent altogether in some species; in cubozoan polyps, there is a nerve net *within* the gastrodermis. Some hydrozoan medusae possess one or two additional nerve nets, whereas in the polyps of hydrozoans and cubozoans there appears to be only a single epidermal nerve ring. Both bi- and multipolar neurons enable the conduction in either direction, allowing a stimulation to progress quickly throughout a network. Despite the seeming simplicity of cnidarian nervous systems, it has been shown that they possess at least some of the classic interneuronal and neuromuscular synapse neurotransmitters seen in Bilateria, including serotonin, suggesting that both catecholamine and indolamine neurotransmitters may be present (at least in sea anemones). Neuronal communication in cnidarians uses transmission through both chemical synapses and electrical synapses mediated by gap junctions. There is also evidence for epithelial conduction through junctions between epithelial cells in some cnidarians.

A few nerve cells and synapses are polarized and allow for transmission in only one direction, but most cnidarian neurons and synapses are nonpolar—that is, impulses can travel in either direction along the cell or across the synapse. Thus, sufficient stimulus sends an impulse spreading in every direction. In

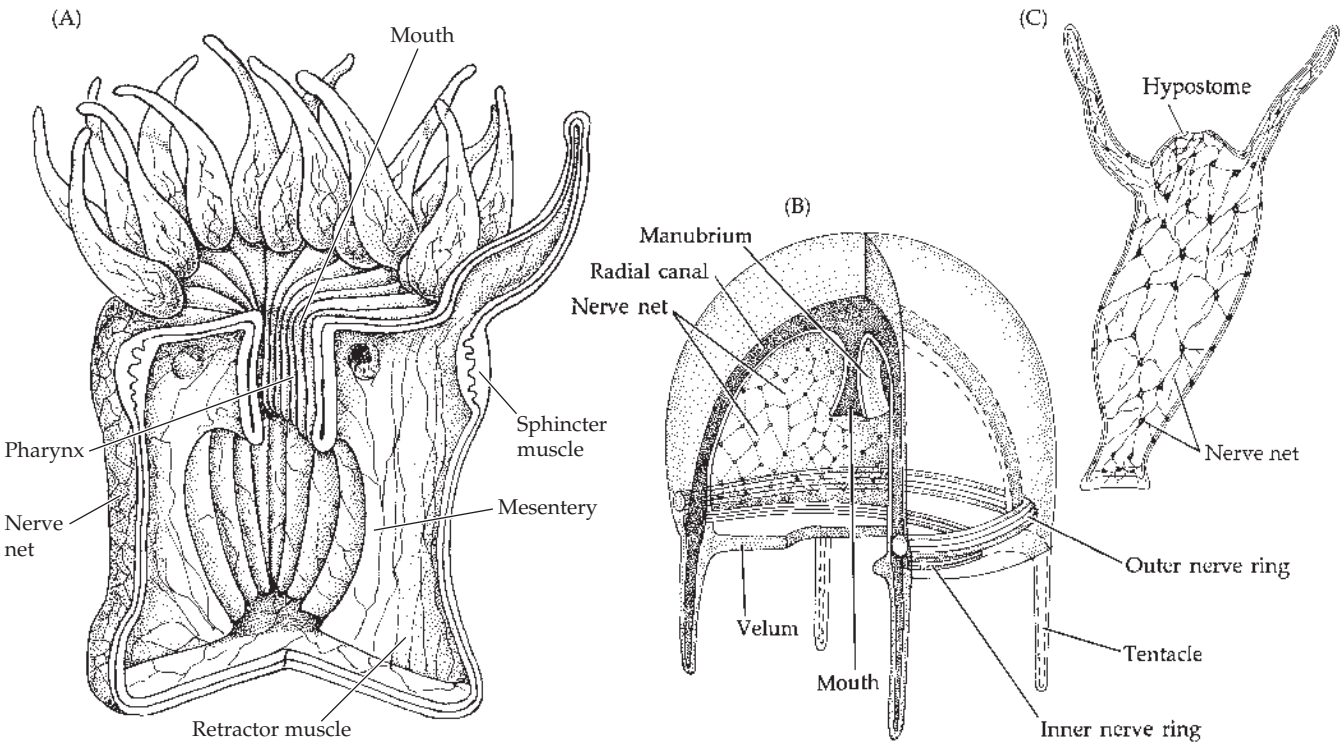
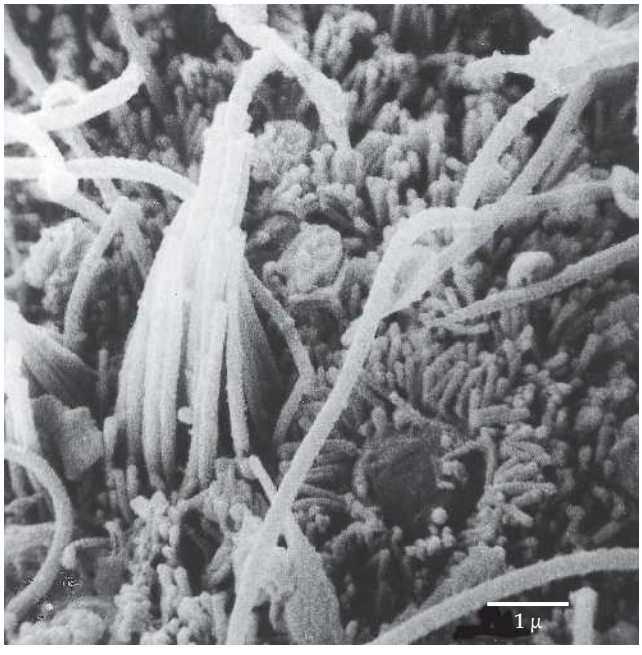


FIGURE 7.33 Cnidarian nerve nets. (A) Nerve net of a typical sea anemone (Anthozoa). (B) Nerve net in a hydromedusa (Hydrozoa). (C) Nerve net of *Hydra* (Hydrozoa).

some cnidarians where both nerve nets are well developed, one net serves as a diffuse slow-conducting system of nonpolar neurons, and the other as a rapid through-conducting system of bipolar neurons.

Polyps generally have very few sensory structures. The general body surface has various minute hairlike structures developed from individual cells. These serve as mechanoreceptors, and perhaps as chemoreceptors, and are most abundant on the tentacles and other regions where cnidae are concentrated. They are involved in behavior such as tentacle movement toward a prey or predator and in general body movements. Some appear to be associated specifically with discharged cnidae, such as the ciliary cone apparatus of anthozoan polyps, which is believed to function in the same way as the cnidocil in hydrozoan and scyphozoan nematocysts (Figure 7.34). Oddly, these structures do not appear to be connected directly to the nerve nets. In addition, most polyps show a general sensitivity to light, not mediated by any known receptor but presumably associated with neurons concentrated in or just beneath the translucent surface of epidermal cells.

The genome of the anemone *Nematostella vectensis* has been sequenced and much of its development mapped. It has been shown to possess a complex neural morphology that is modified during development from the larval to adult (polyp) form (there is no medusa stage in this species). The nervous system is a diffuse nerve net with both ectodermal sensory and effector cells, and endodermal multipolar ganglion cells. *Nematostella vectensis* has specialized neural structures with distinct populations of neurons are located at the pharyngeal nerve ring, at the oral nerve ring, innervating the mesenteries, and at the tentacle tips of the adults, as well as at the larval apical tuft. Thus, the nerve net consists



From R. N. Mariscal. 1974. In A. M. Cameron et al. (Eds.), *Proceedings of the Second International Coral Reef Symposium, Vol. 1*, pp. 519–532. The Great Barrier Reef Committee, Brisbane, Australia

FIGURE 7.34 A ciliary cone on the tentacle of the corallimorpharian anemone *Corynactis californica* lies adjacent to cnidocyte (the circle of microvilli).

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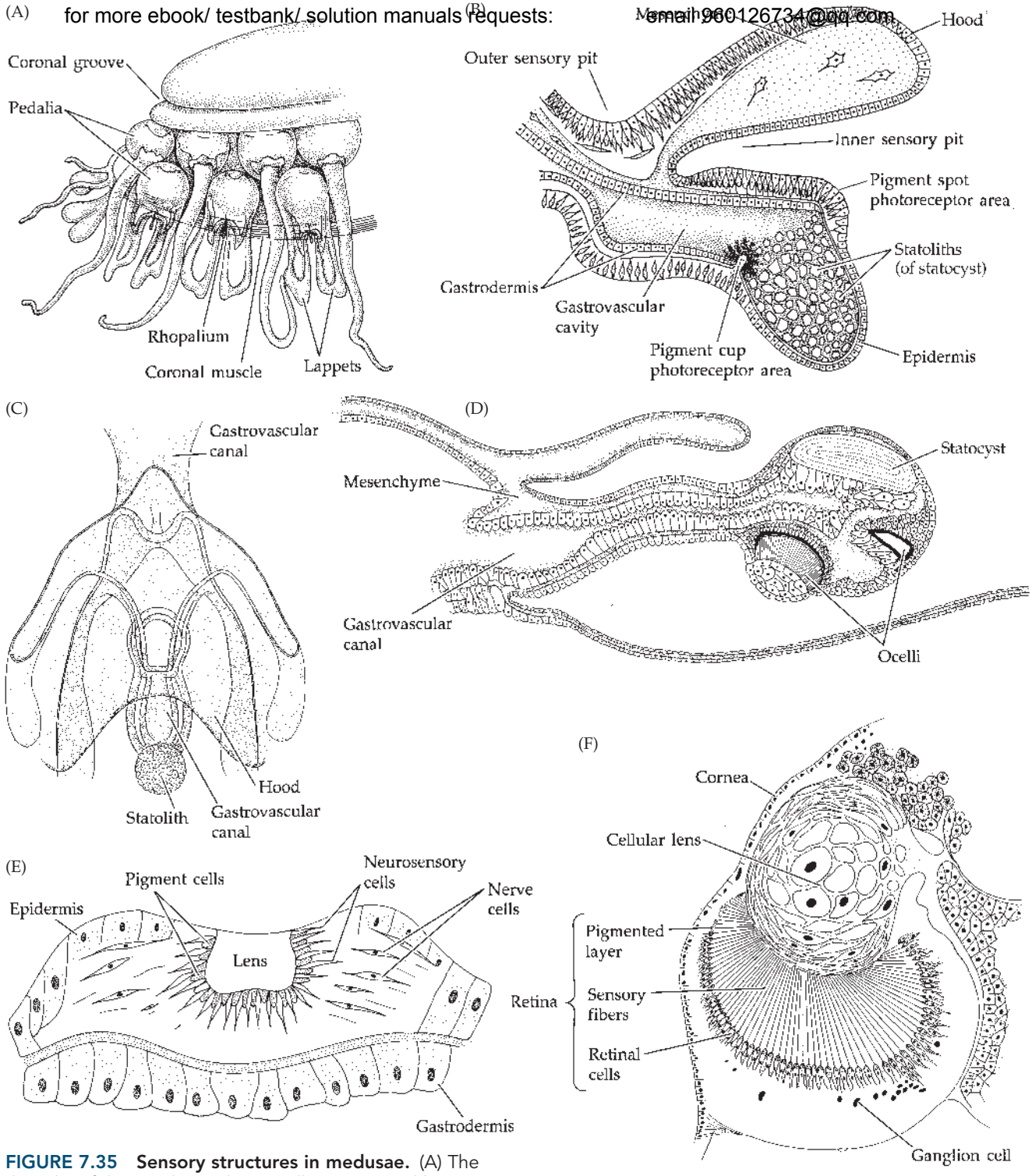

FIGURE 7.35 Sensory structures in medusae. (A) The rhopalia of the scyphomedusa *Atolla* are situated between the marginal lappets. (B) A rhopalium (section) has various sensory regions. (C) A rhopalium of *Aurelia* (diagrammatic). A portion of the gastrovascular/radial canal has been cut away. (D) A cubozoan rhopalium (note the lower eye is not shown in this oblique section). (E) A pigment-cup ocellus (cross section) of a hydrozoan medusa. (F) The eye of a cubozoan (*Carybdea*) (cross section).

of several distinct neural territories. Interestingly, these neuralized regions correspond to expression of conserved bilaterian neural developmental regulatory genes, including homeodomain transcription factors. This suggests that, even though *N. vectensis* lacks a centralized nervous system, its neural systems seems to be patterned along an oral–aboral axis.

As might be expected, motile medusae have more sophisticated nervous systems and sense organs than do the sessile polyps (Figure 7.35). In many groups, especially the hydromedusae, the epidermal nerve net of the bell is condensed into two nerve rings near the bell margin. These nerve rings connect with fibers innervating the tentacles, muscles, and sense organs. The inner ring stimulates rhythmic pulsations of the

bell. This ring is also connected to statocysts, when present, on the bell margin, which is supplied with general sensory cells and with radially distributed ocelli and (probably) chemoreceptors. The general sensory cells are neurons whose receptor processes are exposed at the epidermal surface. The ocelli are usually patches of pigment and photoreceptor cells organized as a disc or a pit. Statocysts may be in the form of pits or closed vesicles, the latter housing a calcareous statolith adjacent to a sensory cilium. When one side of the bell tips upward, the statocysts on that side are stimulated. Statocyst stimulation inhibits adjacent muscular contraction, and the medusa contracts muscles on the opposite side. Many medusae maintain themselves in a particular photoregime by directed swimming behaviors. This action is seen especially in those medusae harboring large populations of zooxanthellae, such as the upside-down jelly *Cassiopea*, which lies upside down on the shallow seafloor, exposing to light the dense zooxanthellae population residing in tissues of its tentacles and oral arms.

There is great variation in eye type and structure among cnidarians, including among hydrozoan medusae. Some cnidarians have structural eyes (even camera-type eyes), but others have pigment-cup ocelli of varying complexity, or only simple eyespots, or just a generally photosensitive neuronal system. Among the hydromedusae, structural eyes are usually well-defined ocelli that vary in complexity from a simple ectodermal layer with sensory and pigment cells, through pigment-cup eyes, to small camera-type eyes with pigmented retina and lens- or cornea-like structures. The axons of the photosensory cells may join in bundles that collect to form an "optic nerve" that runs to the outer nerve ring in the bell. In addition, hydrozoans have been shown to possess a cytoplasmic conducting system similar in nature to that of sponges. Epidermal cells and muscle elements appear to be the principal components of the system. Although the impulse seems to move slowly, it is initiated by nerve cells and relies on gap junctions.

In the codonophoran siphonophores, a linear condensation of the nerve net produces longitudinal "giant axons" in the stem and the nerve tracts in the tentacles. One of these axons is actually a neuronal syncytium that originates by fusion of neurons from the nerve net of the stem. The high-speed impulses in these large-diameter nerve tracts enable codonophorans to contract rapidly and initiate a fast escape reaction.

Image-forming and simpler eyes both exist in cnidarians, and even eyeless species show light-sensing behavior, supporting the idea that ancestors without eyes already sensed light with dispersed photoreceptor cells and that eyes evolved multiple times within the phylum. Cnidae also act as sensory cells by responding to stimuli and are integrated with the nervous system through synapses. The bell margins of cubomedusae and scyphomedusae usually bear club-shaped structures called **rhopalia**, which are situated between a pair of flaps or **lappets** (Figure 7.35A). The rhopalia are complex sensory centers, each containing a concentration of epidermal neurons, a pair of chemosensory pits, a statocyst, and eyes of various design. One pit is located on the exumbrellar side of the hood of the rhopalium, the other on the subumbrellar side.

Cubomedusae are strong swimmers that are able to make rapid directional changes in response to visual stimuli. They have been shown to be attracted to light, to avoid dark objects, and even to navigate around obstacles. They are active predators that "rest" at night. Although cubomedusae have the basic cnidarian nerve net and subumbrellar nerve ring close to the bell margin (sometimes called the "ring nerve"), they also have the most elaborate visual system in Cnidaria, located on four rhopalia. Each rhopalium has six eyes, of four morphological types: paired pit-shaped pigment-cup eyes, paired slit-shaped pigment-cup eyes, and two complex camera-type eyes with cornea, lens, and retina (one small upper lensed eye, and one large lower lensed eye). Although the retina of the camera eye is only one cell thick, it is multilayered, containing a sensory layer, a pigmented layer, a nuclear layer, and a region of nerve fibers. The number of sensory cells, or photoreceptors, in each of these remarkable eyes varies from about 300 to 1,000, depending on the species. Each rhopalium also has a crystalline concretion, the statolith, which is often called a statocyst. Neuronal signals from the rhopalia are presumably transmitted to swimming pacemaker neurons to direct visually guided swimming movements. Giant neurons have been identified on either side of the cubomedusan rhopalium.

Despite the structural simplicity of the cubozoan planula larva, being composed of only six cell types, it possesses rhabdomeric photoreceptors of the pigment-cup ocelli type. These comprise 10–15 ocelli arranged as individual photoreceptor cells. Each contains screening pigment in a cavity filled with microvilli (the sites of photoreception) and a single cilium. The cilium is the typical 9+2 structure and is likely motile, rather than sensory. There is no synaptic or electrical (gap junction) connection between the ocelli and any other cell in the larva. The ocelli of cubozoan planulae appear to represent one of the simplest visual systems in the animal kingdom.

Scyphozoan medusae have structurally simple visual eyespots located in the rhopalia, which also contain gravity-sensing structures, the statocysts. The eyespots are simple ectodermal pigment-cup eyes, consisting of photosensory cells containing pigment granules or of photosensory cells alternating with pigment cells, or they are pigment-cup eyes with ectodermal sensory cells and gastrodermal pigment cells. The sensory cells make contact with the ectodermal nerve net.

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Bioluminescence is common in cnidarians and has been documented in all classes except the Cubozoa and the poorly known Staurozoa. In some forms (e.g., many hydromedusae), luminescence consists of a single flash in response to a local stimulus. In others, bursts of flashes propagate as waves across the body or colony surface (e.g., sea pens and sea pansies). One of the most complicated luminescent behaviors occurs in some hydropolyps, where a series of multiple flashes is propagated. The sea pansy *Renilla* (an octocoral) also has very elaborate luminescent displays. Propagated luminescence is probably controlled by the nervous system, although this phenomenon is not well understood. In at least one hydromedusa (*Aequorea*), luminescence appears not to be the result of the usual luciferin-luciferase reaction; rather, a high-energy protein, named **aequorin**, emits light in the presence of calcium.

Reproduction and Development

Asexual reproduction takes many forms in cnidarians, and regeneration after major injuries is common. Many anemones can be cut in half and then regenerate the two halves flawlessly. Sometimes injuries to the oral region result in the production of two or more mouths, each with its own set of feeding tentacles.

Sexual reproduction in Anthozoa is the least complex, usually involving a motile **planula larva** that settles and grows into a sessile adult polyp. However, sexual reproductive processes in Medusozoa are intimately tied to the alternation of generations that characterizes this clade. As you have already read, medusozoan life cycles commonly involve an asexually reproducing polyp stage, alternating with a sexual medusoid stage that produces a characteristic motile planula larva. Hence, cubozoans have motile planulae, which settle to grow into polyps that in turn produce sexual medusae. Scyphozoans also follow the planula-to-sessile-polyp mode, but the polypoid stage generates multiple juvenile medusae, called **ephyrae**, by transverse fission or **strobilation** at the polyp's oral end; ephyrae later mature as the sexual medusoid stage. Planulae, polyps, and medusae all appear in many hydrozoan species' life cycles. Medusae, when present, develop from a laterally budding tissue mass called the **entocodon**, but polyp or medusa stages may be entirely missing from certain life cycles. Because of these many variations in life cycle, we will discuss the cnidarian classes separately.

Anthozoan reproduction Members of this class are exclusively polypoid, and the variety of ways that new individuals can be produced asexually nearly defies imagination. Asexual reproduction is common in sea anemones, and longitudinal fission of polyps can result in two separate individuals (Figure 7.36A), or the daughter anemones can remain close together to produce large groups (clones) of genetically identical individuals (e.g., seen in some species of *Anthopleura*, *Diadumene*, and *Metridium*). During longitudinal fission, the body column stretches to the point of ripping itself apart, each half then regenerating its missing parts. The less common process of pedal laceration (e.g., seen in some acontiate sea anemones: *Diadumene*, *Haliplanella*, *Metridium*) can also lead to clonal populations. During pedal laceration, the pedal disc spreads and the anemone simply glides away, leaving behind a circle of small fragments of the disc, each of which develops into a young sea anemone. This behavior is easily observed in aquaria, where anemones can affix themselves to the glass walls.

(A)

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(B)

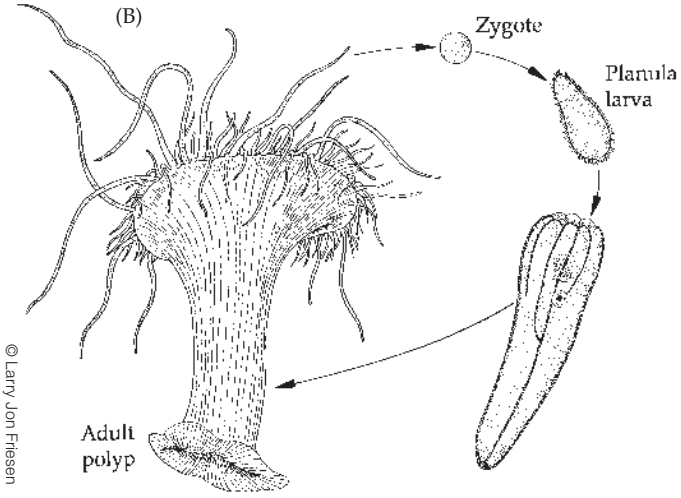

FIGURE 7.36 Reproduction in Anthozoa. (A) Asexual reproduction by longitudinal fission in the aggregating anemone *Anthopleura elegantissima*. (B) A typical anthozoan sexual life cycle: the adult polyp releases gametes that fuse externally, or fertilized eggs are released, and zygotes develop into a planula larva; the larva settles and transforms directly into a young polyp.

In addition to these two common modes of asexual reproduction, at least a few species of sea anemones undergo transverse fission (e.g., *Edwardsiella lineata*, *Nematostella vectensis*). Transverse fission is usually by way of a constriction and then separation in the lower part of the column that results in the formation of a small aboral compartment and a larger oral region, each of which then grows its missing region. Transverse fission has also been reported by a process called "polarity reversal," in which the aboral end spontaneously sprouts new tentacles and a new mouth; eventually a new physa forms in the midsection of the anemone and the two individuals separate (e.g., *Gonactinia*). Certain sagartiid sea anemones engage in intratentacular budding, wherein multiple mouth openings result from repeated longitudinal fission through the pharynges of existing individuals. This process produces bandlike colonies that resemble the elongated polyps of certain meandroid corals. Also, certain populations of *Anthopleura* engage in mesenterial budding of tiny polyps, which are brooded within the gastrovascular cavity before release from the parent anemone. In these anemones, no evidence of gonadal or gametic development has been found, suggesting that these populations are primarily if not entirely asexual.

One family of sea anemones (Boloceroididae) swims actively and produces new individuals by longitudinal fission, pedal laceration, and a bizarre process called tentacular shedding (or tentacle budding) in which tentacle fragments are pinched off at basal sphincters and moved into the coelenteron, where they are brooded as they develop into new polyps before being released. Certain anemones and at least one scleractinian coral (*Pocillopora damicornis*) are known to produce planula larvae parthenogenetically and brood them until release. And, among all these odd asexual modes of reproduction there is the so-called "polyp bailout" of some corals, where under conditions of stress (e.g., high salinity, low pH, acute temperature shock) the nonskeletonized portion of the polyp detaches itself and disperses to a new site, whereupon it settles and builds a new skeleton. The detached polyps appear to retain their endosymbiotic zooxanthellae.

Anthozoans are typically gonochoristic, although most scleractinian corals are hermaphroditic. Fertilization can take place internally, but in most species it occurs externally, in the open sea. A typical anthozoan life cycle is shown in Figure 7.36B. Eggs are free or, occasionally, pooled into a gelatinous egg mass (even through fertilization). Sperm are usually equipped with mitochondria and flagella suited for propulsion, although structural differences among anthozoan sperm are remarkable. Cleavage is typically radial and holoblastic, resulting in a hollow spherical, uniformly ciliated, coeloblastula. Gastrulation occurs by way of ingression or invagination, to produce distinct ectodermal and endodermal germ layers, and thence a ciliated planula larva. When invagination occurs, the blastopore remains open and sinks inward, drawing with it a tube of ectoderm that becomes the adult pharynx. Because the mouth forms at the site of gastrulation (at the animal pole), anemones/cnidarians are, by definition, true protostomes, suggesting that protostomy predated the cnidarian-bilaterian divergence. The planula larva may develop one or a few pairs of tentacles at the oral end, as well as a rudimentary pharynx and mesenteries, before settling. Some anthozoan planulae are planktotrophic, although very yolky ones do not feed. The ability of some larvae to feed allows them a potentially longer larval life, enhancing dispersal and selection of an appropriate settlement site. Some anthozoan planulae (e.g., *Anthopleura*) appear to obtain zooxanthellae by ingestion. In some species, the planulae develop up to eight complete mesenteries before settling, and this is the so-called **edwardsia stage**, named after the octamesenterial genus *Edwardsia*. The larva eventually settles on its aboral end and tentacles grow around the upwardly directed mouth and oral disc. Development in *Nematostella vectensis* includes an early chaotic cleavage stage and a hollow blastula that gastrulates by unipolar invagination to a swimming planula, which settles and grows tentacles surrounding its oral opening to the gut to form a polyp.

Many coral populations undergo synchronous spawning over large areas on reefs, a process mediated by moonlight-sensitive molecules called **cryptochromes**, which have also been associated with control of circadian activity in vertebrates and insects. In some cases this synchrony is restricted to colonies of a single species, or it is only loosely correlated with lunar cycles, but widespread synchronous spawning events involving over 100 different coral species have been reported (on the Great Barrier Reef, Australia), perhaps as an adaptation to satiate predators. The synchronized release of massive numbers of eggs and sperm into the water by individuals in an area is called broadcast spawning. Unfertilized eggs apparently die within hours if not fertilized by sperm. Such events create a pulse of nutrients into the surrounding ecosystem and also may lead to hybridization among scleractinian corals. Verified cases of hybridization between members of different coral genera exist, and this may explain the great range of polymorphism seen in many coral "species." Because hybrid individuals can become secondarily clonal, they may persist within populations for years, but the degree to which interbreeding by hybrids or their introgression into parental populations occurs is unclear. Some coral planula larvae are long-lived, spending several weeks or months in the plankton, an obvious means of dispersal. Other corals release benthic planulae that crawl away from the parent and settle nearby. In the Caribbean coral *Porites astreoides* the larva hosts zooxanthellae, and an analysis of differential gene expression during competency has

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shown that the dinoflagellate endosymbionts may play a significant role in the transition from nonprobing to probing behavior in larvae.

Octocorals are usually gonochoristic and often spawn synchronously, although the timing of gonadal development appears to be highly variable among temperate and tropical species, evidently due to variability in water temperature or resource availability, respectively. Although little is known about the reproductive biology of most ceriantharians, it appears that antipatharians, anemones, and stony corals may be gonochoristic or hermaphroditic. In some species, colonial forms can contain males, females, and hermaphrodites. The gametes arise from patches of tissue on the gastrodermis of all or only some mesenteries. Eggs are fertilized either in the coelenteron, followed by early development in the gut chambers, or more commonly outside the body, in the sea. A number of anemones brood their developing embryos internally or on the external body surface. The northeast Pacific sea anemone *Aulactinia incubans* releases its brooded young through a pore at the tip of each tentacle! Some corals undergo internal fertilization, brooding, and then release of planula larvae. The eastern Pacific solitary coral *Balanophyllia elegans* builds skeletal chambers within which oocytes and embryos may be carried apart from the main digestive cavity, a structural arrangement that allows continued brooding through advanced developmental stages. These calcareous structures are preserved in the fossil record. Some octocorals (e.g., *Briareum*, *Alcyonium*) brood their embryos in a mucous coat on the body surface; then the planula larvae escape. Others shed their gametes and rely on external fertilization and planktonic development. *Heliopora coerulea* is a gonochoristic hermatypic octocoral that broods its planulae at the surface of female colonies before their annual release.

Cylista troglodytes is the only sea anemone known to copulate. The coupling starts when a female glides up to a receptive male, whereupon their pedal discs are pressed together in such a way that they create a chamber into which the gametes are shed and fertilization occurs. The copulatory position, which forms a temporary marsupium, is maintained for several days, presumably until planula larvae have developed. This behavior may be an adaptation to areas of great water movement that might otherwise scatter gametes and reduce the probability of successful fertilization.

Recent work on the sea anemone *Nematostella vectensis* has revealed cnidarians to possess some (but not all) of the genes involved in dorsal–ventral patterning in the Bilateria. Although these homologues are expressed in somewhat haphazard ways during development, their expression has suggested to some workers the possibility that the oral–aboral polarity of cnidarians might be equivalent to the anterior–posterior polarity of bilaterians. In fact, homologues of five Hox genes known to regulate anterior–posterior axis patterning in Bilateria are also known from *N. vectensis* (and other cnidarians), although Cnidaria lack a definitive anterior–posterior axis. These genes show a staggered domain expression in the oral–aboral axis patterning of the anemone. This suggests that the earliest stages of what was to become bilaterality had its roots at least as deep in the evolution of the Metazoa as the Cnidaria. Thus, what we recognize as "biradiality" in anemones (e.g., the right–left arrangement of feeding tentacles, pharyngeal siphonoglyph, coelenteron mesenteries) might, in fact, be a rudimentary form of bilaterality.

Scyphozoan reproduction Most scyphozoan jellyfish species have a metagenic life cycle involving a benthic, asexually reproducing polyp stage and a sexually reproducing medusa stage. However, the life cycles of most species are poorly known because their benthic stages occur in yet unknown locations. The asexual form of scyphozoan cnidarians is a small polyp called the **scyphistoma** (= scyphopolyp; Figure 7.37A). It may produce new scyphistomae by budding from the column wall or from stolons. At certain times of the year, generally in the spring, medusae are produced by repeated transverse fission of the scyphistoma, a process called **strobilation** (Figure 7.37B). During this process the polyp is known as a **strobila**. Medusae may be produced one at a time (**monodisc strobilation**), or numerous immature medusae may stack up like soup bowls and then be released one after the other as they mature (**polydisc strobilation**). Immature and newly released medusae are called **ephyrae** (sing. ephyra). An individual scyphistoma may survive only one strobilation event, or it may persist for several years, asexually giving rise to more scyphistomae and releasing ephyrae annually.

Ephyrae are very small larvae with characteristically incised bell margins (Figure 7.37C,D). The ephyral arms, or primary tentacles, mark the position of what becomes the adult lappets and rhopalia. In some genera (e.g., *Aurelia*) the number of ephyral arms is quite variable. Maturation involves growth between these arms to complete the bell. Development into sexually mature adult scyphomedusae takes a few months to a few years, depending on the species.

The gamete-forming tissue in adult scyphomedusae is always derived from the gastrodermis, usually on the floor of the gastric pouches, and gametes are generally released through the mouth. Most species are gonochoristic. Fertilization takes place in the open sea or in the gastric pouches of the female. Gastrulation is by ingression or invagination and results in a mouthless, double-layered planula larva; when invagination occurs, the blastopore closes. The planula larva eventually settles and grows into a new scyphistoma.

The medusa phase dominates the life cycles of most scyphozoans. The small polyp stage is often significantly suppressed or absent altogether. For

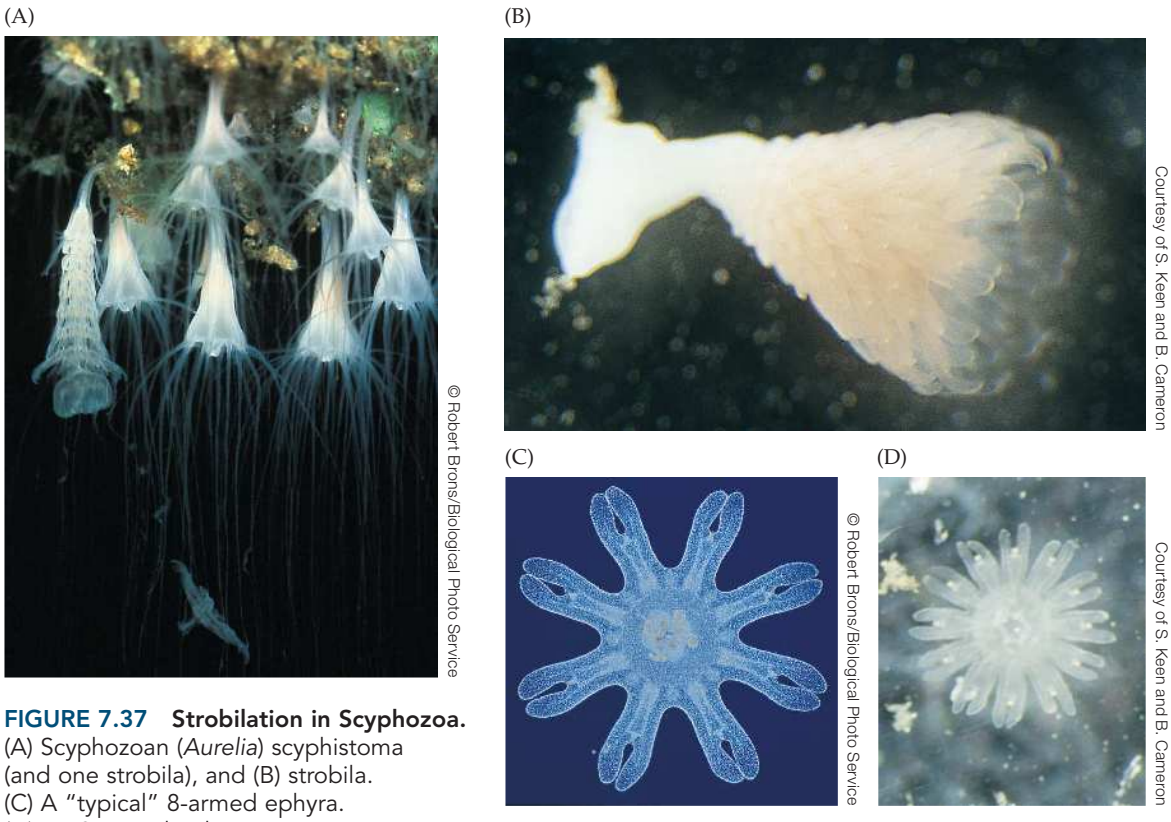

FIGURE 7.37 Strobilation in Scyphozoa.
(A) Scyphozoan (*Aurelia*) scyphistoma (and one strobila), and (B) strobila. (C) A "typical" 8-armed ephyra. (D) A 12-armed ephyra.

example, many pelagic scyphomedusae have eliminated the scyphistoma, and the planula larva transforms directly into a young medusa (e.g., *Atolla*, *Pelagia*, *Periphylla*). In others, the larvae are brooded, developing in cysts on the parent medusa's body (e.g., *Chrysaora*, *Cyanea*). A few genera have branching colonial scyphistomae with a supportive skeletal tube and an abbreviated or suppressed medusoid stage (e.g., *Nausithoe*, *Stephanoscyphistoma*). None, however, has lost the medusoid stage altogether. Some scyphozoan life cycles are shown in Figure 7.38.

Cubozoan reproduction The reproductive biology of cubozoans is only just beginning to be understood. Apparently, each polyp metamorphoses directly into a single medusa, rather than undergoing the kind of strobilation seen in scyphozoan polyps. Some cubozoan medusae are known to engage in a form of copulation, in which the male uses his tentacles to bring the female close enough to transfer a sperm packet, or spermatophore, directly to her. In *Copula sivickisi* and *Tripedalia cystophora*, this courtship results in the female moving the spermatophore to her mouth to be ingested. Once in the gastrovascular system, spermatophores are transferred to specialized structures that function in sperm storage. Females accept spermatophores from multiple males yet may only produce one embryo strand (a packet of fertilized ova that eventually attaches to algae). During courtship, mature females may exhibit conspicuous velar spots that may provide a visual signal to courting males.

Staurozoan reproduction Reproduction in staurozoans has been observed in only a few species. So far as is known, all species are gonochoristic and free-spawn gametes into the water, where fertilization takes place. The zygotes quickly settle and develop into creeping, nonciliated planulae, each with a fixed number of cells. Planulae develop into a nonfeeding "microhydrula" stage and may asexually produce creeping frustules that later develop into stauropolyps, or the microhydrula stage may develop directly into stauropolyps, which later develop into stauromedusae.

Hydrozoan reproduction Hydrozoan polyps reproduce asexually by budding. This is a rather simple process wherein the body wall evaginates as a bud, incorporating an extension of the gastrovascular cavity with it. A mouth and tentacles arise at the distal end, and eventually the bud either detaches from the parent and becomes an independent polyp or, in the case of colonial forms, remains attached. Asexual reproduction in the latter case creates larger and more-complex polypoid colonies that have greater reproductive capacity.

Medusa buds, or gonophores, are also produced by polyps in a similar fashion, although the process is sometimes quite complex. A rather special kind of

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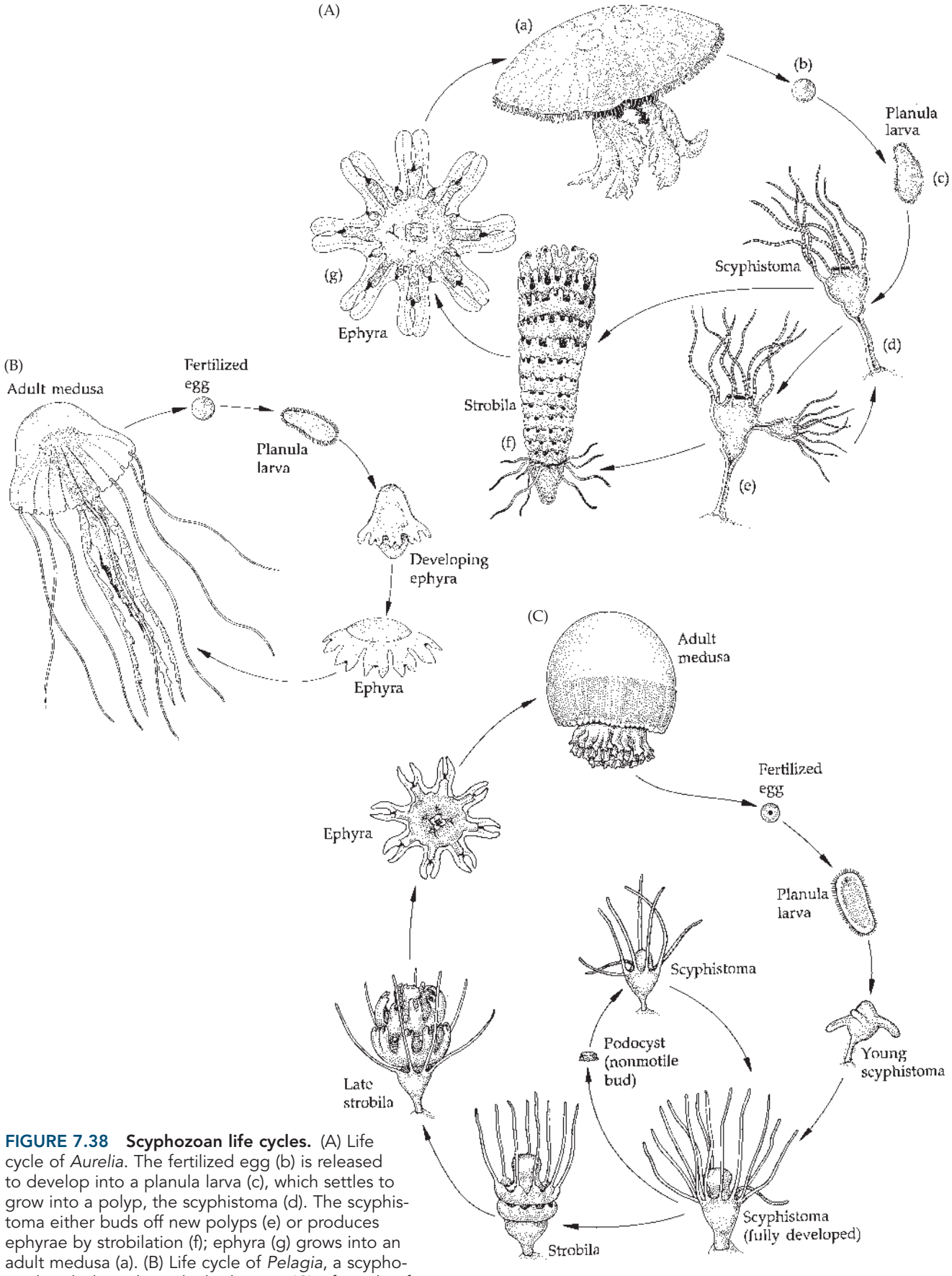

FIGURE 7.38 Scyphozoan life cycles. (A) Life cycle of *Aurelia*. The fertilized egg (b) is released to develop into a planula larva (c), which settles to grow into a polyp, the scyphistoma (d). The scyphistoma either buds off new polyps (e) or produces ephyrae by strobilation (f); ephyra (g) grows into an adult medusa (a). (B) Life cycle of *Pelagia*, a scyphomedusa lacking the polyploid stage. (C) Life cycle of the "cannonball jellyfish," *Stomolophus meleagris*.

budding occurs in the siphonophores, in which the floating colonies produce chains of individuals called **cormidia**, which may break free to begin a new colony.

Certain hydromedusae also undergo asexual reproduction, either by the direct budding of young medusae (Figure 7.39) or by longitudinal fission. The latter process often involves the formation of multiple gastric pouches (**polygastry**) followed by longitudinal splitting, which produces two daughter medusae. In some species (e.g., *Aequorea macrodactyla*), direct fission may take place. Polygastry does not occur during this process; instead, the entire bell folds in half, severing the stomach, ring canal, and velum (Figure 7.40). Eventually the whole medusa splits in half, and each part regenerates the missing portions.

Cnidarians in general have a great capacity for regeneration, as exemplified by experiments on *Hydra*. The eighteenth-century naturalist Abraham Trembley (from the Republic of Geneva) had the clever idea of turning a *Hydra* inside out—and he did. To his delight, the animal survived quite well, with the gastrodermal cells functioning as the "new epidermis" and vice versa. Cells removed from the body of a *Hydra* also have a modest degree of reaggregative ability, like that seen so dramatically in sponges. In some cases, entire animals will reconstruct from cells taken only from the gastrodermis or only from the epidermis.

A typical *Hydra* consists of only about 100,000 cells of roughly a dozen different types. Although distinct epidermis and gastrodermis exist, these tissues are very similar to one another, comprising mainly epitheliomuscular cells. It takes only a few weeks for all the cells in a *Hydra* to replace themselves, or "turn over," including the nerve cells. These attributes make *Hydra* an ideal creature for studies of developmental biology, histogenesis, and morphogenesis.

All hydrozoan cnidarians have a sexual phase in their life cycle (Figure 7.41). However, in solitary species such as those in the genus *Hydra*, and perhaps in many colonial forms, the medusoid phase (typically the gamete-producing stage) is suppressed or absent. Instead, the polyp epidermis develops simple, transient gamete-producing structures called **sporosacs** (Figure 7.5B). Most colonial hydroids produce medusa buds (gonophores) either from the walls of the hydranths or from separate gonozooids. The gonophores may grow into medusae that are released as free-living sexually reproducing individuals, or they may remain attached to the polyps as incipient medusae that produce gametes in place. For example, *Gonothyraea loveni* has reduced medusae that remain attached to the colony, and the embryos are brooded within these medusae. The embryos of *G. loveni* lack a blastocoel, and gastrulation proceeds through delamination to produce a parenchymula (a developmental stage in which flagellated ectodermal cells surround a mass of parenchyma-like endodermal cells), which then grows to become the free-swimming planula larva. The planula settles and grows into a primary polyp that initiates a new colony.

Milleporid hydrozoans produce short-lived sexual medusae that are released over several days during particular seasons. Temporal segregation of spawning seems to occur among colonies of different species. Colonies within species are gonochoristic and so release exclusively male medusae, bearing a sperm sac

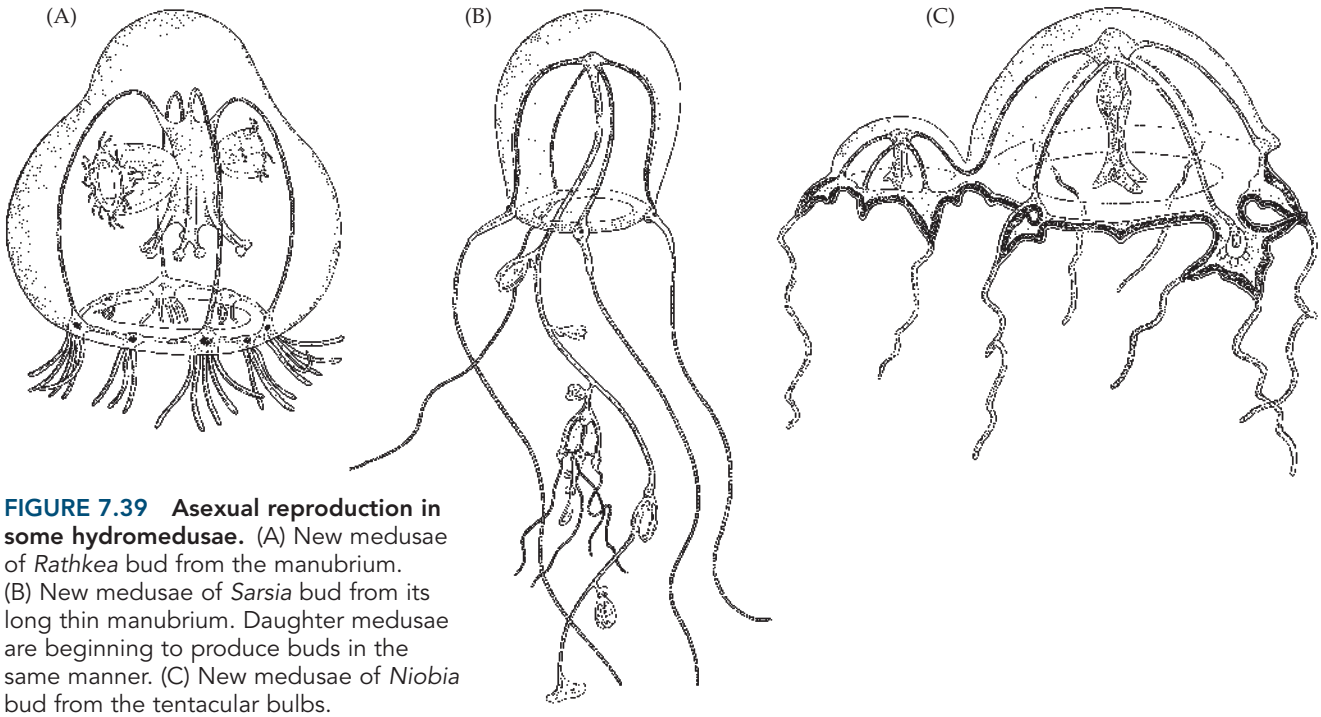

FIGURE 7.39 Asexual reproduction in some hydromedusae. (A) New medusae of *Rathkea* bud from the manubrium. (B) New medusae of *Sarsia* bud from its long thin manubrium. Daughter medusae are beginning to produce buds in the same manner. (C) New medusae of *Niobia* bud from the tentacular bulbs.

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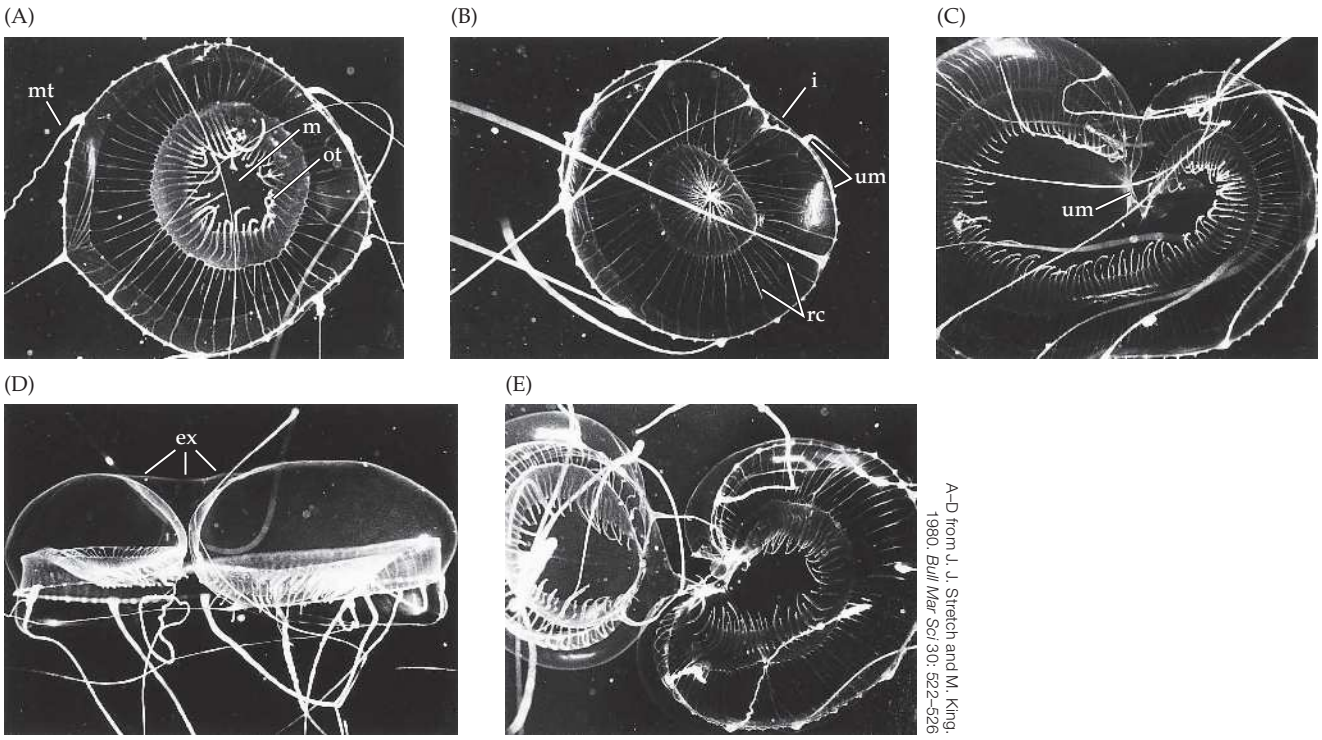


A–D from J. J. Stretch and M. King. 1980. *Bull Mar Sci* 30: 522–526

FIGURE 7.40 Asexual reproduction in the hydromedusa *Aequorea*. The sequence of photographs shows the direct fission of *A. macrodactyla*. (A) This oral view shows a nondividing medusa with its marginal fishing tentacles (mt) deployed. (B) Initiation of invagination (i). (C–E) A progression of the direct fission process. The oral (C) and marginal (D) views illustrate the severing of the umbrellar margin (um) and the separation of exumbrellar (ex) halves. (E) The exumbrellar surface beginning to pull apart, producing free-swimming daughter medusae; healing is nearly complete in the smaller daughter medusa on the left. ot: oral tentacles; m: mouth; rc: radial canals.

located at the vestigial manubrium, or female medusae bearing three to five ova in the subumbrellar cavity. Male medusae appear to be released into the water column by their corallae a few hours before female medusae are released. Gametes are released by both medusa types, and fertilization occurs externally.

In free-living hydromedusae, germinal cells arise from interstitial epidermal cells that migrate to specific sites on the bell surface, where they consolidate into a temporary gonadal mass. Subsequently, gametogenic tissue appears on the surface of the manubrium, beneath the radial canals, or on the general subumbrellar surface. Hydromedusae are typically gonochoristic, with either sperm or eggs usually being released directly into the water, where fertilization occurs. In some, only sperm are released and fertilization occurs on or in the female medusa's body. Free hydromedusae are especially common in temperate waters, where they may be very abundant seasonally and easily collected in plankton nets. Siphonophores appear to be ancestrally gonochoristic, but hermaphroditic forms exist among the Physonectae and exclusively among the Calycophorae (Codonophora). Planktonic dispersal of sexual forms would seem to mitigate against genetic differentiation of coastal populations, but considerable genetic population structure has been demonstrated among morphologically similar populations of *Obelia geniculata*, with estimated divergence times among reciprocally monophyletic lineages exceeding several million years.

One of the most famous of the hydromedusae is *Turritopsis dohrnii*, known as the "immortal jellyfish," which lives most of its life as a small hydromedusa found worldwide in cooler waters. It has the ability (as do a few other cnidarian species) to revert from a solitary, sexually mature adult medusa to a sexually immature, clonal polypoid stage on the seafloor. The clonal stage resembles that of the postplanula colony that originally gave rise to the medusa. The transformation is apparently triggered by environmental stress, predation, or "old age," and it is accomplished by a cell developmental process called transdifferentiation. Theoretically, the process can go on indefinitely, rendering the organism immortal.

Hydrozoans display remarkable variety in their embryonic and early postembryonic development. In most cases, cleavage is total and subequal, with a unilateral cleavage furrow during early cell divisions, leading to a coeloblastula or morula; gastrulation occurs in practically all known patterns except invagination (e.g., unipolar and multipolar migration, syncytial delamination, epiboly, etc.), typically resulting in a stereogastrula. However, the overall motif is fundamentally radial and holoblastic. The interior cell mass is endoderm; the

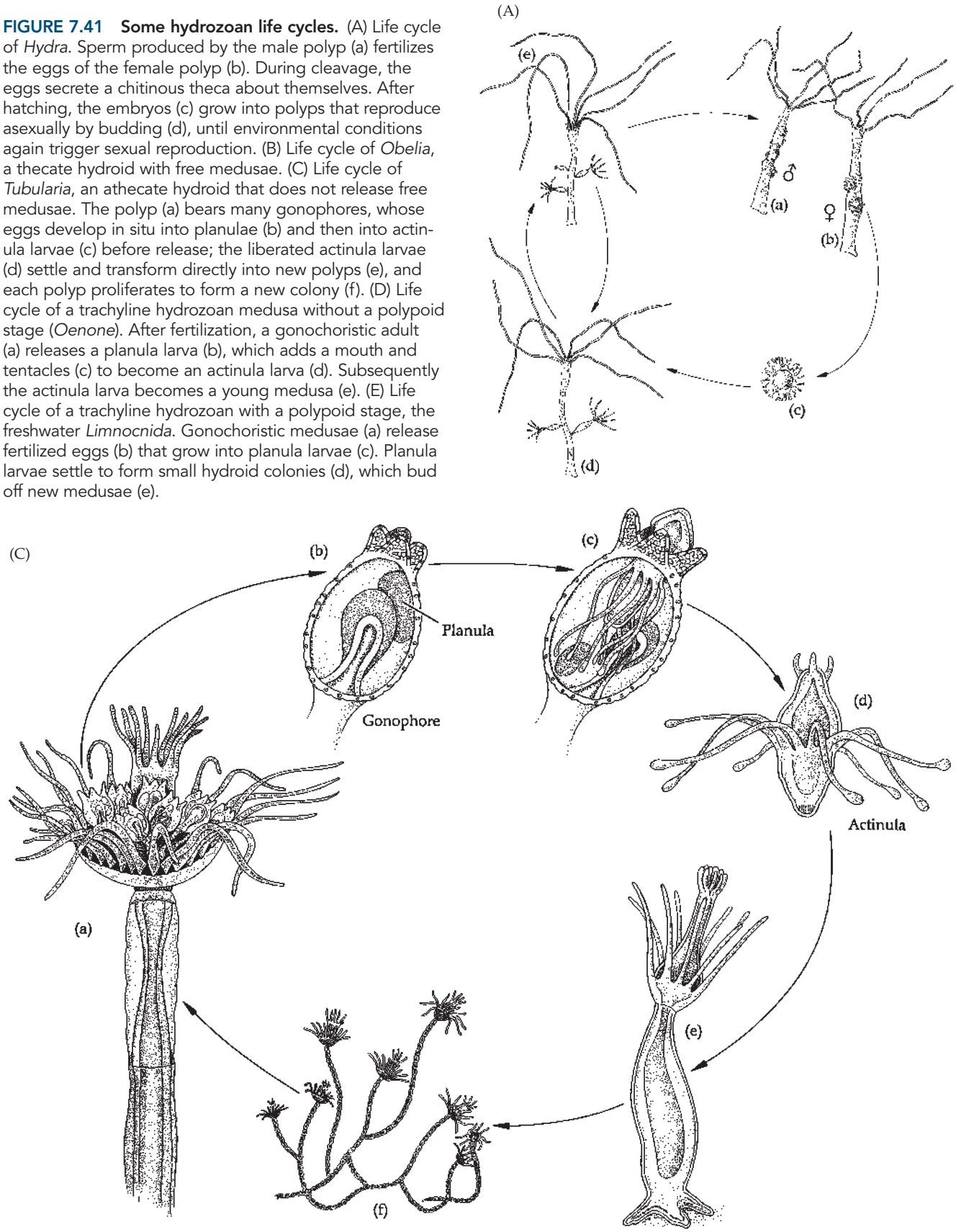
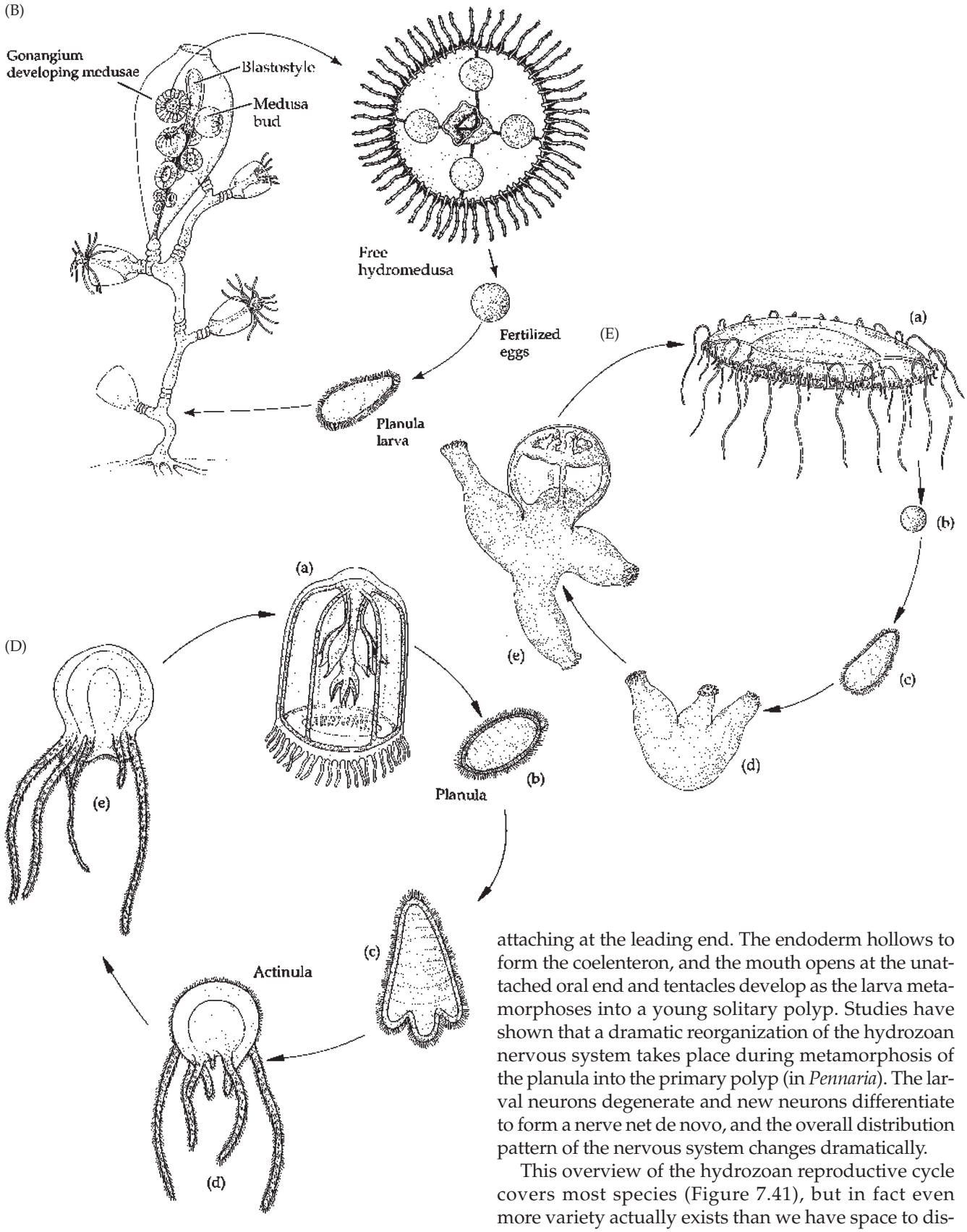


FIGURE 7.41 Some hydrozoan life cycles. (A) Life cycle of *Hydra*. Sperm produced by the male polyp (a) fertilizes the eggs of the female polyp (b). During cleavage, the eggs secrete a chitinous theca about themselves. After hatching, the embryos (c) grow into polyps that reproduce asexually by budding (d), until environmental conditions again trigger sexual reproduction. (B) Life cycle of *Obelia*, a thecate hydroid with free medusae. (C) Life cycle of *Tubularia*, an athecate hydroid that does not release free medusae. The polyp (a) bears many gonophores, whose eggs develop in situ into planulae (b) and then into actinula larvae (c) before release; the liberated actinula larvae (d) settle and transform directly into new polyps (e), and each polyp proliferates to form a new colony (f). (D) Life cycle of a trachyline hydrozoan medusa without a polypoid stage (*Oenone*). After fertilization, a gonochoristic adult (a) releases a planula larva (b), which adds a mouth and tentacles (c) to become an actinula larva (d). Subsequently the actinula larva becomes a young medusa (e). (E) Life cycle of a trachyline hydrozoan with a polypoid stage, the freshwater *Limnocnida*. Gonochoristic medusae (a) release fertilized eggs (b) that grow into planula larvae (c). Planula larvae settle to form small hydroid colonies (d), which bud off new medusae (e).

exterior cell layer is ectoderm (Figure 7.42). The stereogastrula elongates to form a unique, solid or hollow, nonfeeding, usually free-swimming **planula larva** (Figure 7.43). The planula larva is radially symmetrical, but it swims with a distinct "anterior–posterior" orientation. The ectodermal cells are monociliated and destined to become the adult epidermis; the endoderm is destined to become the adult gastrodermis. The trailing end of



the larva (of all cnidarians) becomes the oral end of the adult, and even in the larval stage a mouth sometimes develops at this end. Hydrozoan planulae swim about for a few hours to a few weeks before settling by attaching at the leading end. The endoderm hollows to form the coelenteron, and the mouth opens at the unattached oral end and tentacles develop as the larva metamorphoses into a young solitary polyp. Studies have shown that a dramatic reorganization of the hydrozoan nervous system takes place during metamorphosis of the planula into the primary polyp (in *Pennaria*). The larval neurons degenerate and new neurons differentiate to form a nerve net de novo, and the overall distribution pattern of the nervous system changes dramatically.

This overview of the hydrozoan reproductive cycle covers most species (Figure 7.41), but in fact even more variety actually exists than we have space to discuss. For example, in some trachylines, the polypoid stage is apparently lost altogether. The medusae produce planula larvae that develop into actinula larvae, which metamorphose into adult medusae, bypassing any sessile polypoid phase. Some trachylines and some

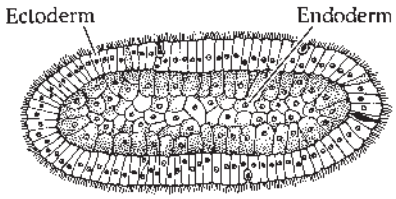


FIGURE 7.42 **A typical solid hydrozoan planula larva resulting from ingression.**

siphonophores undergo direct development, bypassing the larval stage altogether. Within the Trachylina, members of the family Rhopalonematidae (a trachymedusae formerly classified in Actinulida) exhibit minute interstitial polyps that lack a medusoid stage (or possibly these forms represent creeping medusae) and have suppressed the larval phase. The adult polyp is ciliated and resembles an actinula larva (hence the prior placement within Actinulida).

Myxozoan reproduction Myxozoan cnidarians have such aberrant life cycles that it is difficult to identify either polypoid or medusa stages within them. No planula stage is known to exist. Such marked differences from other cnidarian taxa have contributed to the uncertain status of myxozoans within the phylum to date, although recent phylogenomic work suggests they may be the sister group of Medusozoa. Nevertheless, an alternation of sexual and asexual generations within vertebrate and annelid hosts does occur, albeit as parasitic forms as described above. Asexual reproduction occurs within the vertebrate host, producing infective myxospores as already described (Figure 7.29). Sexual reproduction occurs within annelids and other coelomate worms, generating infective actinospores. The separation of the sexual and asexual stages of the life cycle of these parasites is similar to that which occurs in other parasitic species and could suggest that some developmental genetic homologies exist between the asexual and sexual stages of myxozoans and the polyp and medusa stages of other cnidarians. However, the reproductive modes of most myxozoans remain poorly known. Recent genomic studies have revealed myxozoan genomes to be among the smallest across all Metazoa, with only about 5,500 genes and lacking key factors for signaling pathways typically needed for multicellular development.

Cnidarian Evolutionary History

Earliest Cnidaria

Cnidarians have one of the longest fossil histories among the Metazoa. They are well represented from the early Cambrian onward, and the major lineages of the phylum had already diversified by the Fortunian Age. A possible sea pen, a hydroid, and two sea anemones have been described from the Fortunian Chengjiang biota in China. But the first apparent cnidarian fossils date from the Precambrian Ediacaran Period, from the famous Ediacara Hills of South Australia, which contain possible medusae and polypoid colonies (e.g., sea pen–like creatures) that lived nearly 600 million years ago. However, these early circular and frond-like impressions cannot be unequivocally assigned to any modern Cnidarian taxa. Some researchers doubt that they represent true cnidarians, even though some of the circular forms have marginal tentacles such as those seen in most medusae. Other possible Neoproterozoic polypoids include impressions that may be the floats of the pelagic "chondrophorans" and fossils with triradiate symmetry (e.g., *Tribrachidium*), as well as pentaradiate and octoradiate symmetry, thus differing fundamentally from any living cnidarians. Some workers consider these fossils to be parts of other organisms, such as isolated holdfast structures; others have placed them in an extinct class of Cnidaria, the Trilobozoa. Still others view them as primitive triradiate echinoderms.

In the 1980s, the German paleontologist Adolf Seilacher, frustrated by attempts to assign these Neoproterozoic Era fossils to modern phyla, created an entirely new phylum, the Vendobionta (or Vendozoa), suggesting that it might be a sister group to the Eumetazoa (metazoans above the poriferan grade). The Vendozoa, Seilacher noted, seemed to have a quiltlike construction of thin, lightly sclerotized but flexible, outer skin separated into compartments by more rigid internal struts (which in fossil impressions appear to be sutures). Later workers placed these fossils in an extinct cnidarian order, the Rangeomorpha, and called other, more bilaterally symmetrical forms Erinettomorpha. One of the most famous of these latter forms is the oval-shaped *Dickinsonia*, which may

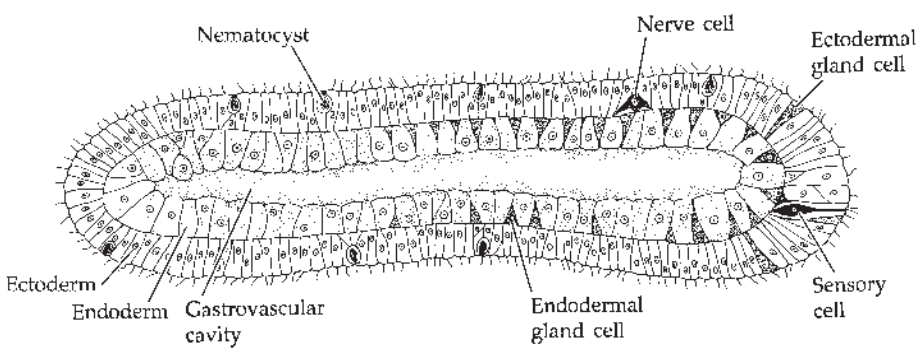


FIGURE 7.43 **The hollow planula larva of the hydroid *Gonothyraea* (longitudinal section).**

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have measured over a meter in length but been only a few millimeters in thickness. Some workers consider *Dickinsonia* to be medusa-like, but it has also been assigned to the Platyhelminthes, to the Annelida (due to hints of possible body segmentation), to an extinct phylum (Proarticulata), to Placozoa, and to an entirely new kingdom! Today, *Dickinsonia* is identified as being a mobile organism, but like many Ediacaran macrofossils it lacks any structures that can be convincingly interpreted as a mouth or gut, and thus it cannot be placed in any existing phylum. The presence of cholesteroids as the dominant lipids in *Dickinsonia* and allied taxa supports an affinity of these organisms with Filozoa, the clade that unites metazoans with Filasterea and Choanoflagellatea.

Attempts to place the Ediacaran fossils within the Cnidaria (or other extant phyla) met with limited success until 2014. For example, differences in apparent growth patterns and frond structure between extant cnidarians (e.g., pennatulaceans) and frond-like Ediacaran species had argued against a direct cnidarian relationship. Then, in 2014, a 560-million-year-old (Ediacaran) cnidarian-like fossil (named *Haootia quadriformis*) was reported from Newfoundland, with quadraradial symmetry and clearly preserved bundled muscular fibers. *Haootia* appears to be a nearly 6 cm long polyp, or perhaps an attached medusa. Another strong candidate for Ediacaran ancestry is *Corumbella werneri*, recovered from both South American and U.S. sites, which bears strong resemblance to coronate Scyphozoa. Remarkable embryos of probable scyphozoan affinity have also been reported form the lower Cambrian of China. Exceptionally well-preserved jellyfish fossils (including phosphatized fossil embryos) are known from early Cambrian (~535 Ma) Chengjiang and Kuanchuanpu formations in China and the middle Cambrian (~505 Ma) of Utah. Early trace fossils have also been assigned to the phylum Cnidaria. Burrows assigned to sea anemones occur in the early Cambrian, and some strata have meandering tracks that appear to be traces left from mucous trails of creeping anemones (some modern anemones move in this fashion, using ciliary activity).

Cnidarian Phylogeny

Like Porifera, cnidarian body plans appear to have remained essentially unchanged since the Cambrian, and molecular phylogenetic analyses clearly position Cnidaria below the origin of bilaterality and possibly as the sister group to Bilateria. In Chapter 4 we reviewed the important embryological differences between the coelomate metazoan clades known as the protostomes and deuterostomes. To the extent that these traits occur in noncoelomate Metazoa, it is of phylogenetic importance to note them. For example, radial cleavage is characteristic of the deuterostomes (but also occurs in a few protostomes), but it probably arose very early in metazoan evolution; it occurs in cnidarians and, in a slightly different form, in most sponges. Thus it appears to be the plesiomorphic type of cleavage among animals. Spiral cleavage, on the other hand, defines an entire clade of protostomes (the Spiralia), suggesting it is a more derived cleavage pattern in Metazoa.

The phylogeny of Cnidaria has been argued for decades, nearly all possible relationships among the major lineages have been hypothesized, and there has been a long debate about whether the polyp or the medusa came first. Anatomical evidence has been equivocal on the question of which living class of Cnidaria resembles the most ancestral members of the phylum. Some workers have favored a view that the first cnidarian was a medusa, based largely on the conjecture that the sexual stage must have appeared first (the **medusoid hypothesis**), suggesting that the medusoid stage was lost in the class Anthozoa. Other workers have favored the view that the polypoid form is primitive within Cnidaria, because polyps occur in all classes of the phylum (except the parasitic Myxozoa) and thus must be part of the primitive cnidarian body plan (the **polypoid hypothesis**).

Phylogenetic studies inform us that the phylum comprises three major living clades: Anthozoa, Endocnidozoa, and Medusozoa. Phylogenomic analyses strongly support a basal split in Cnidaria into two clades, Anthozoa and Medusozoa (Myxozoa aside), which does not provide strong support for either the polypoid or the medusoid hypothesis (i.e., the ancestral cnidarian could have been an anthozoan-like polyp, or it could have had a medusa stage that was lost in the Anthozoa line) (Figure 7.44). Microbial symbioses appear to have evolved multiple times independently among the Cnidaria (e.g., in hexacorals, octocorals, scyphozoans, and hydrozoans). The origin of a medusa stage probably occurred only once. The polyp stage was lost in the lineages leading to Endocnidozoa and within Trachylina. In addition, we now know that, among cnidarians, only the anthozoans possess circular mitochondrial DNA, a trait they share with most other Metazoa (including the Placozoa). Members of the Medusozoa clade all have linear mtDNA and the unique cnidocil, both viewed as derived traits within cnidarians. Over half of the described species of Cnidaria belong to the polyp-only clade Anthozoa (e.g., sea anemones, corals, sea fans, and sea pens). Medusozoa consists of four clades: Scyphozoa, Cubozoa, Hydrozoa, and Staurozoa. Endocnidozoa is an entirely parasitic clade that includes about 2,200 species of Myxozoa and a single known species of Polypodiozoa—minute endoparasites of invertebrates and vertebrates with complex life cycles.

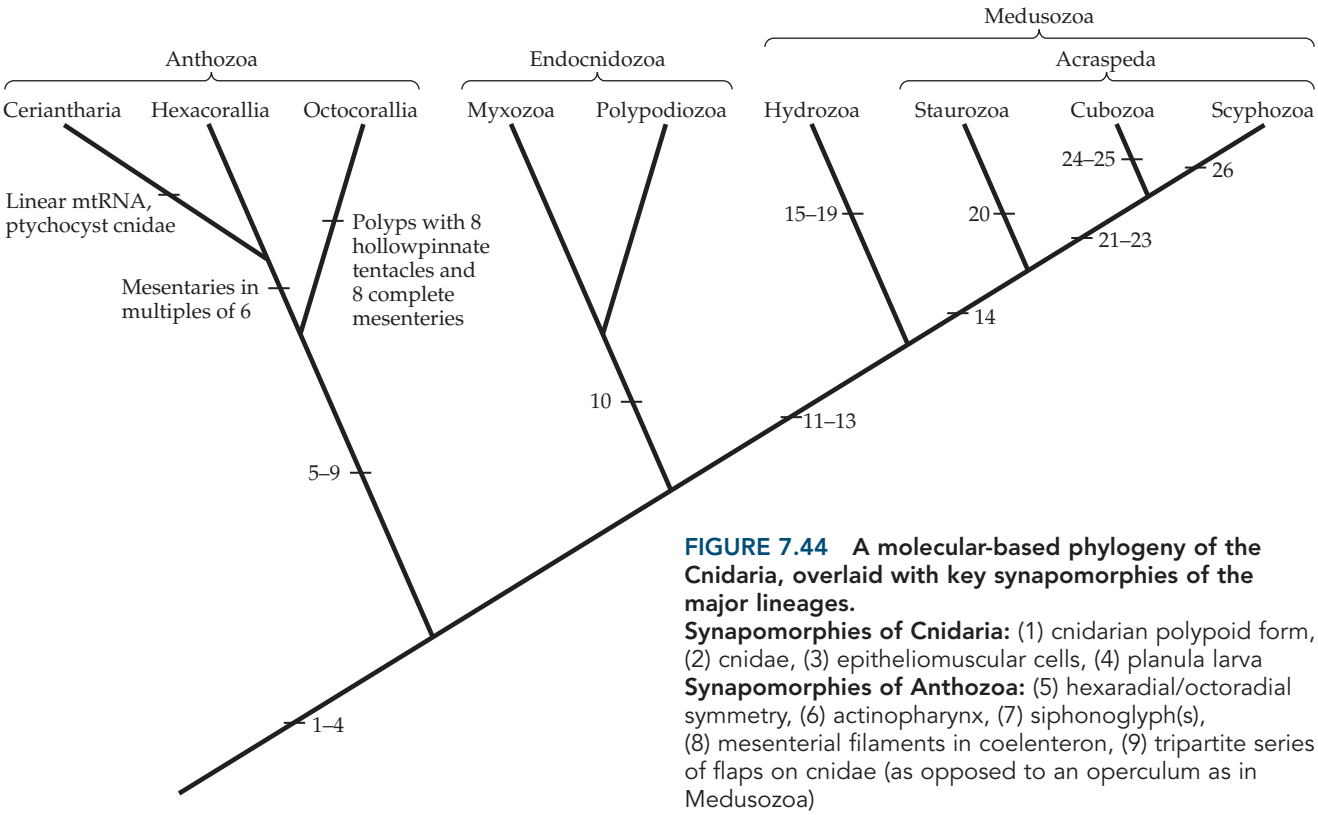

FIGURE 7.44 A molecular-based phylogeny of the Cnidaria, overlaid with key synapomorphies of the major lineages.
Synapomorphies of Cnidaria: (1) cnidarian polypoid form, (2) cnidae, (3) epitheliomuscular cells, (4) planula larva
Synapomorphies of Anthozoa: (5) hexaradial/octoradial symmetry, (6) actinopharynx, (7) siphonoglyph(s), (8) mesenterial filaments in coelenteron, (9) tripartite series of flaps on cnidae (as opposed to an operculum as in Medusozoa)
Synapomorphies of Endocnidozoa: (10) obligatory endoparasitism and complex life cycle
Synapomorphies of Medusozoa: (11) with medusae and alternation of generations, (12) linear mtDNA (also seen in ceriantharian Anthozoa), (13) operculate cnidae (with cnidocil)
Synapomorphies of Acraspeda: (14) medusae acraspedote (without a velum)
Synapomorphies of Hydrozoa: (15) relocation of gamete-forming tissue to epidermis, (16) absence of gut mesenteries, (17) simplification of middle layer to an acellular mesoglea, (18) craspedote medusae, (19) loss of gastrodermal nematocysts
Synapomorphies of Staurozoa: (20) evolution of unique life cycle, with stauropolyps and sessile stauromedusae
Synapomorphies of Cubozoa-Scyphozoa: (21) reduction or loss of polyp, (22) rhopalia, (23) lensed rhopaliar eyes
Synapomorphies of Cubozoa: (24) boxlike medusa form, (25) velarium
Synapomorphies of Scyphozoa: (26) strobilation

Phylogeny within each of the cnidarian classes is equally interesting but largely beyond the scope of this text. However, a few generalizations can be made about some important events. Coloniality has been a common and important evolutionary theme within Cnidaria. Coloniality in the hydrozoans may have arisen by retention of young polyps during asexual reproduction, and this development ultimately led to the highly specialized colonial groups such as the Siphonophora, Milleporidae, and Stylasteridae. In the class Scyphozoa, evolution favored increasing specialization of the pelagic medusoid form and diminishing importance of the polypoid stage in the life cycle. Scyphomedusae and cubomedusae have evolved large size, special musculature, a cellular or fibrous mesenchyme, a complex gastrovascular system, and a fairly sophisticated sensory system.

Anthozoans are characterized by several unique synapomorphies: hexaradial or octoradial symmetry (transformed into biradial symmetry in most); the actinopharynx, siphonoglyphs, and unique mesenterial filaments in the coelenteron; absence of a cnidal operculum and cnidocil; tripartite flaps on the cnidae; and special ciliary cones associated with the cnidocytes. Anthozoans also possess a more complex gastrovascular and nervous system than seen among the Medusozoa, as well as a greater degree of cellularity of the mesenchyme. Although the position of Ceriantharia is not yet fully resolved, most data support a sister-group relationship with Hexacorallia.

Among members of the class Anthozoa, evolution has produced a grand series of experiments in colonial polypoid living, resulting in such "superorganisms" as stony corals, octocorals, pennatulaceans, and zoantharians. Within the Hexacorallia, stony corals (scleractinians) first appear in the fossil record at the base of the Late Triassic Epoch, about 237 million years ago, although the first scleractinians were not reef builders. Scleractinian origins (and radiations) are still not well understood. Suggested extinct ancestors of Scleractinia include three Paleozoic coral groups: the Rugosa, the

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Heterocorallia, and the Tabulata. The Rugosa (sometimes called horn corals) and Heterocorallia had their polyps divided by septa into four cycles (rather than six as in Scleractinia), and the septa arose in a pinnate fashion (rather than cyclically as in Scleractinia). Tabulate corals were nonseptate. The connection between rugose corals, which formed calcite skeletons, and modern scleractinians, whose skeletons are aragonitic, is tightened by the discovery of Cretaceous scleractinians with calcite skeletons. Rugose corals, which ranged in size from a centimeter or so to over a meter in length, lived from the Ordovician Period to the late Permian and were solitary or colonial.

Within the Scleractinia, molecular evidence appears to confirm the existence of two clades, "robust" species with solid, heavily calcified skeletons forming massive or platelike structures, and "complex" species with lighter, more porous and more complex skeleton structures. Within these clades, only the Poritiina and Dendrophylliina appear to be monophyletic, suggesting that relationships based on morphology alone are likely to be misleading in this group. Possibly contributing to this diversity, recent evidence suggests that coloniality and symbiosis with zooxanthellae have been repeatedly acquired and lost throughout the history of stony corals, a tendency that may have allowed scleractinians to diversify within reef and nonreef communities, as well as recover from repeated local extinctions over evolutionary time. An increase in polyp size within the Anthozoa seems to have occurred over time, along with the evolution of complex structural components of the mesenchyme and increasingly efficient musculature. Anthozoans, of course, have greatly exploited a commensal relationship with zooxanthellae—more so than members of the other classes. Convergent evolution has occurred frequently throughout the Cnidaria, as witnessed by such features as colonies, calcareous skeletons, the velum-velarium structures, and various means of suppressing the medusoid or polypoid stage in the life cycle.

Chapter Summary

Cnidaria is a clade of diploblastic metazoans that arose in the Precambrian, before bilaterality had been achieved in the Animal Kingdom. They are notable for their possession of cnidae, radial symmetry, a gastrovascular cavity with a single opening, unique myoepithelial cells, planula larvae, and a life cycle that may be dimorphic and include both polyp and medusoid stages. Cnidae are housed in a cnidocyte cell and have a variety of functions, including prey capture, defense, locomotion, and attachment. Most cnidarians are marine, free-living forms but some freshwater species and parasites (notably the endoparasitic Polypodiozoa and Myxozoa) are also known. Colonialism and symbiotic relationships with dinoflagellates are common among the free-living species and have evolved multiple times independently. The phylum comprises three major lineages: Anthozoa, a polypoid lineage lacking medusae; Medusozoa, a diverse clade including species exhibiting primarily motile medusoid forms as well as forms with both medusoid and polypoid life stages; and Endocnidozoa, a clade of highly simplified obligate endoparasites. Polypoid forms, especially colonial species, have an impressive array of flexible (chitin–based) and hard ($CaCO_3$–based) skeletons. Corals and other cnidarians hosting symbionts, when stressed (e.g., warming ocean waters), may loose their symbiotic dinoflagellates (zooxanthellae) through a process known as "coral bleaching." With over 13,300 described living species and an old fossil record dating at least to the Cambrian, Cnidaria is a highly successful phylum.

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CHAPTER 8

A Brief Introduction to the Bilateria and Its Major Clades

Courtesy of G. Rouse

While the relationships of the nonbilaterians still remain stubbornly unresolved, the monophyly of Bilateria is strongly supported. However, our understanding of the relationships among the phyla *within* Bilateria has changed considerably since the emergence of molecular phylogenetics in the 1990s. Our current view of bilaterian relationships is shown in Figure 8.1 (and in more detail in subsequent chapters). In this short chapter, we will walk you through the bilaterian tree, step-by-step, before sending you off to the following chapters where you will dive into the individual subclades and phyla. There may be some taxonomic names here that are new to you and also some names whose meanings have changed in recent years. Several long-standing groups, such as Protostomia and Deuterostomia, have changed in their phylum memberships, and a number of new higher-level clades have emerged.

The Bilateria

The Bilateria (or Triploblastica) is a clade of animals whose adult tissues are derived from three embryonic germ layers—endoderm, mesoderm, and ectoderm—and whose body axis is anteroposterior. This type of axial patterning makes individuals divisible into two symmetrical halves, left and right, a pattern known as bilateral symmetry. In addition, the presence of bilaterality and an anterior–posterior axis has led to regional specialization, perhaps most importantly the concentration of nerves and sensory structures in the anterior area—a process known as cephalization (i.e., the formation of a head end). The concept of Bilateria was codified (and the name created) by Hatschek in 1888, and the clade is supported by all modern phylogenetic analyses. Developmentally, Bilateria is also supported by the presence of the three classes of Hox genes: anterior, central, and posterior; in contrast, only anterior and posterior ones are found in nonbilaterians. Further, the presence of mesoderm in bilaterians has led to the development of numerous derivative tissues, such as mesodermal muscles, blood, and various organs. Mesoderm is also associated with the formation of a true body cavity in most bilaterians, or coelom (also called a secondary body cavity, as opposed to the primary embryonic body cavity, or blastocoelom). A true coelomic cavity can be recognized as mesodermal by the fact that its lining is a true epithelium, with polarized cells interconnected by apical adherens junctions.

The recently recognized phylum Xenacoelomorpha (Chapter 9) is seen as the sister group to all the remaining living bilaterian phyla, which form a clade called Nephrozoa (the name recognizes that these are mostly "kidney-bearing" animals, although all these "kidneys" may not be homologous). The clade Nephrozoa is sometimes also called "Eubilateria." Most animals are nephrozoans—26 of the 31

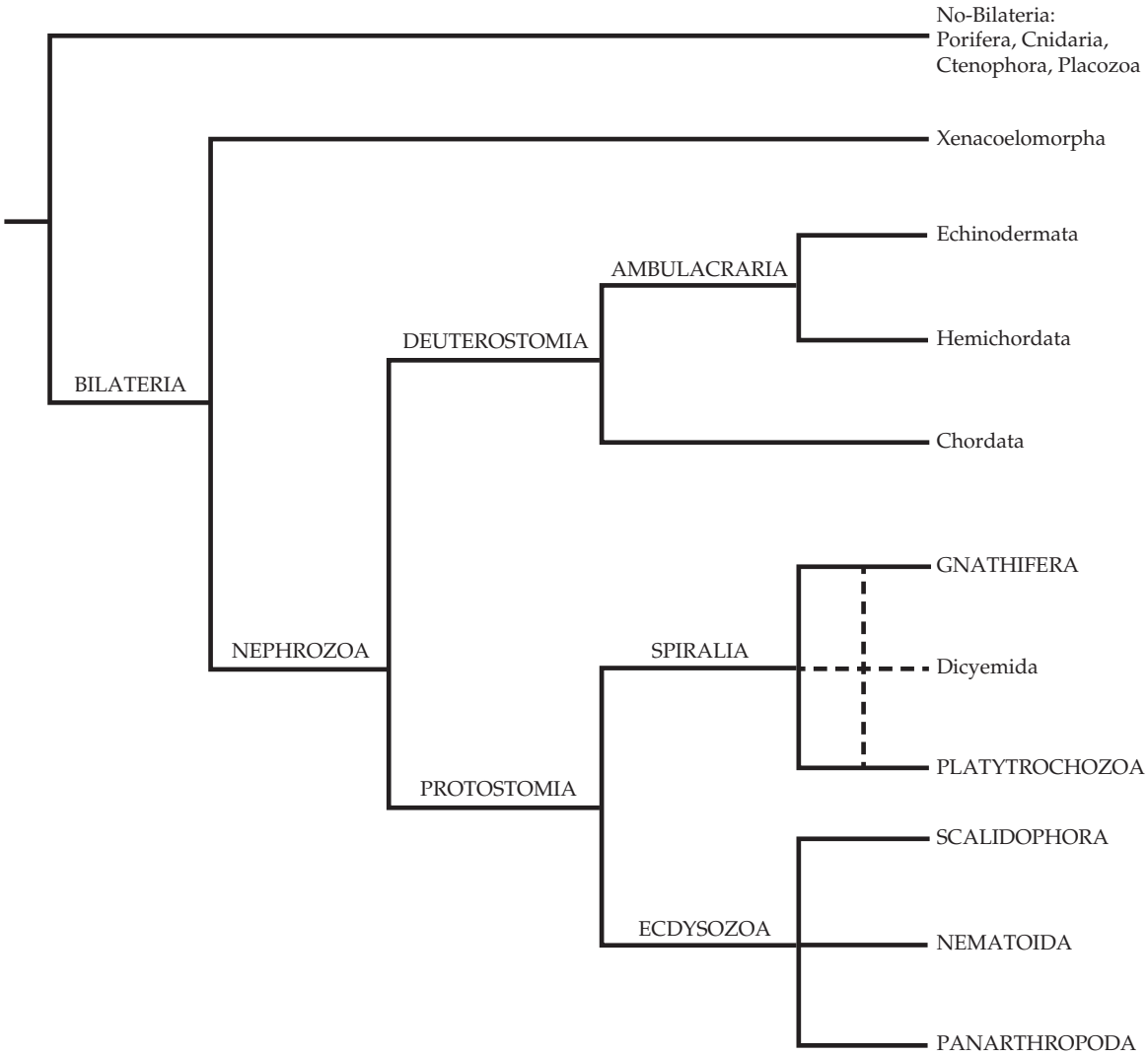

FIGURE 8.1 A phylogenetic tree of the Bilateria showing major clades. Most of the bilaterian clades (indicated in all capital letters) are also defined by morphological apomorphies. Apomorphies of Bilateria include bilateral symmetry, cephalization, three germ layers, and the presence of mesodermally derived organs. Apomorphies of Nephrozoa include the presence of a through gut (complete gut, with an anus), complex organ structures, and the *Hox3* gene. Probable apomorphies of Deuterostomia are pharyngeal gill slits and possibly enterocoelic development and a trimeric condition of coelomic cavities. Probable apomorphies of Protostomia are a circumesophageal brain and ventral nerve cords. An important apomorphy of Ecdysozoa is molting of the cuticle during the life cycle. Other possible apomorphies of Ecdysozoa are a trilayered cuticle, formation of the epicuticle from the tips of epidermal microvilli, lack of locomotory cilia, and a terminal position of the mouth. Spiral cleavage is a likely apomorphy for the Spiralia, although it was apparently secondarily lost in some groups (e.g., Lophophorata). Ambulacraria share a unique excretory heart-kidney system and the probably homologous tornaria/dipleurula larvae.

The clade Gnathifera includes the phyla Chaetognatha, Gnathostomulida, Micrognathozoa, and Rotifera. The clade Platytrochozoa includes the phyla Cycliophora, Entoprocta, Nemertea, Mollusca, Annelida, Phoronida, Bryozoa, and Brachiopoda (the last three comprising the Lophophorata). The clade Nematoida includes the phyla Nematoda and Nematomorpha. The clade Scalidophora includes the phyla Kinorhyncha, Priapula, and Loricifera. The clade Panarthropoda includes the phyla Tardigrada, Onychophora, and Arthropoda.

living phyla. Simply put, the Nephrozoa are bilaterians that evolved large body sizes and the need to develop complex organs for circulation, gas exchange, osmoregulation, excretion, muscular movement, structural support, etc. A through gut (a complete gut, with an anus) is an apomorphy of the Nephrozoa (with a reduction in several clades, most notably Platyhelminthes). Although most have protonephridia or some kind of metanephridium, many small-bodied nephrozoans (e.g., Chaetognatha, Bryozoa) may still rely on diffusion across the body wall. In addition to the three main classes of Hox genes found in all bilaterians (anterior, central, posterior), which have increased in complexity in Nephrozoa; the nephrozoans have also acquired a unique family of *Hox3* genes (not present in Xenacoelomorpha).

Deuterostomes and Protostomes

Within the Nephrozoa are the two great clades Deuterostomia and Protostomia (Figure 8.1). These are legacy

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names that have been around since the nineteenth century, and they are names zoologists are very familiar with. The names were originally based on what was known at the time about early embryonic development, especially the fate of the blastopore. Deuterostomia were those animals in which the blastopore became the adult anus, the mouth thus forming de novo, secondarily, from the bottom of the archenteron. Hence the name: *deutero* = "second," *stoma* = "mouth." In Protostomia (*proto* = "first"), on the other hand, the blastopore gave rise to the mouth, and the anus formed elsewhere. However, we now know that some Protostomia have deuterostomous development (e.g., nematomorphs and priapulans, some brachiopods), and in some Deuterostomia the anus does not originate from the blastopore. In fact, it seems that the blastopore, the mouth, and the anus have a degree of developmental independence. Egg development with radial cleavage was also sometimes used to define the Deuterostomia, but that type of cleavage also occurs in a number of nondeuterostome phyla, so it cannot be an apomorphy of deuterostomes. Enterocoelic coelom formation (see Chapter 4) was also once thought to define the Deuterostomia, with schizocoelic coelom formation being typical of Protostomia; but we now know that schizocoely occurs in some deuterostomes. Thus, as more and more animals are studied, modern phylogenetic research has revealed that these developmental patterns are more varied than originally thought and show inconsistencies with phylogenetic patterns. And further, the new tree of life reveals that three phyla once classified in Deuterostomia are actually nested within the Protostomia. These are the three lophophorate phyla: Phoronida, Bryozoa, and Brachiopoda (the clade Lophophorata; see Chapter 16).

Thus, Deuterostomia includes only 3 phyla: Chordata, Hemichordata, and Echinodermata. When these are compared with the 23 phyla in Protostomia, deuterostomes may seem like an early, spurious, evolutionary experiment, or perhaps even appear to be a "dead-end" lineage, probably originating in the Precambrian. However, 2 of the 3 deuterostome phyla have been hugely successful. With 7,300 living species, Echinodermata is one of the most important animal groups in the sea, and of course the Chordata (with 63,000 species) includes the large land animals—the vertebrates (and, therefore, us).

What morphological characters define the Deuterostomia? There is a strong indication that the ancestral deuterostome had pharyngeal gill slits. These are present in hemichordates and chordates, and in some extinct stem-group echinoderms. Another likely apomorphy is a widely conserved deuterostome-specific cluster of six ordered genes, including four transcription factors expressed during the development of pharyngeal gill slits and the branchial apparatus. Another possible apomorphy of Deuterostomia is enterocoelic development and a trimeric condition of coelomic cavities, at least in the first deuterostomes, although this feature is lacking in the phylum Chordata. It could have been lost in the evolution of chordates (and thus it would be an "underlying apomorphy"), or alternatively it could be a feature only of Ambulacraria—the clade uniting Echinodermata and Hemichordata. The deuterostomes are introduced in Chapter 25 and covered in Chapters 25, 26, and 27.

Protostomia is a monophyletic lineage containing the two large clades, Spiralia and Ecdysozoa. Protostomia is introduced in Chapter 10. Although strongly supported by molecular phylogenetics, Protostomia is tricky to define by any morphological synapomorphies. A ventral nerve cord is probably a good apomorphy, although it is not distinct in the soft-bodied, flattened, platyhelminth and nemertean worms. And in some cigar-shaped animals (e.g., Priapula), "ventral" is defined by the position of the nerve cord, and thus it becomes a circular argument. Similarly, protostomes tend to have a circumesophageal brain (leading to the ventral nerve cords), but deviations from this occur. Protostomes constitute 95% of Earth's known species diversity, and they include 15 phyla in the clade Spiralia and 8 in the clade Ecdysozoa.

Spiralia includes all those bilaterians with spiral cleavage—a highly stereotyped egg cleavage pattern described in detail in Chapter 4. However, Spiralia also includes some phyla without spiral cleavage (e.g., the Lophophorata), suggesting this embryonic patterning has been lost in some cases through evolutionary reversal. Robust morphological apomorphies for Spiralia are not yet known, and the hunt for them is one of the more exciting things going on in biology today. Our tree shows the odd parasitic phylum Dicyemida having three possible origins, because the phylogenetic position of these animals in molecular analyses is still unstable (see Chapter 10). The two relatively well-supported clades Gnathifera (4 phyla) and Platytrochozoa (10 phyla) are discussed in Chapters 11 and 12.

Ecdysozoa is composed of animals that molt their cuticles during their life cycle as a solution for growth. The clade is strongly supported by both molecular and morphological analyses. In addition to ecdysone-based molting, other apomorphies for Ecdysozoa have been proposed, such as a trilayered cuticle, formation of the epicuticle from the tips of epidermal microvilli, lack of locomotory cilia, and a terminal position of the mouth. There are some deviations in these characters among the Ecdysozoa, but they may still prove to be good apomorphies of the first ecdysozoans. A terminal mouth is prevalent in Cambrian fossils assigned to stem-group ecdysozoans, including arthropods and onychophorans, and it is present in scalidophorans and some tardigrades. Segmentation is found in 4 of the 8 ecdysozoan phyla, but it is still uncertain how many times it might have evolved. Relationships within this clade remain in flux, and our tree shows an unresolved trichotomy of three subclades that are largely defined by morphological, not molecular, characters.

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Courtesy of Greg Rouse

CHAPTER 9

Phylum Xenacoelomorpha

Basal Bilaterians

As you read in Chapter 8, the invention of a third (middle) germ layer, the true mesoderm, and evolution of a bilateral body plan opened up vast new avenues for evolutionary expansion among animals. The appearance of this inner body layer led to greater specialization in tissue formation, including highly specialized organ systems and condensed nervous systems (e.g., central nervous systems). In addition to derivatives of ectoderm (skin and nervous system) and endoderm (gut and its derivatives), triploblastic animals have mesodermal derivatives—which include musculature, circulatory systems, excretory systems, and the somatic portions of the gonads. Bilateral symmetry gives these animals two axes of polarity (anteroposterior and dorsoventral) along a single plane that divides the body into two symmetrically opposed parts—the left and right sides. The evolution of bilaterality also resulted in cephalization: the concentration of sensory and feeding structures at the anterior end, thus forming a "head." And, except in Xenacoelomorpha, bilaterians further evolved a complete gut (or through gut), with a mouth and an anus, and excretory organs in the form of protonephridia and metanephridia (i.e., the clade Nephrozoa). The origin of the Bilateria was probably in the Ediacaran, around 630–600 million years ago, although some dated phylogenies have estimated the origin was even earlier.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

The Basal Bilaterian

Phylogenetic research strongly suggests that the Xenacoelomorpha split early from the remaining bilaterian lineage. All members of this phylum share a number of characteristics, including a soft flattened body, mesodermally derived musculature, absence of a coelom or excretory or circulatory systems, a completely ciliated epidermis, and

BOX 9A Characteristics of the Phylum Xenacoelomorpha

1. Soft-bodied, dorsoventrally flattened, acoelomate; almost exclusively marine worms
2. Epidermis with unique pulsatile bodies, found in no other metazoan phylum
3. Cilia of epidermis with distinctive arrangement of microfilaments: the standard 9+2 arrangement extending for most of the shaft but microfilament doublets 4–6 failing to reach the end of the cilium (the "xenacoelomorph cilia")
4. Mouth, when present, ventral; with an incomplete gut (i.e., lacking an anus)
5. Largely lacking discrete organs (e.g., no discrete circulatory system, protonephridia or nephridia, or organized gonads)
6. Cerebral ganglion with a small neuropil; with anterior statocyst and a diffuse intraepithelial nervous system
7. With a frontal organ (Acoelomorpha) or frontal pore (Xenoturbellida), possibly homologous
8. With circular and longitudinal muscles
9. Hox and ParaHox genes present (but fewer in number than in other metazoans)
10. With direct development (no larval forms)

direct development (no larval stage). These features resemble a hypothetical creature known as the **Urbilateria**, the putative first bilaterian or triploblastic animal with anterior–posterior and dorsal–ventral axes. These soft-bodied worms also have a centralized nervous system, with multiple parallel longitudinal nerve cords, although the "brain" is little developed and the main sensory structure appears to be a statocyst. Importantly, research suggests that their mouth—the single gut opening—does not derive from the blastopore (i.e., they are deuterostomous in their development). Thus, the origin of the Bilateria may have been accompanied by an embryological shift in the origin of the mouth from the blastopore (as seen in Cnidaria and Ctenophora) to elsewhere.

Phylum Xenacoelomorpha

The phylum Xenacoelomorpha (Box 9A) comprises three clades of acoelomate worms (Acoela, Nemertodermatida, and Xenoturbellida) that are sometimes recognized as two or three separate phyla. Evidence from both molecular and morphological data suggests that Acoela and Nemertodermatida are sister groups (the Acoelomorpha), and these are a sister group to Xenoturbellida; thus we include them here in a single phylum (see Figure 9.26). In addition to molecular support, xenacoelomorphs also have a suite of unique features that define them among the Bilateria: they lack a through gut (also seen in the phylum Platyhelminthes, but presumably secondarily derived), have unique pulsatile bodies, have ciliated epidermal cells with a distinctive arrangement of microfilaments, and possess a frontal organ (Acoelomorpha) or frontal pore (Xenoturbellida). Xenacoelomorpha currently contains about 400 species, 6 in the subphylum Xenoturbellida (all in the genus *Xenoturbella*) and the rest in the subphylum Acoelomorpha (mostly in the class Acoela). No fossils have been identified. All described species are small, flattened, unsegmented worms without an anus or discrete excretory organs. Almost all are microscopic, but a few reach several centimeters in length. All but a few are free-living; at least two species are endosymbionts in holothuroids. Almost all are marine, although two species of Acoela inhabit fresh waters.

The xenacoelomorph clades have had long taxonomic journeys. Initially Nemertodermatida and Acoela were viewed as the most primitive living Platyhelminthes, due to their simple anatomy. As ultrastructural work revealed increasing complexity, opinion shifted, and from the 1960s to the turn of the century these worms were widely regarded not as primitive, but as secondarily reduced platyhelminths. However, as multigene phylogenetic analyses began to explore these small worms, it became apparent that they were actually very early bilaterians, probably diverging even before the protostome-deuterostome split. All three groups also have unique epidermal bodies that represent degenerating ciliated cells that are resorbed into the body and called **pulsatile bodies** or "restitution cells." In Acoela, the cilia are retained in vacuoles prior to digestion, whereas in nemertodermatids the cilia appear to be lost before resorption begins. A type of pulsatile body also occurs in the xenoturbellids (which may or may not be homologous with those of Acoelomorpha). Pulsatile bodies are unknown from any other metazoan phylum. All Xenacoelomorpha lack discrete excretory systems, the presence of which unites all other Bilateria as the clade Nephrozoa, and their cerebral ganglion has a very small neuropil, although it can be considered a true brain. Furthermore, xenacoelomorphs share a unique pattern of neurotransmitter activity, body wall musculature, and mode of embryonic development.

A close relationship between the acoel and nemertodermatid worms is supported by their unique ciliary rootlet system, frontal organ, perhaps their cleavage pattern (i.e., the horizontal orientation of the second, asymmetric cleavage plane), and several other features. The musculature of acoels and nemertodermatids is also strikingly similar, yet different in some key aspects; acoels have a grid of orthogonal musculature with mainly ventral diagonal musculature and, in some species, a muscular pharynx. More derived acoels have more complex layers of diagonal muscles. Nemertodermatids

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have an orthogonal grid and well-developed diagonal muscles throughout the body, and little evidence of a muscular pharynx.

Although *Xenoturbella bocki* was initially considered to be a free-living flatworm, its unusual anatomy quickly came to distinguish it from platyhelminths, as well as from the Acoelomorpha. Phylogenetic (and even some morphological) studies initially linked *Xenoturbella* to deuterostomes. Sequences of Hox genes in *X. bocki* also suggested it could be a basal deuterostome with a reduced Hox gene complement, and lack of typical deuterostome characteristics suggested that *Xenoturbella* might belong at the very base of the deuterostome tree. Some earlier phylogenetic analyses suggested that *Xenoturbella* might be closely tied to the clade known as Ambulacraria (Echinodermata and Hemichordata). However, no developmental evidence has been found of structures common to other Ambulacraria, such as gill slits, endostyle, and enterocoelic coelom formation.

By 2009, large-scale molecular phylogenetic studies had begun suggesting *Xenoturbella* is the sister group of Acoelomorpha, at the base of the Bilateria as the sister group to Nephrozoa. The anatomical data seemed to agree with this linking, and it was eventually suggested that together they warranted phylum status as Xenacoelomorpha. Acoels have only three Hox genes (one each of the anterior, central, and posterior groups). Nemertodermatids have only two (a central and a posterior group). *Xenoturbella* has one anterior, two (or three) central, and one posterior gene. Platyhelminths, on the other hand, as most nephrozoans, have a nearly complete Hox cluster. We discuss each of the three curious worm groups in the class Acoela, class Nemertodermatida, and subphylum Xenoturbellida sections below. There is no fossil record attributed to any xenacoelomorphs.

CLASSIFICATION OF PHYLUM XENACOELOMORPHA

Generally small, flattened or semicylindrical, acoelomate marine worms with anterior statocyst; diffuse intraepithelial nervous system, an intraepithelial or basiepidermal nerve net (sometimes condensed into basiepidermal neurite bundles with a condensed brain and submuscular cords); midventral mouth and incomplete gut (i.e., lacking an anus); unique pulsatile bodies (unknown from any other Bilateria). Largely lacking discrete organs (e.g., without a discrete excretory or circulatory system, or organized gonads). Cilia of epidermal cells with distinctive arrangement of microfilaments wherein the standard 9+2 arrangement extends for most of the ciliary shaft, but toward the end, microfilament doublets 4 through 7 end, leaving doublets 1–3 and 8–9, which continue to the end of the cilium. These **xenacoelomorph cilia** are not known in any other animal phylum (although similar cilia have been described from the pharynx of some enteropneust hemichordates). With both circular and longitudinal muscles. With direct development and no distinct larval forms. Two subphyla, Acoelomorpha and Xenoturbellida.

SUBPHYLUM ACOELOMORPHA With small cerebral ganglia with a neuropil, a unique pattern of neurotransmitter activity, and unique body wall musculature; with a distinctive mode of embryonic development. Acoelomorphs lack a well-developed basement membrane (basal lamina), but they do have small islands of extracellular material between the epidermal cells and underlying muscle that might be homologous with the basement membrane of other bilaterians. Hox and ParaHox genes are present in both classes, although these are not strictly similar.

CLASS ACOELA About 400 species. Gut a digestive syncytium, lacking a permanent digestive cavity or with a small transient gut lumen; with unique anterior statocyst containing one statolith; parenchyma may contain chordoid vacuoles; biflagellate sperm, each flagellum with axonemes incorporated into the sperm cell; endolecithal ova; without epithelial basal lamina. Small (1–5 mm) worms, common in marine sediments (a few in fresh water); some are planktonic or symbiotic. (e.g., *Amphiscolops, Antigonaria, Conaperta, Convoluta, Convolutriloba, Daku, Diopisthoporus, Eumecynostomum, Haplogonaria, Hofstenia, Isodiametra, Myopea, Oligochaerus* [with freshwater species], *Paratomella, Polychoerus, Praesagittifera, Proporus, Solenofilomorpha, Symsagittifera, Thalassoanaperus, Waminoa*)

CLASS NEMERTODERMATIDA About 20 species of interstitial or endosymbiotic marine worms possessing a ciliated, glandular epidermis and an anterior statocyst containing 1 to 4 statoliths; parenchyma without chordoid vacuoles; mouth may be present or absent; with small transient or permanent gut cavity; a proboscis with extensible filaments is present in some species; with true epithelium and gland cells; uniflagellate sperm; with endolecithal ova; with limited basal lamina beneath the epidermis. One genus (*Meara*) contains species that are symbionts in sea cucumbers. (e.g., *Ascoparia, Flagellophora, Meara, Nemertinoides, Nemertoderma, Sterreria*)

SUBPHYLUM XENOTURBELLIDA Six species, all in the genus *Xenoturbella*; fleshy pink worms, a few millimeters to over 20 cm in length. Xenoturbellids have a humplike structure in the anterior third of the body but lack other structural organs (other than a statocyst) and possess a diffuse nervous system. A thick basement membrane (the "subepidermal membrane complex") is present beneath the epidermis. An anterior frontal pore, which is continuous with a ventral glandular network, may be homologous with the frontal organ of acoelomorphs. These worms live in holes on sandy coastlines or deeper offshore muds and many appear to be specialized to eat bivalves.

Subphylum Acoelomorpha

These soft, flattened or subcylindrical, acoelomate worms have the body completely covered by locomotory cilia on multiciliated epidermal cells. The cilia form a unique network of interconnecting rootlets, and the epidermal cells have a unique mode of withdrawing and being resorbed. The space between the gut and body is filled with parenchymal cells. The digestive system (and digestive cavity) may be permanent or transient but always lack an anus. There is a weakly ganglionated brain and well-developed subepidermal or intraepidermal nerve plexus. There is an anterior statocyst and frontal organ opening at the anterior tip, some with simple ocelli. All have direct development, and there are no discrete or organized gonads. About 420 species have been described.

Class Acoela

Acoels are mostly minute, sediment- or surface-dwelling worms in marine or brackish water. They range in size from less than a millimeter to about 4–5 cm in length. Those inhabiting interstitial habitats are generally long and slender, whereas those inhabiting surfaces tend to be more disc shaped, broad, and flat. Swimming species are cylindrical with tapered ends or occasionally enrolled sides. Epiphytic species are usually cone shaped with ventrally enrolled sides that may give the appearance of trailing "fins." A few species of acoels have also been found in the guts of echinoderms, in fresh water, and at hydrothermal vent sites (Figure 9.1A–H).

Acoels lack a structural gut. Instead, they possess a multinucleated mass (a syncytium) that phagocytizes ingested food particles (Figure 9.2). Larger species often supplement their nutritional requirements with endosymbiotic algal partnerships, which can contribute to the bright coloration seen in many (Figure 9.3A). Acoels living in the guts of other animals often have symbiotic bacteria inhabiting their epidermis.

Acoels possess both circular and longitudinal muscles. Their nervous system consists of an array of paired longitudinal nerve cords with a concentration of anterior sensory cells and a cerebral commissure (the brain) (Figure 9.4). The anterior statocyst with a single statolith is distinctive in acoels and (along with simple, light-sensitive eyes in some species) appears to assist in maintaining the animal's orientation (Figure 9.1). Acoels lack sclerotized structures other than those associated with genitalia, although some species manufacture crystalline spicules in the parenchyma. They also possess aberrant, complex, biflagellate sperm that vary in the structure of the usual 9+2 arrangement of microtubules possessed by many metazoans. They have direct development and exhibit no distinct larval forms.

FIGURE 9.1 Acoela. (A) *Diopisthoporus lofolitis* (Diopisthoporidae). st = statocyst, e = egg, ph = pharynx simplex. (B) *Paratomella rubra* (Paratomellidae). (C) Color variation in 33 specimens of *Hofstenia miamia* (Hofsteniidae) from the Caribbean. (D) *Philactinoposthia novaecaledoniae*, living specimen (Dakuidae). (E) *Waminoa* sp. (Convolutidae) on bubble coral (*Plerogyra sinuosa*). (F) *Daku riegeri* (Dakuidae). (G) *Eumecynostomum evelinae* (Mecynostomidae). (H) *Paramecynostomum diversicolor* (Mecynostomidae).

Acoels were first described at the turn of the nineteenth century from northeast Atlantic coastlines. These and other early descriptions placed them among the free-living Platyhelminthes and distinguished major subtaxa on the basis of the female reproductive system. Later revisions in the middle of the twentieth century established over 20 families, and most of the nearly 400 described species were based primarily on details of male copulatory structures. Similarities in internal anatomy, epidermal ciliation, and the appearance of epidermal "pulsatile bodies" led to combining Acoela with another group, Nemertodermatida, as the Acoelomorpha.

The lack of hard anatomical features in these worms led workers to studies of microscopic ultrastructure using scanning and transmission electron microscopy, including investigations of muscle fiber orientation and structure (which distinguished several major lineages), sperm morphology, and spermatogenesis (which identified biflagellate sperm and unusual patterns of microtubules within sperm acrosomes), as well as neuroanatomy. Studies increased in number near the end of the twentieth century as the diversity of habitats investigated increased, including anoxic sulfide sands. Further systematic refinements within major acoel clades (notably the polyphyletic family Convolutidae), and developmental analyses, corroborated genetic results that place acoels outside the Platyhelminthes. In addition, 18S and 28S rRNA, mitochondrial DNA, and myosin heavy chain type II nucleotide sequences have all placed acoels outside the Platyhelminthes, as do all recent genomic and transcriptomic analyses. Much taxonomic revision is still under way, and about 9 to 20 families are currently recognized, depending on whose schema is followed.

Both molecular phylogenetics and EvoDevo research provide evidence that acoels likely split off near the base of the bilaterian tree. For example, the pattern of expression of *ClEvx* (a gene responsible for sensory specificity brain neurons) anterior and posterior to the statocyst in hatchling acoels is more similar to that found in cnidarians than it is to more derived bilaterians. Other studies indicate that *brachyury* (*bra*) and *goosecoid* (*gsc*), genes associated with the formation of the acoel mouth, are also expressed during mouth development in protostomes as well as deuterostomes, suggesting that acoel and bilaterian mouths are homologous. Studies of

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(A)

(B)

(C)

A–C courtesy of M. Hooge

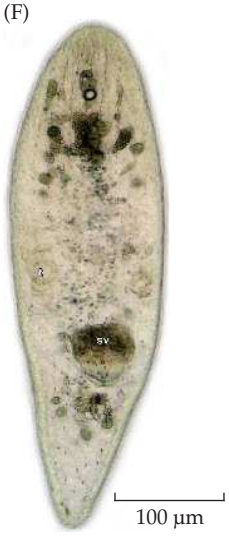
(D)

Courtesy of U. Jondelius

(E)

Courtesy of R. Groeneveld

(F)



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F,G courtesy of M. Hooge

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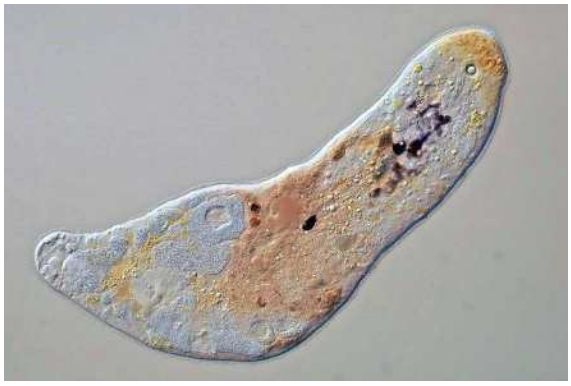

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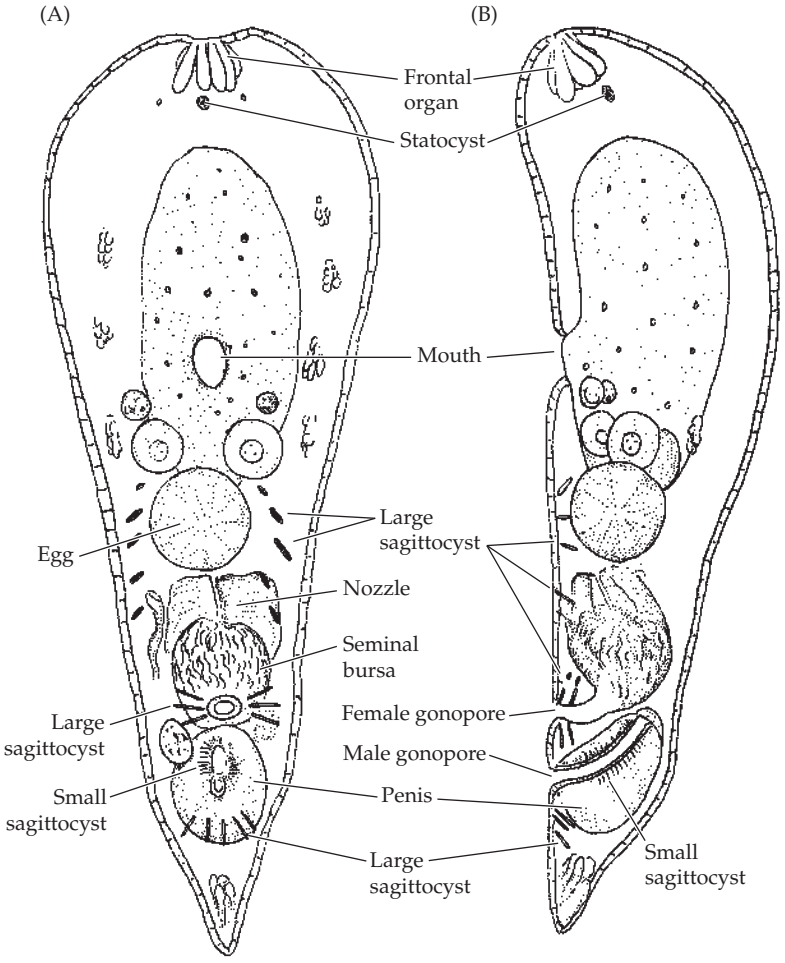
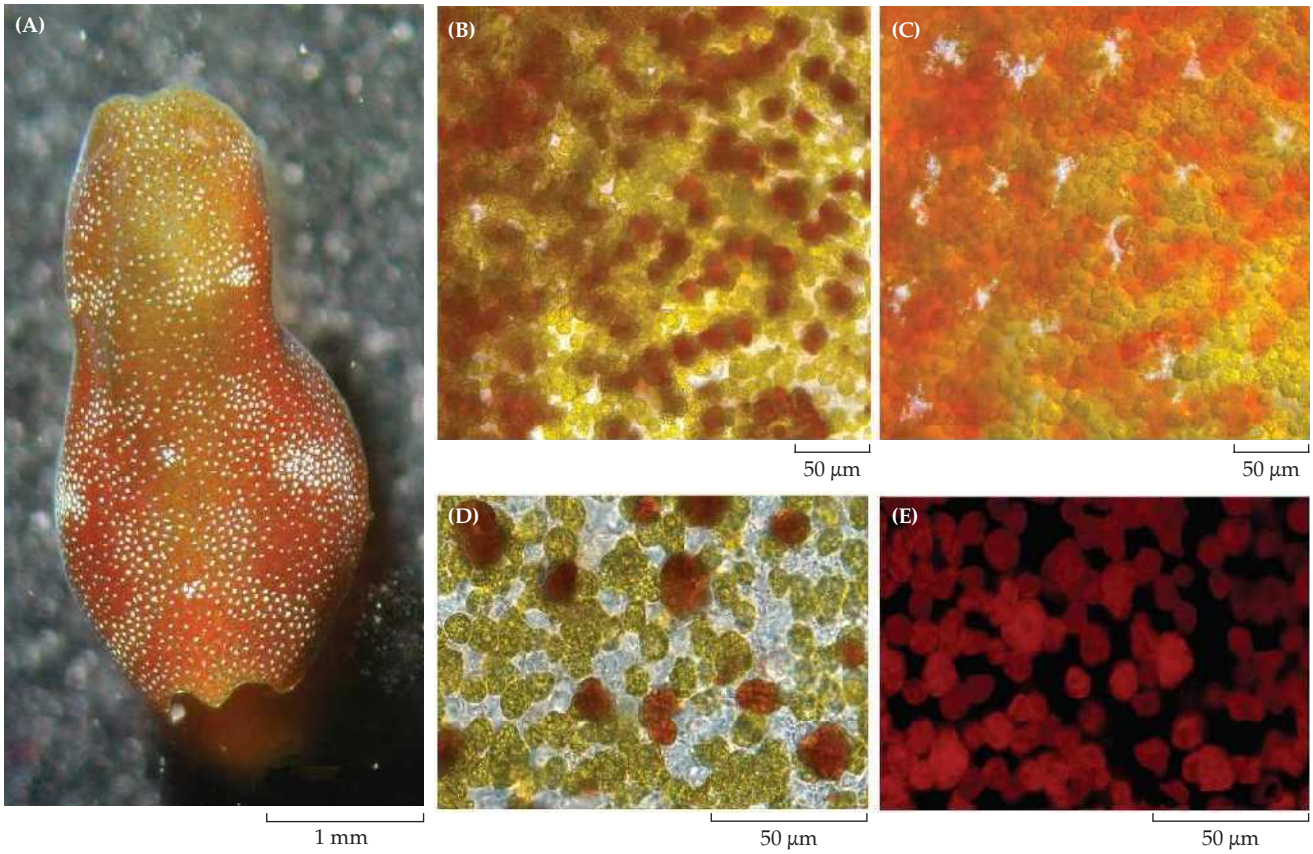


FIGURE 9.2 The anatomy of *Praesagittifera shikoki* (Acoela). (A) Dorsal view. (B) Lateral view. (After T. Yamasu. 1991. *Hydrobiologia* 227: 273–282. https://link.springer.com/article/10.1007/BF00027612)



A–E from E. Hirose and M. Hirose. 2007. *Zool Sci* 24: 1241–1246

FIGURE 9.3 Bright coloration in *Convolutriloba longifissura* (Acoela). (A) Whole body (dorsal view). (B–E) Closeup views of the dorsal surface showing endosymbiotic algae: (B,D) transmission light, (C) incident light, (E) epifluorescent light (blue excitation). Note that (B,C) and (D,E) are paired images.

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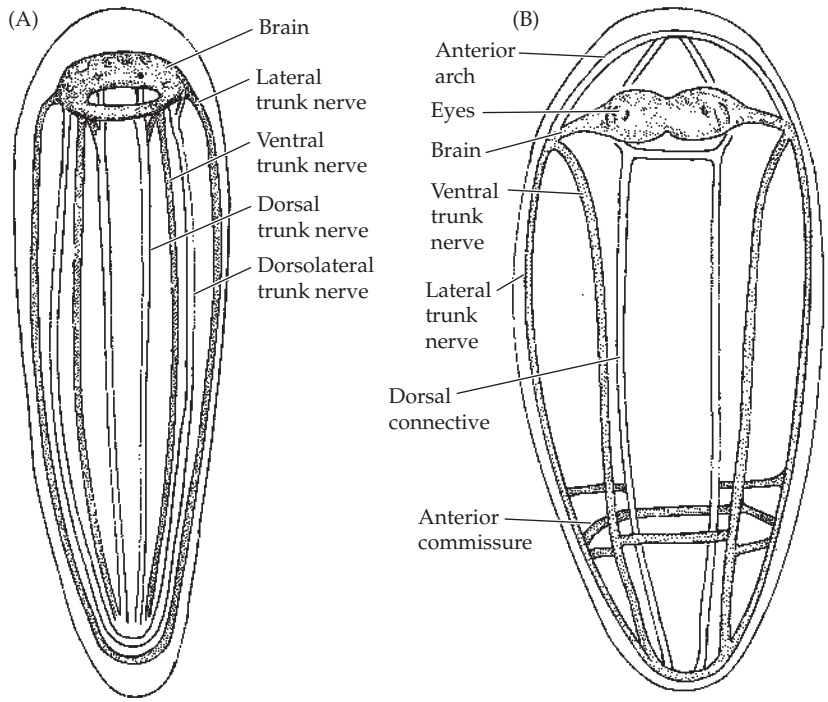

FIGURE 9.4 Comparison of central nervous systems. (A) An acoel (*Actinoposthia beklemischevi*). (B) A free-living flatworm (Platyhelminthes: *Gieysztoria expedita*). (After E. A. Kotikova and O. I. Raikova. 2008. *Zhurnal Evolyutsionnoi Biokhimii i Fiziologi* 44: 83–93. https://link.springer.com/article/10.1134%252FS002209300801012X)

neural development and structure in the acoel *Symsagittifera roscoffensis* show that genes associated with brain-like structures are present, suggesting that such genetic machinery was in place in the urbilaterian ancestor (if indeed acoels reflect such an ancestor). The overall "primitiveness" of Acoela is also seen in their lack of a clearly differentiated gut or excretory system, unencapsulated gonads, absence of ciliary or rhabdomeric eyes, lack of a well-developed basal lamina under the epidermis, and absence of a larval stage.

The Acoel Body Plan

Body Wall and External Appearance

Most acoels are tiny, just a few millimeters long. The smallest species tend to be interstitial, feeding on bacteria and organic particulates available on the surfaces or between the spaces of the sediments they inhabit. Infaunal species tend to be more elongate (Figure 9.1A,B,F,H). Larger species usually inhabit the surfaces of rocks, large algae, or cnidarians (Figure 9.1C–E,G). These faster-moving species are often predatory, gliding quickly on their ciliated surfaces and capturing prey with a raptorial "hood" that consists of lateral extensions of the body.

Large-bodied species, reaching lengths of 4–5 cm, in some families (e.g., Convolutidae) have anterior ocelli (Figure 9.1G), whereas small-bodied species tend to lack these. Larger-bodied species also often have photosynthetic endosymbionts under their epidermis (Figures 9.1E and 9.3). The association with endosymbiotic algae probably evolved more than once, and both zoochlorellae and zooxanthellae have been identified among the various species. Algae are usually obtained during feeding by juvenile worms but in some species can also be transmitted within oocytes by parents to their offspring (vertical transmission). In *Heterochaerus langerhansi*, the dinoflagellate *Amphidinium carterae* resides below the epidermis and has been shown, using radioactively labeled carbon and nitrogen, to receive these substances from its host in the forms of CO_2 from respiration and excreted ammonia from protein metabolism. The rate of transfer is light dependent.

It has been suggested that acoel body pigmentation may have several functions. One might be to provide protection from UV radiation for their symbiotic photosynthetic protists. A second might be to provide cryptic coloration, either to make acoels inconspicuous to visual predators, or possibly to make them less visible to their prey. *Hofstenia* species, also known as "panther worms," are highly polymorphic in dorsal pigmentation, with diverse patterns of dappling and striping of brown, yellow, and white colorations (Figure 9.1C).

The acoel body is completely covered with cilia, which may or may not also line the mouth and entrances to reproductive structures. The epithelium lacks a well-defined basal lamina (extracellular matrix, or ECM). Early researchers identified **pulsatile bodies** embedded within the epidermis of acoels (and nemertodermatids), which later proved to be clumps of ciliated cells in the process of being resorbed and replaced by the epidermis.

Mucus-producing **frontal organs**, which superficially resemble those of flatworms but are probably not homologous in structure, occur in most families. These are gland complexes that open at the anterior end of the worm. The ciliated epidermis of acoels also bears **rhabdoid glands** distributed over the body. The **rhabdoids** themselves are composed of mucopolysaccharides and are chemically as well as structurally distinct from the rhabdites of free-living flatworms, although their role in producing mucus to assist ciliary gliding appears to be similar. Some Acoela also have **sagittocysts** (Figure 9.5), complex needle-shaped secretory products (5–50 μm long) that are ejected with force in prey capture or for defense and probably also to assist in sperm transfer during copulation (perhaps

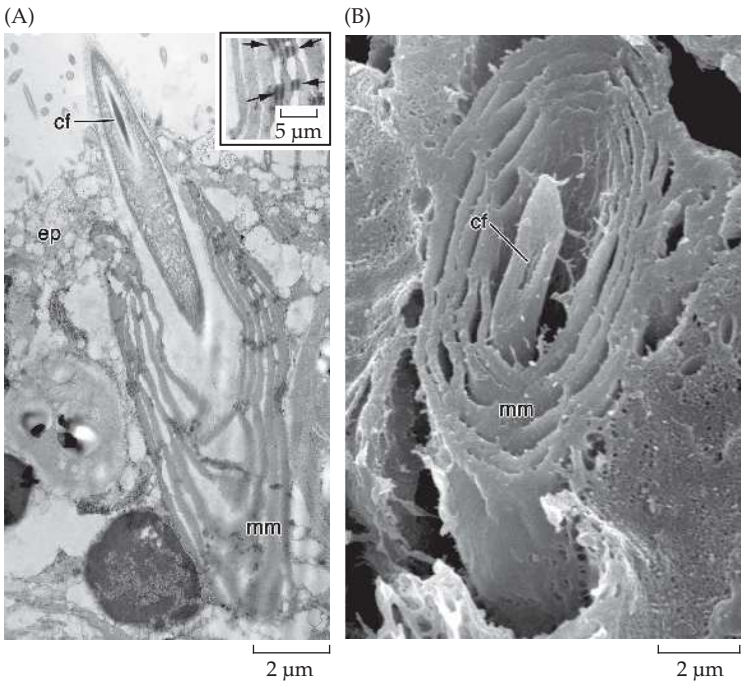

FIGURE 9.5 TEM images of *Convolutriloba longifissura* (Acoela) sagittocysts. (A) A sagittocyst (cf = central filament of sagittocyst) during extrusion from the muscle mantle (mm) and penetration of the epidermis (ep). Inset shows higher magnification of the muscle mantle; arrows indicate the location of desmosomes linking the mantle layers. (B) Close-up of the cut surface of a sagittocyst within the muscle mantle.

by perforating the partner's epidermis). Each sagittocyst arises from a **sagittocyte**, which is surrounded by tightly spiraled muscle filaments that expel the sagittocyst upon contraction (Figure 9.6).

The position of the mouth in acoels is highly variable. In some families, the mouth opens at the posterior end of the animal and leads to a distinct pharynx (Figure 9.1A). Other families have anteroterminal mouths, although most acoel mouths open midventrally (Figures 9.2 and 9.7B). Both a circulatory system and an excretory system, even in the form of protonephridia, are lacking in the Acoela. Male and female reproductive organs are visible through the body wall of smaller acoels (Figure 9.1A,F,H). In larger species they may protrude from the body surface (Figures 9.7D and 9.12B).

Body Musculature, Support, and Movement

The mesodermally derived musculature of acoels provides the primary means of support, whereas the body cilia (assisted by body muscles) provide for their gliding movement. The shape of the cilia is distinctive, having a marked shelf at the tip where doublets 4–7 terminate. The rootlet system that connects the cilia is also unique and plays a role in acoel systematics. Two lateral rootlets project from each cilium and connect to the tips of the adjacent cilia. From a caudal rootlet, two bundles of fibers project to join the kneelike bend of those same adjacent rootlets. Epidermal cilia of acoels beat in a coordinated fashion to create metachronal waves that move from anterior to posterior. The parenchyma between the epidermis and gut sometimes contains chordoid vacuoles (or chordoid cells) that are insunk bodies of epidermal and gland cells.

Abundant dorsoventral muscles serve to flatten the body, and muscles in the body wall generate bending, shortening, and lengthening movements (Figures 9.7 and 9.8). The body wall musculature includes circular, diagonal, longitudinal, crossover, spiral, and even U-shaped muscles. Species lacking a pharynx appear to have specialized, complicated ventral musculature to compensate for the lack of a muscular food-moving structure, and this allows body movements to force food through the mouth.

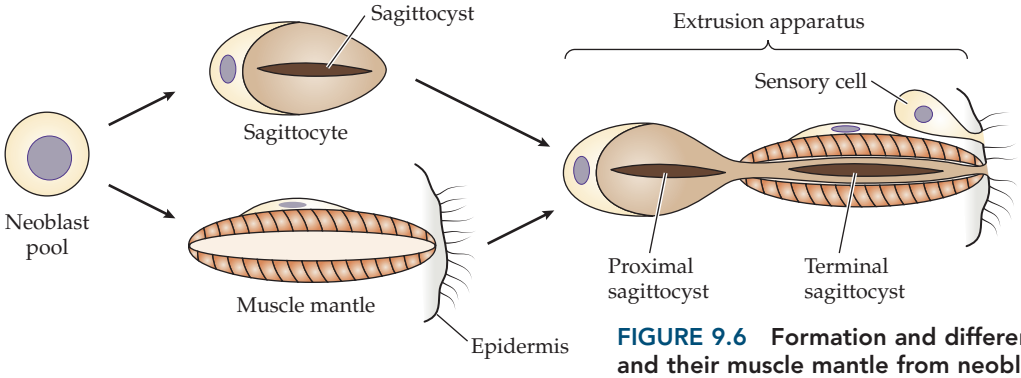

FIGURE 9.6 Formation and differentiation of sagittocytes and their muscle mantle from neoblast cells in Acoela. See text for description.

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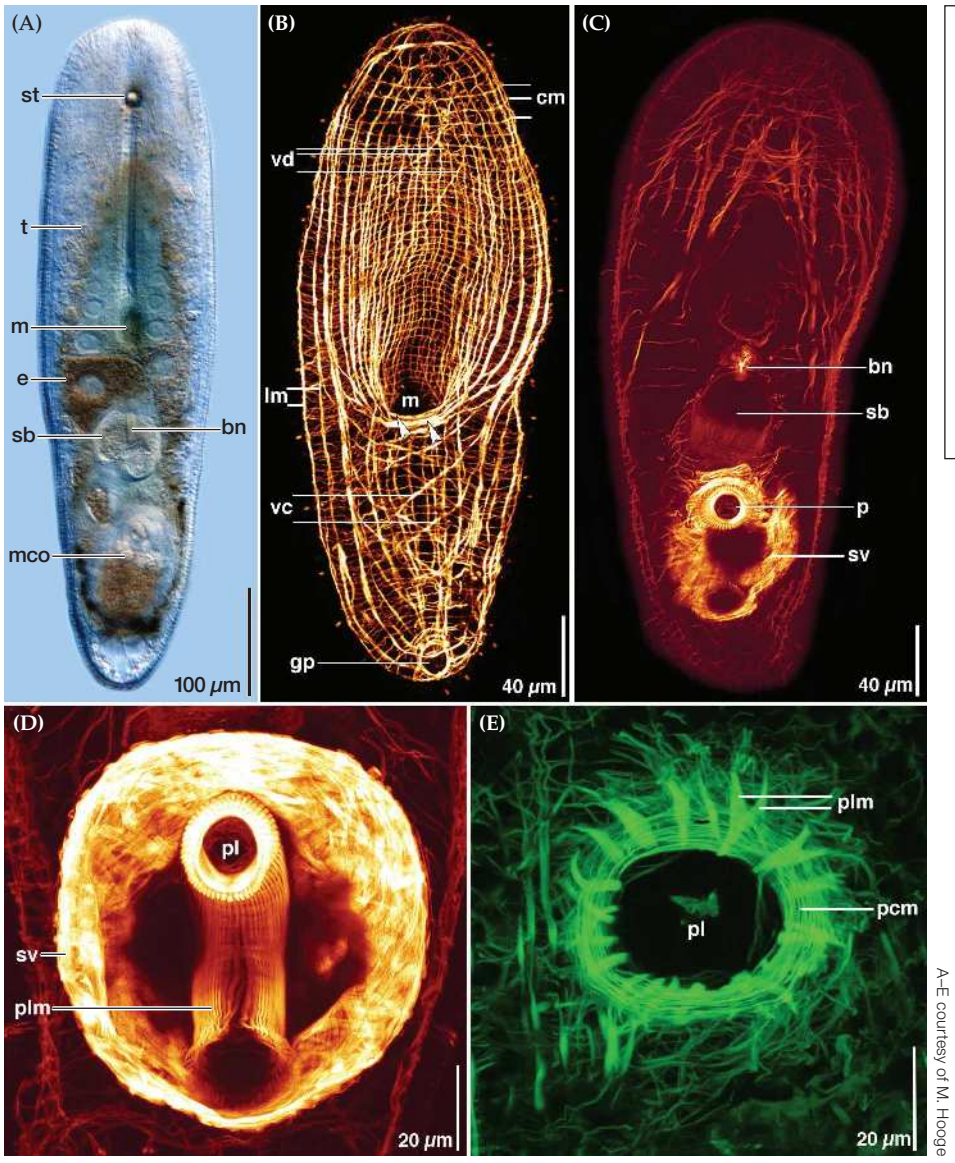

bn = bursal nozzle
cm = circular muscle of body wall
e = egg
gp = gonopore
lm = longitudinal muscle of body wall
m = mouth
mco = male copulatory organ
p = penis
pcm = circular muscle of penis
pl = penis lumen
plm = longitudinal muscle of penis
sb = seminal bursa
st = statocyst
sv = seminal vesicle
t = testes
vc = ventral crossover muscle
vd = ventral diagonal muscle

FIGURE 9.7 Musculature of acoels. (A) Whole mount of living specimen of *Isodiametra earnhardti*. (B) Ventral body-wall musculature of *Haplogonaria amarilla*. (C) Parenchymal musculature of *Isodiametra divae*, showing portions of copulatory organs. (D) Male copulatory organ of *I. divae*, showing musculature of seminal vesicle and invaginated penis. (E) Penis musculature of *Convoluta henseni*. Projections of musculature in whole-mount specimens of acoels stained with Alexa-488-labeled phalloidin and viewed using CLSM. Phalloidin is a naturally occurring toxin in the death cap mushroom (*Amanita phalloides*). Its toxicity is due to its ability to stabilize actin filaments within cells, and this attribute has led to its wide use (fluorescently labeled) in research to visualize filamentous actin, such as muscle fibers. CLSM = confocal laser scanning microscopy.

Nutrition, Excretion, and Gas Exchange

As juveniles, most acoels appear to feed on protists, including unicellular algae such as diatoms. Smaller species may continue this diet throughout their lives, whereas larger species (e.g., *Convoluta convoluta*) are often predaceous, hunting minute crustaceans but also feeding on other worms and larval molluscs. Smaller protists are captured as acoels glide over them with the syncytial gut extruded through the mouth such that it engulfs food with "ameboid"-like action. Larger prey are grasped with the anterior margin of the body and entrapped with mucus before being pressed toward the mouth. Swimming prey may also be rapidly captured and ingested, whereas dead material seems to be actively avoided.

Some acoels possess a pharynx, in some cases known as a **pharynx simplex** (Figure 9.1A), and this structure is variable among the families. In some species the pharynx is a flexible, tube-shaped structure that can be everted from the mouth. In species where no distinct pharynx exists, muscle fibers encircle the mouth to form a sphincter.

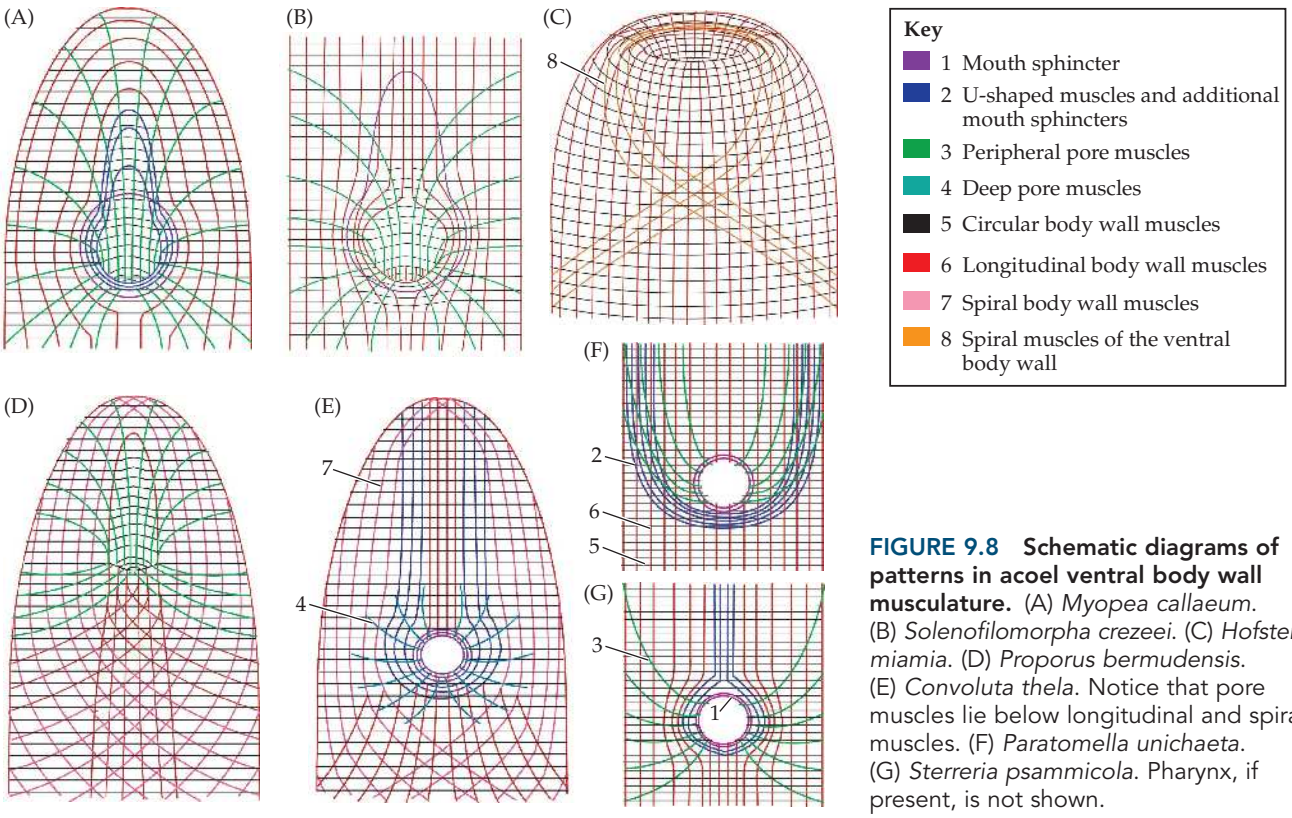

FIGURE 9.8 Schematic diagrams of patterns in acoel ventral body wall musculature. (A) *Myopea callaeum*. (B) *Solenofilomorpha crezeei*. (C) *Hofstenia miamia*. (D) *Proporus bermudensis*. (E) *Convoluta thela*. Notice that pore muscles lie below longitudinal and spiral muscles. (F) *Paratomella unichaeta*. (G) *Sterreria psammicola*. Pharynx, if present, is not shown.

Ingested prey is enclosed within vacuoles that drift within the digestive syncytium, and food is completely absorbed within 18 to 24 hours. A few species, when feeding, develop a small transient gut lumen that is lined with a double layer of cells. The exoskeletons of hard-bodied prey such as crustaceans are voided through the mouth. Fat globules and occasional glycogen vacuoles stored within cells appear to be the primary forms of food reserve. A number of acoel species associate with corals (including *Waminoa* [Figure 9.1E] and several species of *Convolutriloba* [Figure 9.3]). These associations appear to primarily benefit the acoels, which likely feed on mucus produced by these cnidarians. The small size of acoels is sufficient to allow them to eliminate waste nitrogen and carbon dioxide, as well as obtain oxygen from the surrounding water, without a need for specific excretory or circulatory systems.

Nervous Systems and Sense Organs

The central nervous system of acoels usually includes an anteriorly located cluster of large commissures and a few cell bodies that form a paired ganglion system with a minute neuropil (which is quite rudimentary compared with those of other bilaterians). Arising from this are three to five pairs of longitudinal nerve cords connected by an irregular network of transverse fibers (Figure 9.9). Typically there are single or paired dorsal nerve cords and paired lateral and ventral cords. Peripheral neurons connect to epidermal sensory cells and to anterior light-sensitive cells that serve as simple eyes. There is no indication that the eyes have ciliary or rhabdomeric elements, and they are probably simple pigment cells with refractive inclusions and one to several nerve cells to relay the stimulus. This organization contrasts markedly with that of platyhelminths, where the brain consists of a comparatively dense ganglionic mass, the nervous system is primarily developed ventrally, and the nerve cords form an orthogonal nervous system composed of eight orthogons largely developed laterally and ventrally (Figure 9.4). It has been suggested that the bilobed brain of some acoels evolved independently from those found in spiralians and that it may be homologous with the ring-commissural brain seen in nemertodermatids.

The acoel statocyst is a fluid-filled, proteinaceous spherical capsule, 10–30 μm in diameter, surrounding a single retractile statolith (Figure 9.1). The statolith appears to be a single spherical cell. The capsule enclosing the statolith comprises two unciliated cells. Behavioral observations indicate that acoels are capable of precise geotactic orientation, suggesting that movements of the statolith within the statocyst are detectable by the animal. Three pairs of muscle fibers insert into the membrane of the statocyst, evidently assisting in maintaining its position. While the cerebral commissure is closely associated with the statocyst, specific innervation of the structure is difficult to clearly identify, although a small nerve cushion created by two nerve bundles inserting on the capsule, and a cell body located at the ventral

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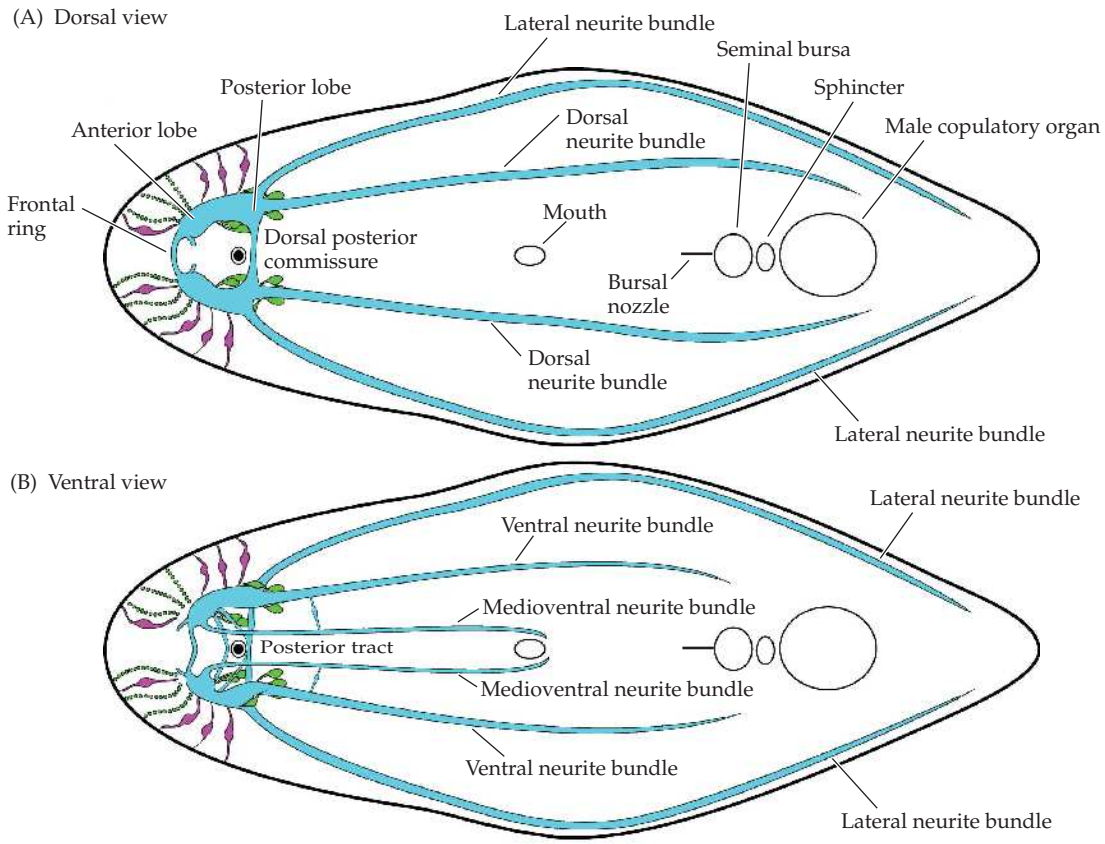

FIGURE 9.9 Diagram of the nervous system of *Isodiametra pulchra* (Acoela) revealed using nervous-tissue-specific staining. (Green and magenta colors denote separate types of neural tissue in the bilobed acoel brain; cyan color shows the central nervous system.)

pole, may be responsible for detecting deformation of statocyst fluid. Positional information might also be conveyed by the stretching of muscle fibers surrounding the statocyst. While statocysts appear in other metazoans, including cnidarians, ctenophores, platyhelminths, annelids, and others, statolith movements within the statocyst in these taxa are generally detected by cilia along the internal surface of the statocyst. The lack of these modifications within the Acoela appears to be unique. Acoels (as well as nemertodermatids and xenoturbellids) also have a **frontal organ**, or frontal gland complex, the function of which is not entirely clear. Some acoels have photoreceptive ocelli, the nature of which is still poorly understood. One clade of acoels (the "convolutimorphs") have the unique extrusomes called sagittocysts (Figure 9.6), somewhat like nematocysts of cnidarians and rhabdites of flatworms.

Reproduction and Development

Acoels are all hermaphroditic but capable of both sexual and asexual reproduction. They also have considerable ability to regenerate cells through the actions of multipotent, mesodermally derived, neoblasts. These neoblasts were originally described in the Platyhelminthes, but analogous (or homologous) cells appear in the Acoela. These cells replace damaged or missing body components and appear to have few limitations in how they are able to repair or replace tissues.

Three distinct forms of asexual reproduction have been documented within the Acoela: transverse fission, longitudinal fission, and budding (Figure 9.10). In at least some (e.g., *Paratomella rubra*), chains of smaller animals form from budding at the posterior end of the animal, a process known as **paratomy.**

Most acoels are simultaneous hermaphrodites (Figure 9.11), although some (e.g., all members of the family Solenofilomorphidae) are protandrous. Ovaries and testes may be paired or unpaired, with testes usually dorsal and ovaries more ventral (Figure 9.12A). In some species a single mixed gonad exists. In no cases are the gonads saccate—that is, the germ cell mass is not lined or discretely separated from the surrounding parenchyma.

Genitalia are usually visible near the posterior end of the animal. The penis is a muscular and glandular, or needlelike structure, often with multiple styletlike elements (Figure 9.12B). Male intromittent organs, regardless of form, can be retracted into a seminal vesicle. During copulation the penis is everted through the

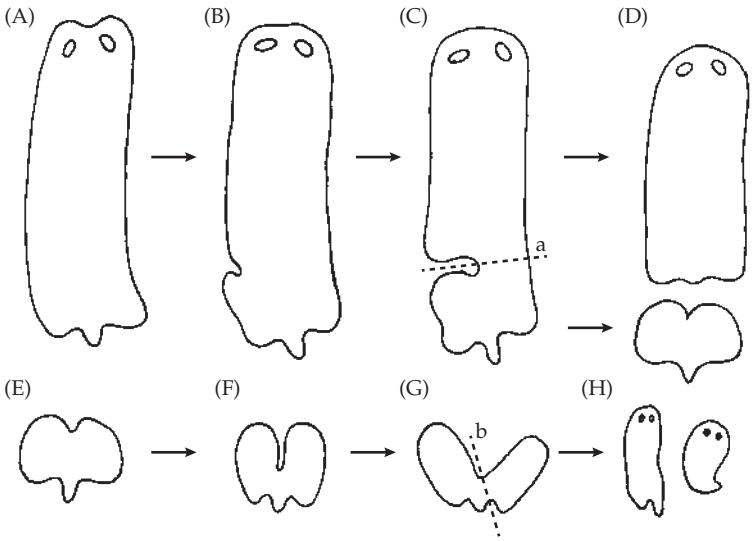

FIGURE 9.10 Modes of asexual reproduction in *Convolutriloba longifissura* (Acoela). (A) Intact animal. (B–D) Transverse fission; lower element of (D) shows "butterfly" stage preceding transverse fission (E–H).

male gonopore that typically lies in a distinct antrum, or vestibule on the body surface. A separate female gonopore exists in some species. In others, the female pore connects directly to the male pore. In still others, no external female opening exists and insemination is hypodermic. Most, but not all, acoels have the vagina positioned anterior to the penis.

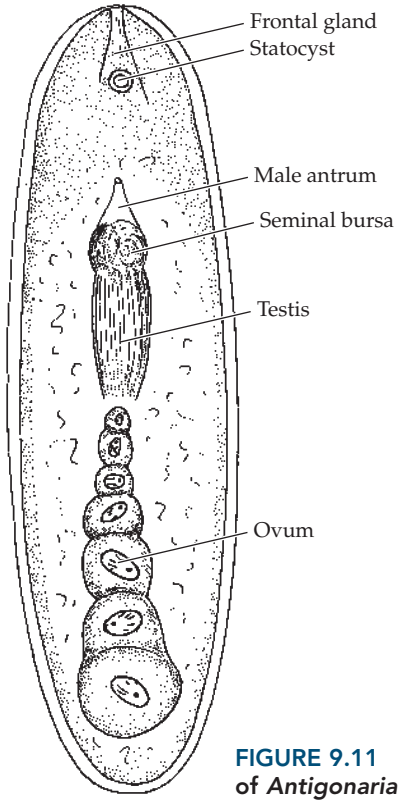

FIGURE 9.11 Internal organization of *Antigonaria arenaria* (Acoela).

A **seminal bursa** may exist that appears to receive sperm from mating partners either during copulation or after hypodermic insemination, and a sclerotized **bursal** or **vaginal nozzle** or sphincter regulates the passage of sperm to eggs. These are among the few sclerotized structures in these soft-bodied worms, and they were considered important in early taxonomic treatments of Acoela. Like many persistent terms in invertebrate zoology, the name "nozzle" was coined by Libbie Hyman, who thought these structures resembled the nozzle of a hose. In certain Convolutidae, multiple bursal nozzles may exist in the same individual (Figure 9.12B). While highly variable in form, seminal bursae and their associated structures appear to be homologous among all acoels.

During copulatory behavior individuals approach one another and exchange quick touches or "nips" of the anterior ends. Larger individuals appear to initiate copulation, which proceeds after both individuals roll into a ball and then unroll with their genitalia firmly engaged. In simultaneous hermaphrodites, each individual can mutually insert its penis into its partner's female gonopore and direct sperm and seminal fluid into the female bursa.

Acoel sperm are filiform and distinctively biflagellate, with the two axonemes of the flagella incorporated into the cell body (a condition also seen in Platyhelminthes) and a 9+2 microtubule pattern. Several well-defined patterns exist in acoel sperm morphology, and these seem to be phylogenetically informative. Combined studies of 18S rRNA sequence data and sperm morphology have revealed remarkable concordance between these two sources of data. Seminal bursae and bursal nozzle complexity also appear to correlate with variation in sperm morphology.

Fertilization is always internal, and zygotes are released either through the mouth, via the female gonopore, or through a rupture created in the epidermis by the growing embryos. Zygotes may be brooded or protected by encapsulation but are usually deposited singly and undergo direct development. Egg clusters appear to be laid primarily at night, in flat gelatinous masses.

Embryonic development is direct, and the cleavage pattern of acoels includes a unique mode called **duet cleavage** that is unlike anything seen in other metazoans. Nemertodermatids, while exhibiting "duet cleavage" in the four-cell stage, do not exhibit the spiral duet pattern seen in acoels. As in spiral quartet cleavage, the first horizontal cleavage in acoels is unequal and so produces micromeres, but it occurs at the two-cell stage instead of the four-cell stage, so the micromeres appear as duets instead of quartets. One

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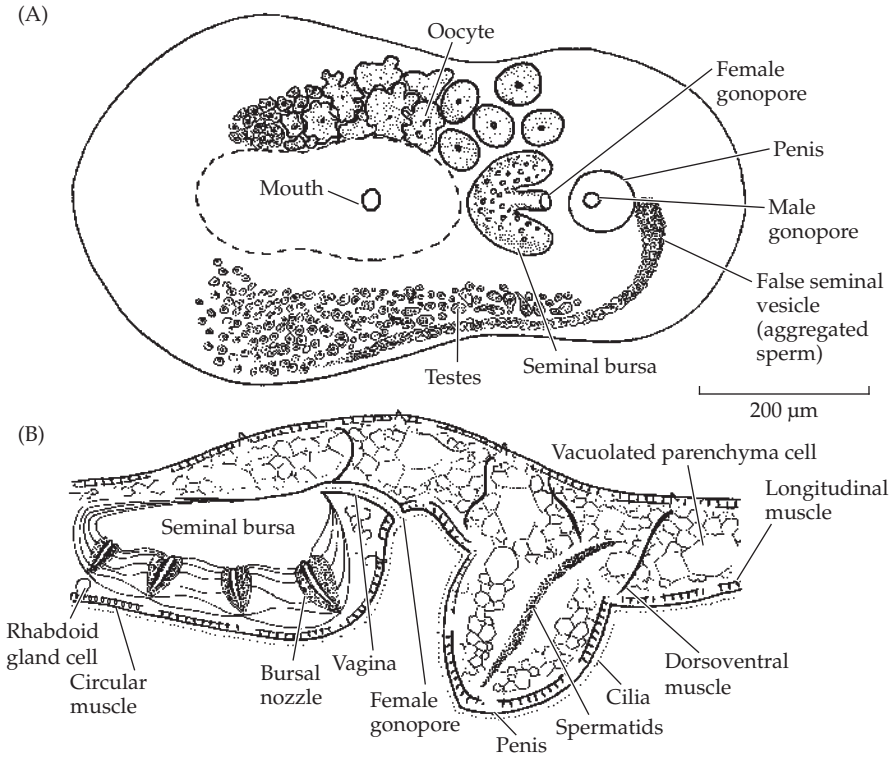

FIGURE 9.12 Acoela: reproductive anatomy of *Polychoerus gordoni*. (A) Dorsal view; note that in this species, as in other Convolutidae, male and female gonads are paired, but they are shown singly here. (B) Sagittal view of female and male reproductive anatomy.

is tempted to call this "bilateral cleavage," rather than spiral cleavage, and it is quite different from that of all other spiral-cleaving Metazoa. So far as is known, acoel embryos generate only endomesoderm, whereas most spiral-cleaving animals tend to also produce some ectomesoderm. Internal tissues arise either by delamination or by immigration of cells that form the ectoderm and mesoderm. By the time gastrulation is complete, the embryo has a layered appearance, with an outer epidermal primordium, and a middle layer of progenitor cells of muscles and neurons, while the innermost cells are those that will develop into the digestive syncytium. Endomesoderm forms from both of the third duet macromeres at the vegetal pole, whereas the mouth forms anteriorly as 1a micromere descendants expand around the posterior pole. Acoels hatch as juvenile worms (direct development) with all major organ systems except the reproductive tract. An anus never forms.

Class Nemertodermatida

Nemertodermatida comprise 18 species of marine worms described mostly from northern Atlantic coastlines. Nearly all known species are free-living, usually in fine sand, mud, or gravel; however, *Meara stichopi* is a symbiont in the foreguts of holothurian echinoderms (sea cucumbers). Nemertodermatids range in length from a few millimeters to nearly a centimeter. They can be leaf shaped or narrow and elongated, and they may creep over the substratum or swim with serpentine movements. Their bodies are densely covered with locomotory cilia, and as a group they are easily recognized by an anterior statocyst containing two statoliths in separate chambers (Figure 9.13A,B)—although a few reports of one to four statoliths also exist. Some species possess an eversible proboscis associated with feeding (oddly, some of these species lack a distinct mouth), with numerous branches that extend anteriorly "like a witch's broom" (Figure 9.14).

The epidermal cells of nemertodermatids lack a true basal lamina but are connected to underlying muscle cells and to each other by a narrow extracellular matrix. Septate junctions between epidermal cells are lacking. As in the acoels, old or damaged ciliated epidermal cells are withdrawn into the body and resorbed, creating temporary structures called pulsatile bodies, although these were called restitution bodies in nemertodermatids (Figure 9.15). Also as in acoels, species living in the guts of other animals often have symbiotic bacteria inhabiting their epidermis (Figure 9.16). The form of the mouth and gut vary among species, from temporary structures to a porelike opening and a narrow intestinal lumen, although a complete gut is lacking (there is no anus, nor is there a discrete pharynx). They lack discrete circulatory or excretory structures. Asexual reproduction has not been reported. Male sexual structures may consist of a simple, ciliated invagination of the epidermis or an eversible penis; seminal vesicles may be present. Where these structures are lacking, sperm appear to simply be ejected from the male antrum. The female gonopore with an

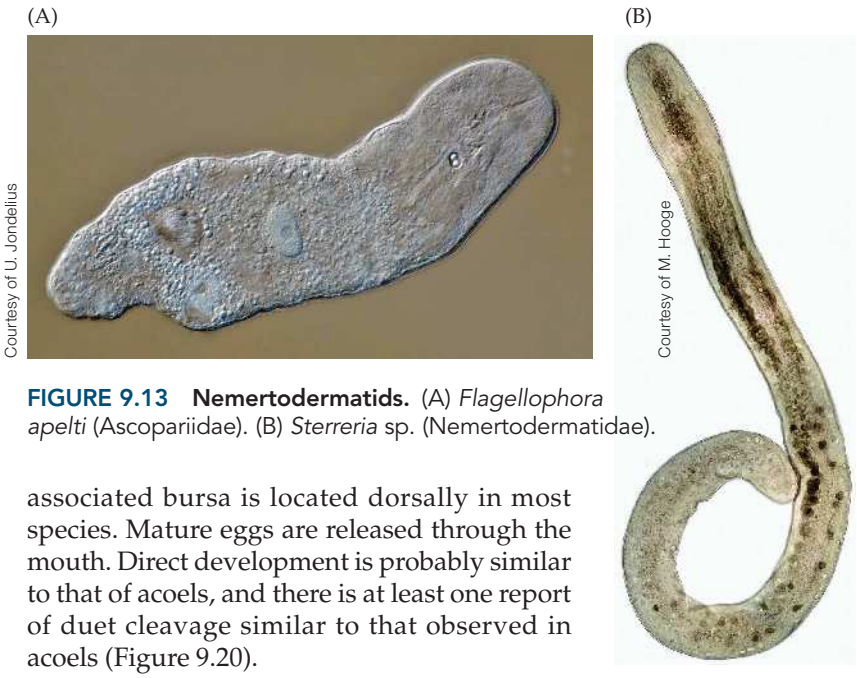

FIGURE 9.13 Nemertodermatids. (A) *Flagellophora apelti* (Ascopariidae). (B) *Sterreria* sp. (Nemertodermatidae).

associated bursa is located dorsally in most species. Mature eggs are released through the mouth. Direct development is probably similar to that of acoels, and there is at least one report of duet cleavage similar to that observed in acoels (Figure 9.20).

The first described nemertodermatid was classified within the acoel Platyhelminthes by Otto Steinböck in 1930. Steinböck, a colorful individual known to express himself in double-spaced capital letters with exclamation marks for emphasis, announced his discovery as "the mother of all turbellarians," possessing a "novel, two-stoned statocyst, an unusually thick and gland-rich epidermis, a peripheral nervous system, and a mixed, lacunar gonad without accessory organs." In 1940 Tor Karling removed the Nemertodermatida from the Acoela because of their well-formed intestinal lumen, a structure lacking in acoels. The Acoela and Nemertodermatida were combined as sister taxa within the Platyhelminthes in 1985 with Ulrich Ehlers' recognition of the taxon Acoelomorpha. Additional work on Nemertodermatida has proceeded slowly because specimens are difficult to come by and because many characters can be highly variable within populations, but the group has seen a sort of revival in the past decades due to realization of their phylogenetic position outside of Platyhelminthes.

The relationship of *Meara stichopi* to its echinoderm hosts is poorly understood but does not appear to be parasitic—hosts do not appear to be harmed by the presence of the worms. In fact, the relationship could be mutualistic, as nematodes have been found within the guts of endosymbiotic *Meara*. Symbiotic species of both *Meara* and *Nemertoderma* are known to possess elongated, Y-shaped symbiotic bacteria (Figure 9.16). In *Meara*,

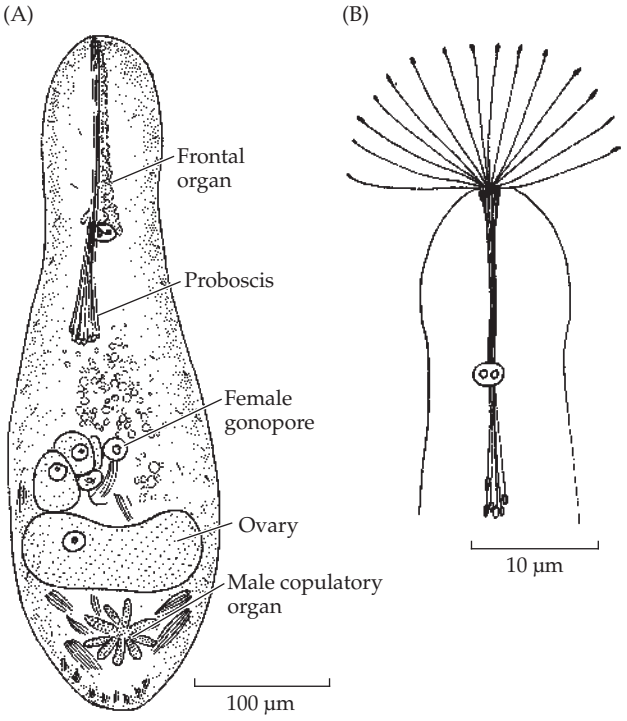

FIGURE 9.14 Nemertodermatids. *Flagellophora apelti.* (A) Dorsal view of mature specimen. (B) Protruded "witch's broom" proboscis.

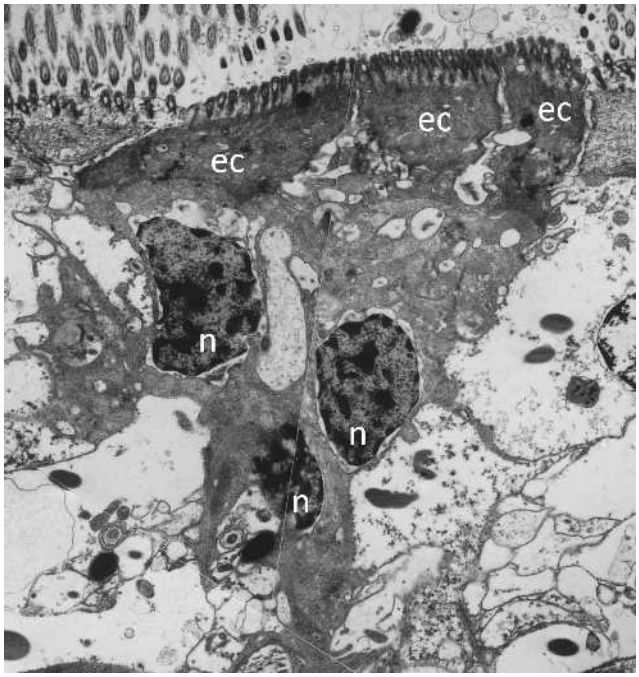

FIGURE 9.15 TEM micrograph showing a cross section the epidermis of the nemertodermatid *Meara stichopi*. Three ciliated epidermal cells (ec), presumably worn or damaged and bearing only the dark stubs of locomotory cilia, are being compacted and withdrawn into the integument to be dissolved; the three dark structures (n) are the epidermal cell nuclei.

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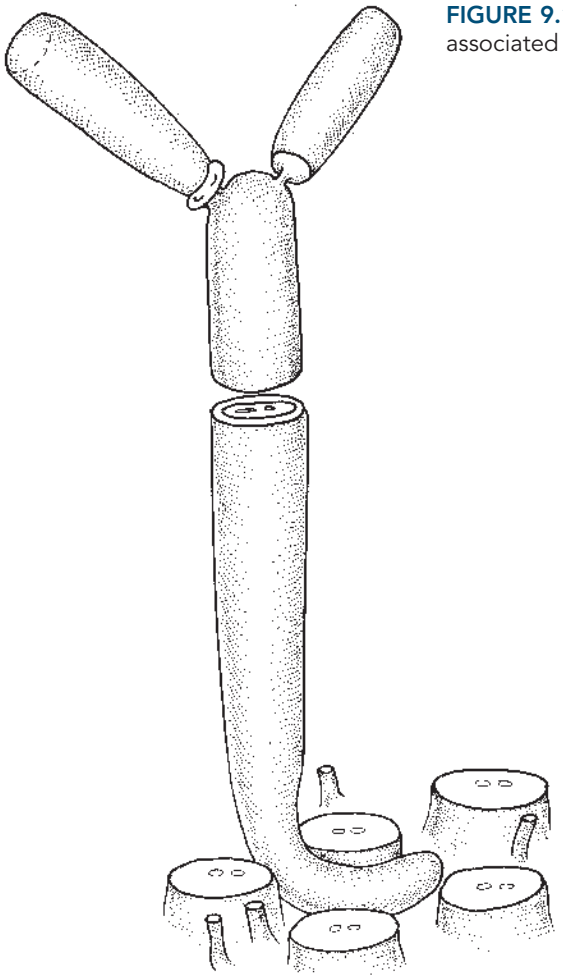


FIGURE 9.16 Nemertodermatida. Y-shaped elongated symbiotic bacteria associated with the epidermis of *Meara stichopi*.

these symbionts are found primarily on the ventral side of the body. Ultrastructural studies indicate that bacteria occur only on the outside surface of their worm hosts, suggesting that the association between bacteria and host does not represent infection.

The Nemertodermatid Body Plan

Body Structure

In general, nemertodermatids are small. The endosymbiotic *Meara stichopi* is usually less than 2 mm in length, free-living *Nemertoderma* average about 3 mm in length, and a few "giant" nemertodermatids grow to nearly 1 cm. Most individuals are colorless to yellow or red, but pigmentation can be variable within populations. The epidermis of most species appears to contain numerous bottle-shaped mucous glands. Overall, the epidermis resembles that of nemertean worms, which led to the namesake "nemertodermatid." In the genus *Nemertoderma*, these glands are more abundant at the apical pole, forming an anterior gland complex with separated, outwardly directed gland openings or necks. However, these openings are not grouped together in a regular way at an apical pore and thus do not form a "frontal organ" like that described for Platyhelminthes.

Cell and Tissue Organization

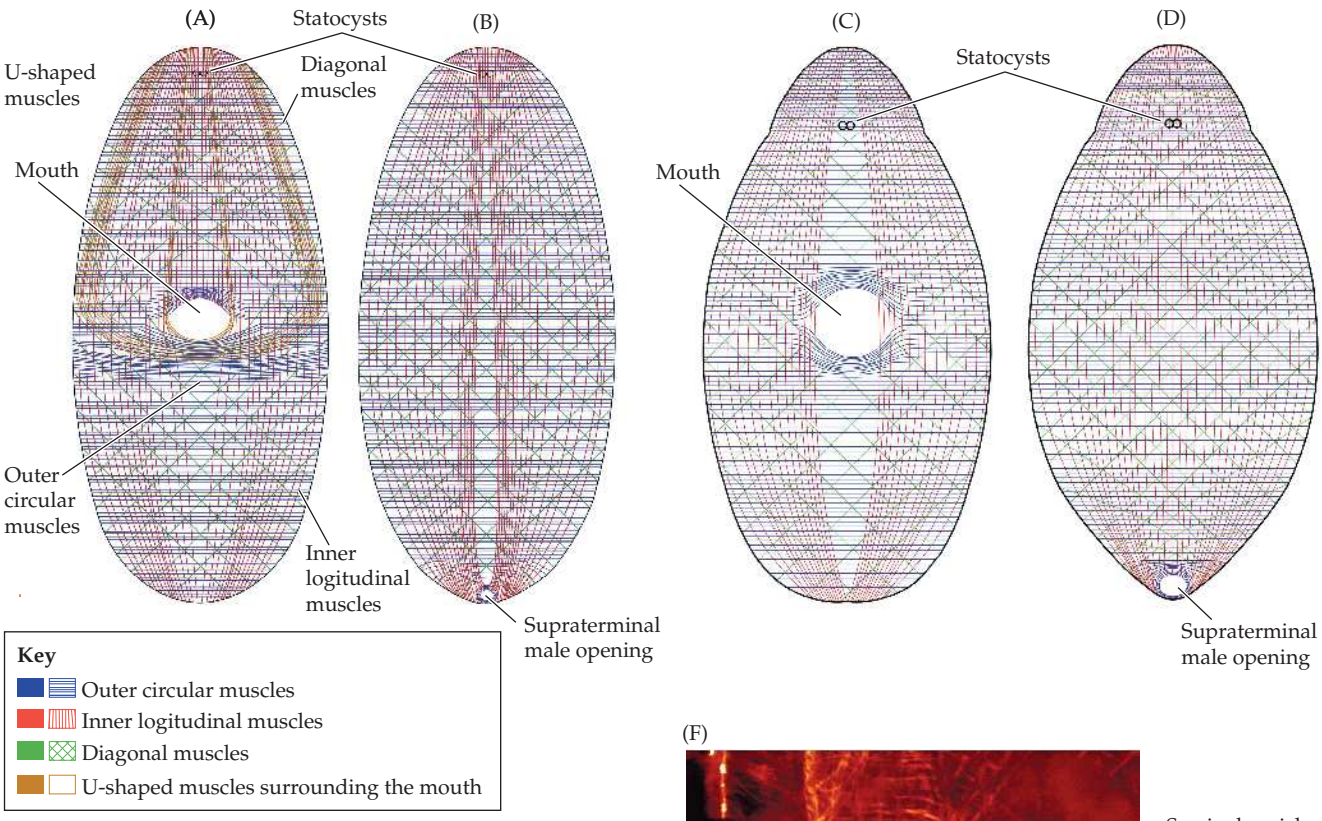
The epidermis of nemertodermatids is entirely ciliated. The cells are connected by an intracellular terminal web—a stratified structure composed of a closely woven inner layer of intensely staining fibrils overlain with more loosely packed fibrils, which bulges at the cell borders. Epidermal cells are joined apically by belt-like adherens junctions (belt desmosomes) called **zonula adherens**. Interspersed among the cells are the necks of various glands and sensory receptors, particularly in the anterior region of the animal. The necks of glands appear to have associated muscular rings that may regulate the flow of gland contents (Figure 9.17E).

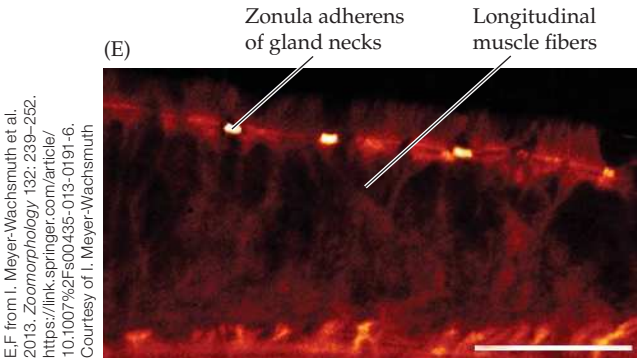
The ciliary rootlet structure is similar in Acoela and Nemertodermatida, one of the primary reasons workers grouped these two taxa together (as the Acoelomorpha). The rootlets of nemertodermatids include a rostrally oriented rootlet and a caudally oriented rootlet. In its original description, *Meara stichopi* was reported to possess "restitution cells" that appeared to contain ciliary structures in the process of being resorbed. Indeed, these cells represent structures similar to the pulsatile bodies reported in acoels, wherein worn cells are encapsulated and transported to the digestive tract for resorption (Figure 9.15). However, this feature is distinct in the nemertodermatids because the cilia detach from their basal apparatus before encapsulation, eliminating their ability to pulsate, causing some researchers to refer to them as "degenerating epidermal bodies."

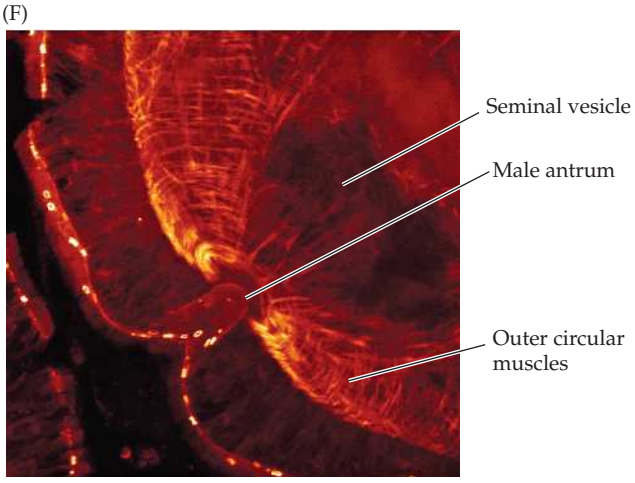
Support and Movement

As in most acoels, body musculature in nemertodermatids consists of outer circular and inner longitudinal muscle layers. Diagonal musculature typically is also present and varies among species, with fibers forming connections between layers in some (e.g., *M. stichopi*; Figure 9.17A,B) and forming distinct layers in others (e.g., *Nemertoderma westbladi*; Figure 9.17C,D). Musculature surrounding the mouth also varies, being best developed in species with a permanent mouth. Musculature is also well developed around permanent genital openings (e.g., *M. stichopi*) but is less so in species with transient genital orifices (e.g., *N. westbladi*).

The opening of the male gonopore and its associated antrum appear as an invagination of the entire body wall, and musculature associated with the seminal vesicle consists of a thin layer, present only in individuals with mature male organs (Figure 9.17F). Parenchymal







E,F from I. Meyer-Wachsmuth et al. 2013. *Zoomorphology* 132: 239–252. https://link.springer.com/article/10.1007%2Fs00435-013-0191-6. Courtesy of I. Meyer-Wachsmuth

FIGURE 9.17 Nemertodermatid musculature. (A–D) Schematic diagrams. (A) Ventral and (B) dorsal views of *Meara stichopi* (graphic showing muscle patterns). (C) Ventral and (D) dorsal views of *Nemertoderma westbladi* (graphic showing muscle patterns). Outer circular muscles (blue); inner longitudinal muscles (red); diagonal muscles (green); U-shaped muscles surrounding the mouth (orange) on ventral side. (E,F) Phalloidin-enhanced micrographs. (E) Lateral view of epidermis in *N. westbladi*, showing longitudinal muscle fibers beneath circular ones in central space. Above this are two thin stained layers: the lower layer corresponding to the intracellular web, the upper layer corresponding to microvilli of the epidermal surface. The zonula adherens of the gland necks appear as brightly stained areas at this level. (F) Posterior body region of *N. westbladi*, with invagination of body wall to form the male antrum; finer musculature of the seminal vesicle is visible in open space. (A–D from I. Meyer-Wachsmuth et al. 2013. *Zoomorphology* 132: 239–252. https://link.springer.com/article/10.1007%2Fs00435-013-0191-6. Courtesy of I. Meyer-Wachsmuth.)

muscles may also be present in individuals in all life stages, forming a three-dimensional network throughout the parenchymal tissue. The statocyst is supported by muscles that attach dorsoposteriorly and anterolaterally to other body wall musculature. Nemertodermatids move by creeping on their ciliated surfaces or, in more elongated species, by undulating their bodies in a serpentine way.

Nutrition, Excretion, Gas Exchange

The gut of nemertodermatids has only a single opening, like that of cnidarians and other xenacoelomorphs. However, unlike in acoels, the gut is not syncytial and instead usually contains a well-defined intestinal lumen. In some nemertodermatid species, a cone of gut tissue has been reported to protrude and retract like a tongue to collect food particles. However, no known

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nemertodermatid possesses a structure recognizable as a muscular pharynx. Other species appear to lack a mouth altogether. In such species (e.g., *Flagellophora apelti*), an anterior **broom organ** is reported, although this structure does not seem to be directly connected to the gut. Instead it seems to consist of a bundle of up to 30 glands whose necks are protrusible through a canal at the anterior end of the body (Figure 9.14B). When opened, the broom organ appears to possess distal ends that are slightly swollen and possibly adhesive. Some researchers have suggested that the mouth of nemertodermatids is a transient structure that appears during a limited part of postembryonic life, with the duration of persistence dependent upon the species.

Meara stichopi inhabits the foregut of the holothurian *Parastichopus tremulus*, a species common on Scandinavian coastlines, and appears to feed on detritus as well as upon nematodes within the gut of its host. Free-living species of Nemertodermatida have been found with comparatively large turbellarians and nematodes within their guts. As in acoels, the small body sizes of nemertodermatids allow them to eliminate waste nitrogen and carbon dioxide, as well as obtain oxygen from the surrounding water, without a need for discrete excretory or circulatory organs.

Nervous System

The nervous system of nemertodermatids is still not well understood. Immunoreactivity studies with the neurotransmitter serotonin (5-hydroxytryptamine; 5-HT) and the regulatory neuropeptide FMRFamide have shown considerable variation in responses in the species examined. In *Meara stichopi*, 5-HT reactivity reveals a subepidermal nerve net and two, loosely organized longitudinal nerve bundles along the length of the animal. In *Nemertoderma westbladi*, 5-HT reactivity shows a two-ringed, anterior commissure, with the rings converging near the statocyst and connected by thin fibers. Two lateral fibers extend longitudinally from the commissure, as does a delicate curtain of evenly spaced finer longitudinal fibers that become indistinct caudally. FMRFamide immunoreactivity follows the same pattern as 5-HT reactivity in *M. stichopi* and *N. westbladi*. These results suggest that the nemertodermatid nervous system is quite distinct from the bilobed ganglionic brain and orthogonal peripheral nervous system of Platyhelminthes (i.e., paired longitudinal ventral nerve cords connected by a regular pattern of transverse commissures). The nemertodermatid central nervous system is also distinct from the commissural brain of acoels (i.e., symmetrical commissural fibers with few cell bodies and three to five pairs of radially arranged longitudinal nerve cords, irregularly connected with transverse fibers). The statocyst may contain one to four statoliths.

Reproduction and Development

The reproductive anatomy and natural history of nemertodermatids is not well studied, and only a few species have been examined in this regard. The male gonopore in nemertodermatids appears to open dorsally (or supraterminally) and is associated with a muscular male antrum. In fully mature specimens, a muscular seminal vesicle and often a male copulatory organ may also evert either posteriorly or slightly dorsally (Figure 9.18). Female genitalia, if present, is located dorsally. *Flagellophora apelti* seems to have a deep, well-defined invagination that may represent a female gonopore (Figure 9.14).

In *M. stichopi*, follicular testicular cells can occupy most of the preoral part of the body. Ovarian cells can occupy the postoral part of the body and the animal often contains one or more large ova within the posterior body region. The male intromittent organ opens terminally to slightly supraterminally in this species.

In general, Nemertodermatida have a 9+2 arrangement of microtubules in their uniflagellate sperm, a condition distinct from the variable microtubule arrangement and biflagellate condition of acoel sperm. Many field-collected nemertodermatids contain two types of sperm. **Autosperm** (sperm produced by the individual in which they are found) in *M. stichopi* are filiform, are about 45–60 μm long, and under phase contrast microscopy show indistinct divisions of individual sperm into head, middle piece, and tail, as is typical of more derived spermatozoan forms within Metazoa (Figure 9.19). Some sperm appear to be coiled, in corkscrew fashion, over half of their length and are nonmotile within the animal producing them. **Allosperm** (sperm not produced by the individual in which they are found) are distinctive because they tend to be uncoiled and motile within the body of recipient individuals.

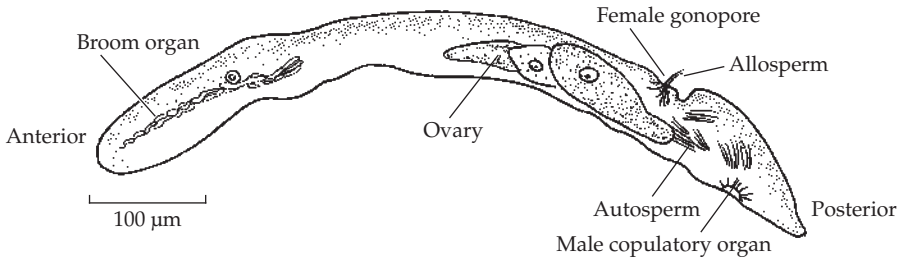

FIGURE 9.18 Nemertodermatida. Diagram of *Ascoparia* sp. showing location of dorsal female gonopore and subterminal male copulatory organ.

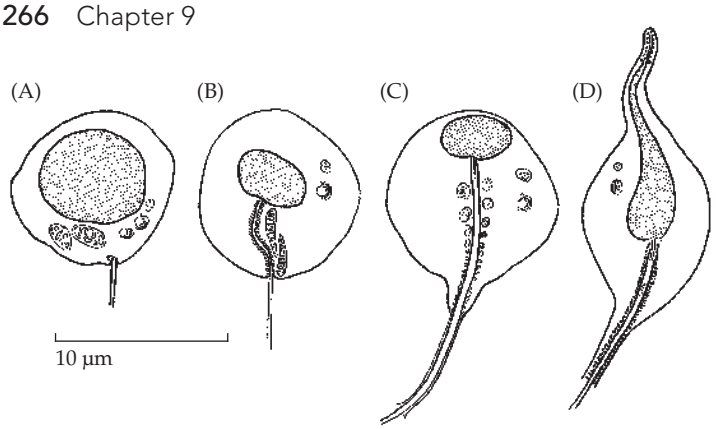

FIGURE 9.19 Nemertodermatida: stages in spermatogenesis in *Meara stichopi*. (A) In early stages of spermatogenesis, the nucleus is large, with heterogeneous electron density; two mitochondria are visible. A single flagellum begins to form from a basal body situated near the cell membrane. (B) The nucleus shrinks and becomes homogenous in density. The mitochondria begin to elongate, and the basal body and associated fibers move into the cytoplasm toward a depression forming in the nucleus. Microtubules coil around the flagellar channel. (C) The mitochondria coil around the flagellar channel, and a sheath grows from the cell to surround the proximal flagellum. (D) The cell and nucleus elongate to form the head of the spermatozoon. The mitochondria form tighter whorls and wander into the length of the flagellar sheath. (After K. Lundin and J. Hendelberg. 1998. *Hydrobiologia* 383: 197–205. https://link.springer.com/article/10.1023%2FA%3A1003439512957)

The pioneering investigator of acoels and nemertodermatids, Einar Westblad, noticed that development of female reproductive structures seemed to precede that of male structures, indicating that some nemertodermatids might be protogynous. On the other hand, other authors have noted that "male maturity seems to precede female maturity," or they have specifically stated that individuals are protandrous. In *N. westbladi*, individuals were found to have matured as males, females, and hermaphrodites, with no clear evidence of either protandry or protogyny. In *Ascoparia neglecta*, an elongate species with no actual mouth in mature individuals (although male and female pores are visible), individuals possess a male copulatory organ, and allosperm have been reported contained in vacuoles near the vagina.

Many species appear to lack female genitalia yet are found to contain both autosperm that are clearly contained within male reproductive structures and allosperm that appear to have been introduced. Individuals bearing allosperm appear to include mature as well as immature individuals, raising the possibility of sperm storage and sperm competition among individuals. Taken together, these findings imply great diversity in reproductive life history among nemertodermatids. Adults in some species appear to be smaller than juveniles, suggesting that maturing individuals may cease to feed and then complete their life history using stored food reserves or other resources.

Copulation has not been observed in any nemertodermatids. However, earlier workers suggested that worms may simply press their posterior ends together long enough for spermatids to get through the epithelium of the recipient worm. Since male structures are located subterminally, this behavior would have to occur with the recipient positioned somewhat dorsally, or an individual transferring sperm would have to undergo dorsiflexion to accomplish impregnation. In species lacking female structures, insemination appears to be hypodermic. Oviposition is accomplished by flexing the body into a dorsiconvex shape, followed by protrusion of the circumoral area of the body to force individual eggs out of the mouth.

Development in nemertodermatids is similar to that of Acoela. The first cleavage division is holoblastic (Figure 9.20). The second division results in the formation of micromeres and macromeres. In later 4-cell stages, the micromeres shift slightly clockwise (dexiotropic), resembling spiral cleavage, but this shift does not occur until well after the division has taken place. Nemertodermatid cleavage starts out radial but then takes place in a duet pattern, the micromeres shifting clockwise to produce a spiral-like pattern. The 4-cell divisions involve both macromeres, resulting in a 6-cell embryo, followed by another division by the micromeres to yield an 8-celled embryo. This alternating pattern is followed until the 16-cell stage, similar to what is known in acoels as "duet cleavage," although in acoels the first division involves a counterclockwise (levotropic)

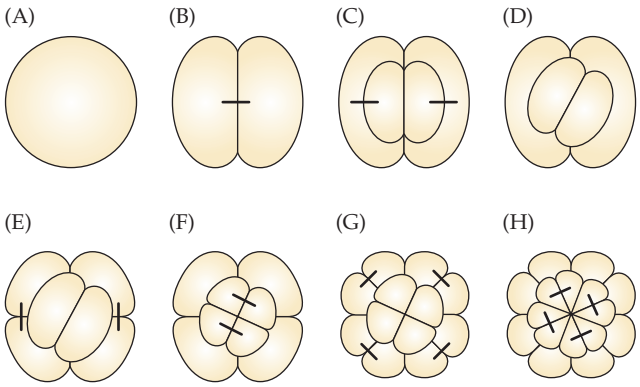

FIGURE 9.20 Diagram of duet cleavage in Nemertodermatida (*Nemertoderma westbladi*), viewed from the animal pole. Lines indicate cleaved relationships among cells. (A) Uncleaved zygote. (B) The 2-cell stage. (C) Early 4-cell stage with micromeres oriented radially. (D) Late 4-cell stage with micromeres shifted. (E) The 6-cell stage. (F) Cleavage of micromeres produces an 8-cell stage. (G) The 12-cell stage with eight macromeres and four micromeres. (H) The 16-cell stage with eight macromeres and eight micromeres. (After U. Jondelius et al. 2004. *Zoomorphology* 123: 221–225. https://link.springer.com/article/10.1007/s00435-004-0105-8)

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shift of the micromeres rather than the clockwise shift documented for *N. westbladi*. Nevertheless, the form of duet cleavage is similar in both taxa, suggesting to some researchers that this trait is ancestral in the Acoelomorpha.

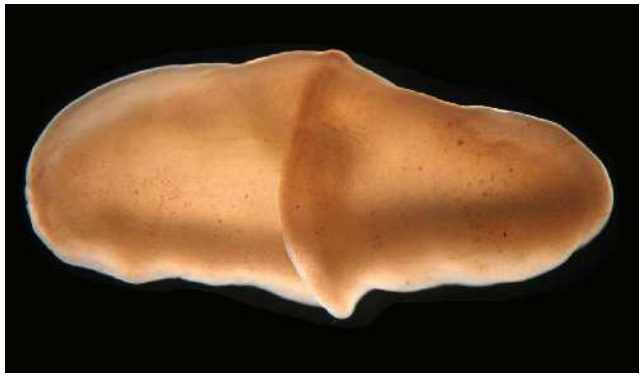
Postembryonic development in *N. westbladi* appears to follow three life history phases. Hatchlings are nearly round, only slightly longer than wide (around 250 × 200 μm). These individuals grow directly into juveniles, which are bottle shaped and may reach nearly 1 mm in length but possess no discernable sexual structures, mouth, or digestive system. Mature specimens may be variable in size (averaging 450 μm in length) and possess a slightly more elongated shape as well as visible male copulatory organs and a small pointed tip at the posterior end formed by the male gonopore.

Subphylum Xenoturbellida

Sixten Bock (1884–1946), the great Swedish platyhelminth specialist, was collecting along the Swedish coast near the Kristineberg Center for Marine Research and Innovation (then known as the Kristineberg Marine Research Station) in 1915 when he came across an odd-looking "flatworm." Bock never got around to identifying the creature, but Einar Westblad, another great platyhelminth specialist, did and initially considered it a free-living archoöphoran platyhelminth, along with similar specimens he had collected near Scotland and Norway. Eventually, in 1949, Westblad described the original specimen as *Xenoturbella bocki*, after its collector (Figure 9.21). The creature caused immediate controversy because of its distinctive appearance. In 1999 a second species was described and named *Xenoturbella westbladi*, but this turned out to be the same species, and thus the name is a junior synonym. The name *Xenoturbella* means "strange turbellarian" because while the creature resembled free-living flatworms overall, its epidermis was reminiscent of hemichordates, and its statocyst seemed similar to that of certain holothuroids.

Since then, five additional species have been discovered and named from the eastern and western Pacific Ocean (Figure 9.22). These worms range in size from a few millimeters to over 20 cm, and they occur in depths from 20 to 3,700 m. Molecular data have shown that xenoturbellids are neither platyhelminths nor closely related to any other nephrozoan phylum, but they are closely related to the Acoelomorpha. Morphological data are in agreement.

Xenoturbella are delicate, free-living, ciliated worms with a very simple body plan. They are easily recognizable by their body furrows: the **horizontal furrows** (= side or anterolateral furrows) and **ring furrow** (= equilateral furrow), the latter nearly crossing the animal's midline (Figure 9.22A). The furrows contain what has been interpreted as high concentrations of sensory cells, so they are presumed to be sensory structures.



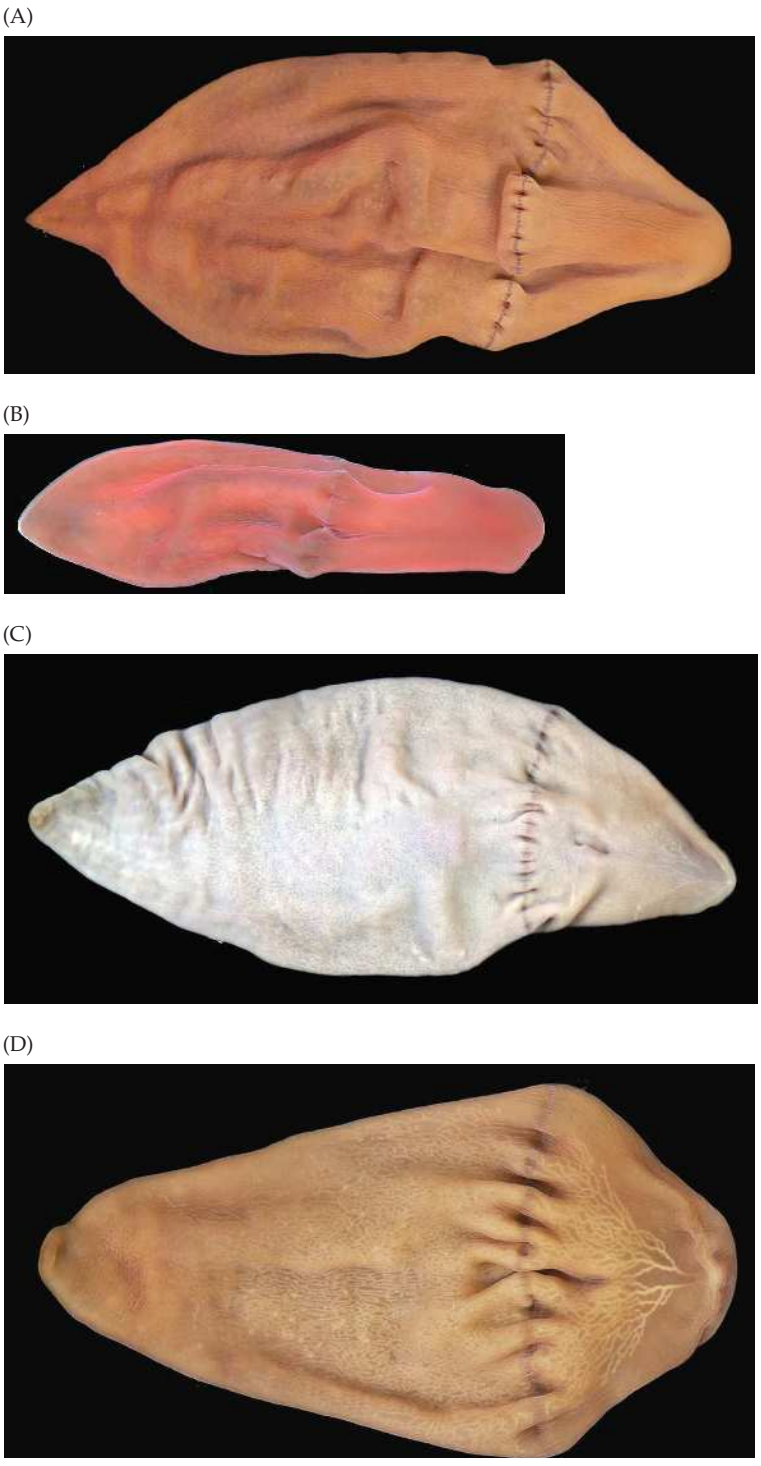
Courtesy of G. Rouse

FIGURE 9.21 ***Xenoturbella bocki.*** Live specimen, from 80 m depth, off the west coast of Sweden.

Like acoels and nemertodermatids, xenoturbellids have distinctive epidermal ciliary rootlets and mode of withdrawal of epidermal cells; they possess a diffuse, basi- or intraepithelial nervous system; they use a statocyst for orientation; and they have circular and longitudinal muscles. They possess a midventral mouth, as some acoelomorphs do. Also like acoelomorphs, *Xenoturbella* lack a complete gut, organized gonads, excretory structures, and coelomic cavities, and they have a poorly developed brain. The nervous system is primarily in the form of an intraepidermal nerve net.

However, unlike acoelomorphs, xenoturbellids possess simple spermatozoa, similar to those seen in externally fertilizing species. Also, muscle layers are connected by extensive interdigitations among the layers of cells, and the longitudinal muscles are exceptionally robust. The nervous system, while diffuse, is concentrated along the sensory furrows. Xenoturbellids also are generally larger in size, with some reaching more than 20 cm in length.

As morphological evidence accumulated on *Xenoturbella*, its relationship to flatworms began to be doubted, and by the late 1950s most researchers agreed that *Xenoturbella* was not a flatworm genus. But there was little consensus about what these animals actually were. Opinions on their identity ranged from considering them "among the coelenterates" to placing them in a sister taxon to the enteropneusts. Then, in the late 1990s, analysis of ribosomal RNA from what appeared to be developing oocytes and embryos in some specimens led to the conclusion that *Xenoturbella* was in fact a highly degenerate mollusc, possibly some form of shell-less bivalve. However, subsequent investigations showed that these RNA samples had been contaminated with gut contents containing molluscan DNA. Subsequent DNA studies suggested *Xenoturbella* might be a highly degenerate deuterostome, near the base of the deuterostome line or perhaps closely related to echinoderms and hemichordates. Continued molecular phylogenetic studies have suggested that *Xenoturbella* is closely tied



A–D courtesy of G. Rouse

FIGURE 9.22 Recently described species of *Xenoturbella*. (A) *Xenoturbella churro* (dorsal view showing ring furrow and oocytes). (B) *Xenoturbella hollandorum* (dorsal view). (C) *Xenoturbella profunda* (ventral view). (D) *Xenoturbella monstrosa* (ventral view).

to acoels and nemertodermatids, and thus the new phylum name Xenacoelomorpha was created to house these three odd, primitive worms.

In 2016 Greg Rouse and colleagues described four new species of xenoturbellids from deep waters of the eastern Pacific (Figure 9.22). A large (>20 cm) species was found in a vesicomyid clam field at 2,890 m depth in Monterey Submarine Canyon (California) and at 1,722 m near a cold-water methane seep in the Gulf of California (Mexico). A second species (~10 cm long) also occurred at 1,722 m in the Gulf of California. A third species (~15 cm long) was found at 3,700 m near a hydrothermal vent in the Gulf of California. The fourth new species was small (~2.5 cm), resembled *X. bocki*, and was found next to the bones of a whale carcass at 631 m in Monterey Canyon. More recently, a sixth species of *Xenoturbella*, *X. japonica*, was added from Japan by Hiroiki Nakano and collaborators (2017), constituting the first finding of the clade in the western Pacific. Whole mitochondrial genome analysis places the three larger species as a sister clade to the smaller Pacific species and *X. bocki*.

The Xenoturbellid Body Plan

General Body Structure

Most specimens of *Xenoturbella* are ovoid in shape, with a flattened ventrum. These worms can be quite active and capable of considerable changes in shape (Figure 9.22B–D). The worms are pink, the anterior region of most individuals being slightly lighter in color, and the horizontal furrows extend posteriorly, on either side, from the head end. Approximately midway down the body, these furrows nearly intersect with a ring furrow. The nervous system appears to be concentrated in these areas, suggesting a sensory function to the structures.

The epidermis of *X. bocki* consists of a layer of tall columnar cells with nuclei situated basally. These cells are densely multiciliated and are interspersed with unciliated or monociliated gland cells and ciliary receptors, the latter being most numerous in the horizontal furrows. The cilia themselves are attached to epidermal cells by several structures (Figure 9.23A). Each cilium ends in a basal body whose protruding **basal foot** has microtubules that extend into the epidermal cell. Two ciliary rootlets project from the basal body deeper into the epidermal cell; the thinner one, located on the same side of the cilium as the basal foot, projects straight into the cell, whereas the thicker rootlet has a kneelike bend. Each cilium has a distinctive arrangement of microfilaments in which the standard 9+2 arrangement extends for most of the ciliary shaft length, but near the end, microfilament doublets 4–7 abruptly end, leaving only doublets 1–3 and 8–9 to continue on to the end of the cilium (Figure 9.23B). This "shelf" arrangement of

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microtubules is also present in Nemertodermatida and Acoela but has not been found in other known metazoan taxa (Figure 9.24).

The basal region of the epidermis houses the cell processes of the multiciliary cells, supporting cells, and a prominent intraepidermal nerve layer. The cell membranes of adjacent epidermal cells intermingle with each other, but tight couplings between the membranes of adjacent extensions do not appear to exist. However, where the cytoplasmic protrusions are shorter, they show a regular arrangement as if the two cells were held together by a zipper, although tight junctions, desmosomes, or gap junctions between cells have yet to be identified.

A number of workers have noted the similarities in both ciliary roots and ciliary tips in *Xenoturbella*, acoels, and nemertodermatids. In all three groups the cilia form a network of interconnecting rootlets. Also as in Acoelomorpha, *Xenoturbella* are capable of withdrawing and resorbing worn-out epithelial cells, although these processes have subtle differences. Whereas nemertodermatids do not withdraw still-motile ciliary cells, the withdrawn epidermal cells in *Xenoturbella* assume an orientation perpendicular to that of the other cells and retain some motility.

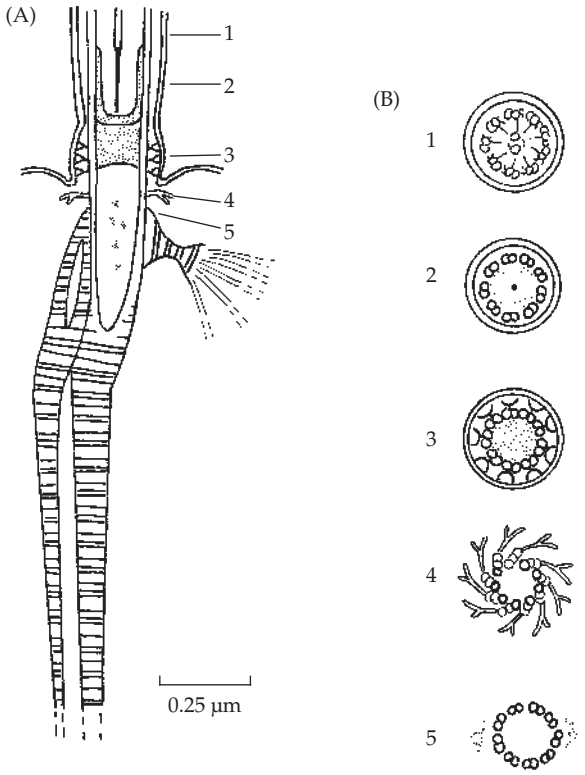

FIGURE 9.23 Diagram of the basal part of the cilium, basal body, and ciliary rootlets of *Xenoturbella bocki*. (A) Longitudinal median section of basal part of cilium. (B) Cross sections of basal part of cilium and the basal body, showing the position of the microtubules at different levels. (1) Basal part of cilium. (2) Cup-shaped structure at the base of cilium. (3) Dense aggregation of granules and champagne-glass structures in the upper part of the basal body. (4) Centriolar triplet part of the basal body with winglike projections (the "alar sheets"). (5) Lower part of the basal body.

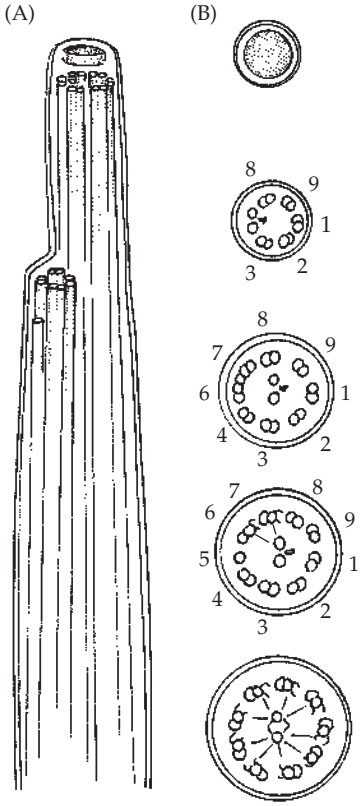

FIGURE 9.24 Diagram of the configuration of axonemal fibers within the distal shafts of epidermal cilia in *Xenoturbella bocki*. (A) Lateral view of the distal shaft showing the "shelf" located approximately 1.5 µm from the cilium tip. (B) Transverse sections of the cilium along its length; a 9+2 arrangement of axonemal fibers begins at the cilium base but microtubule doublets 4–7 end at the shelf.

Support and Movement

Xenoturbella species possess a highly muscular body wall (Figure 9.25A). An outer circular muscle layer surrounds a well-developed inner layer of longitudinal muscles, and radial musculature extends from the gastrodermis to the outer circular layer of muscle cells (Figure 9.25B).

No specialized parenchymal cells exist between the epidermis and the gastrodermis. However, all muscle cells tend to have numerous and well-defined cytoplasmic extensions with extensive mutual interdigitation. Tight attachment of adjacent cell membranes does not appear to exist, but connections resembling the zonula adherens seen in acoels and nemertodermatids are present, as is a fibrous subepidermal layer up to 5 µm thick.

Xenoturbella move by ciliary gliding, without requiring modification of the body profile. The ventral surface is richly supplied with epidermal glands, and

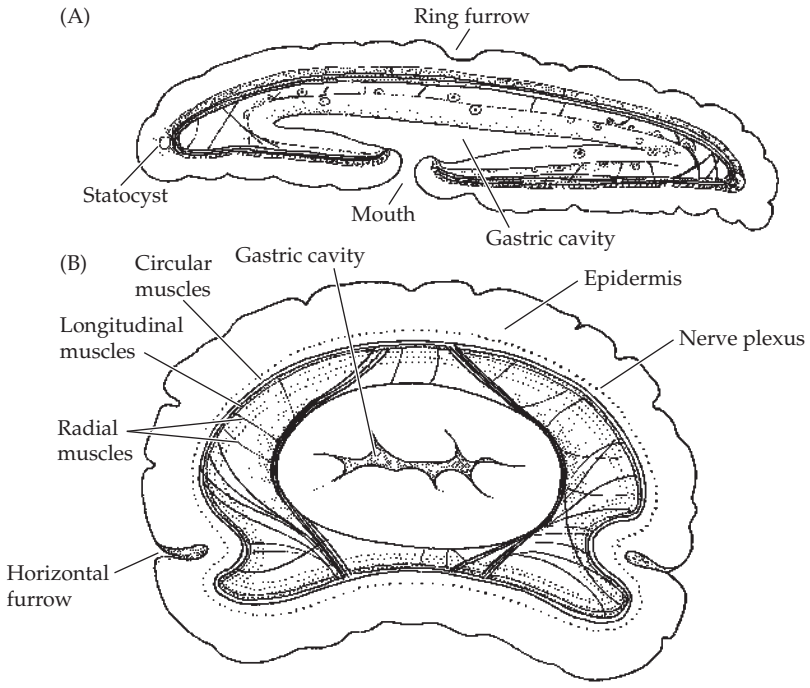

FIGURE 9.25 Internal morphology of *Xenoturbella bocki*. (A) Transverse section anterior to the mouth, showing the gastric cavity. (B) Schematic diagram of longitudinal section anterior to mouth, showing orientation of circular, longitudinal, and radial muscles.

moving animals leave behind a trail of mucus. While they are capable of considerable variation in body configuration due to powerful circular and longitudinal muscles, in most circumstances animals do not require such gymnastics in their basic activities.

Nutrition, Excretion, and Gas Exchange

Feeding by *X. bocki* occurs when individuals open their simple, midventral mouth and protrude their unciliated foregut. Extrusion of this structure appears to take place as a result of contractions of the surrounding body wall musculature, with relaxation of these muscles resulting in foregut retraction. The gut is cellular, but unciliated, and maintains a small cavity. Considerable attention has focused on the gut contents of *Xenoturbella*. Examination of mitochondrial DNA (cytochrome *c* oxidase subunit I sequence data) in the gut contents of *Xenoturbella* suggests that they feed primarily on bivalves, possibly in the form of eggs and benthic larvae. Such specificity suggests that these worms may be specialized predators, a hypothesis supported by the results of stable isotope studies. Two species of endosymbiotic bacteria have been described from the gut of *X. bocki*. Researchers have suggested that these bacteria might assist in nitrogen detoxification (given that excretory organs are lacking) or might supply growth factors or chemical defenses to their hosts. Discrete excretory structures have not been described for *Xenoturbella*.

Nervous System and Sense Organs

The nervous system of *Xenoturbella* is a diffuse intraepithelial (basiepithelial) net with a small anterior concentration forming a small commissural brain. This arrangement is similar to that seen in some acoels and nemertodermatids. The sensory furrows of xenoturbellids appear to have greater concentrations of neurons than other parts of their bodies. Like acoelomorphs, *Xenoturbella* have an anterior statocyst (Figure 9.25A), but the arrangement of muscles and neurons associated with this structure differs in that it appears to be embedded within the nerve net, situated between the epidermis and the muscle layers, rather than specifically supplied with connecting commissures. The statocyst contains motile flagellated cells and a statolith. A frontal pore, continuous with a ventral glandular network, may be homologous with the frontal organ of acoelomorphs.

Reproduction and Development

Xenoturbellids are simultaneous hermaphrodites producing relatively large-diameter, yolky eggs. Neither organized, well-developed ovaries nor testes have been observed in adult individuals. In particular, male gonads appear to consist simply of a layer of male sex cells surrounding the gut. Sperm develop in clumps and appear to be of a "primitive" type, usually associated with external fertilization, wherein spermatids possess a small conical acrosome and a single flagellum. There are no copulatory organs, and gametes appear to be spawned through either the gut or mouth opening. *Xenoturbella* has direct development, as in acoelomorphs, and the hatchlings are elongate/ovoid, swim with a rotating motion with uniform ciliation, and have an apical tuft of cilia. However, no mouth or blastopore has been seen in these juveniles.

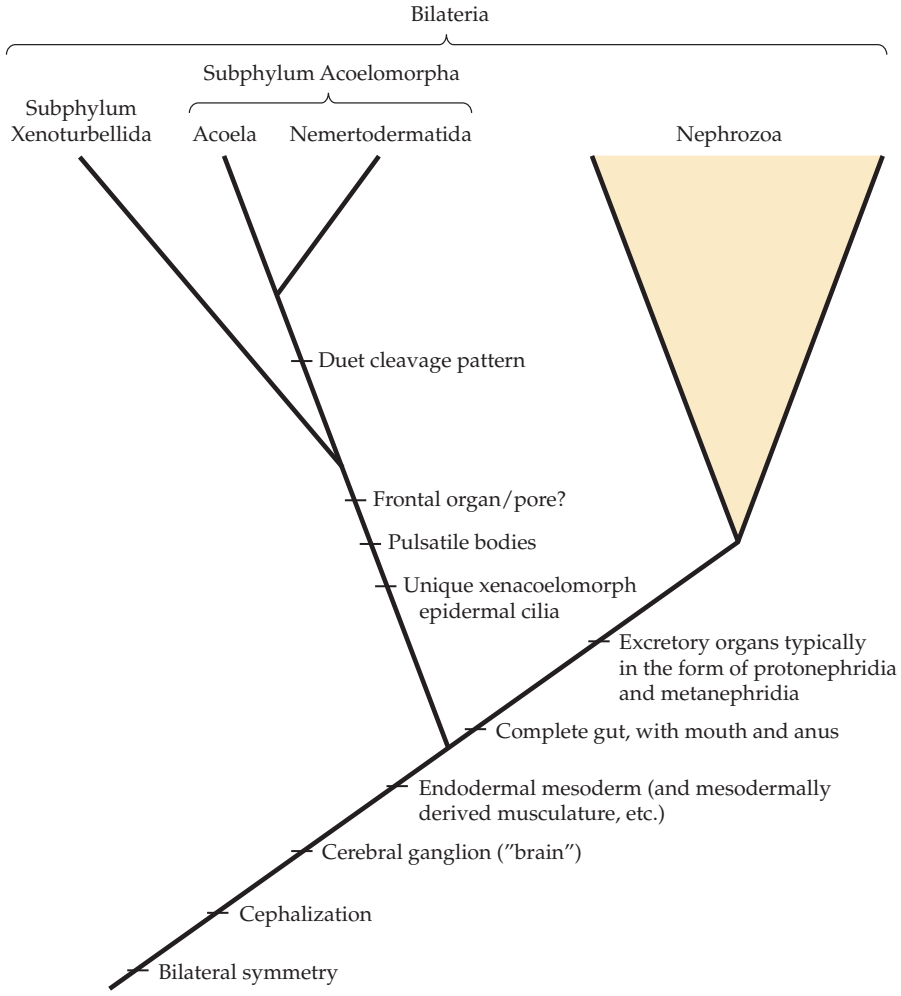

FIGURE 9.26 **The distribution of some important animal features at the base of the bilaterian clade.**

Chapter Summary

This chapter introduced you to one of the most enigmatic animal phyla, composed of relatively simple worms that are now interpreted as the sister group of Nephrozoa and thus often viewed as some of the simplest bilaterians (Figure 9.26). The phylum includes a few hundred species of mostly marine free-living worms (a few inhabit fresh waters, and one is an endosymbiont in sea cucumbers) inhabiting shallow to deep waters. Acoela, with more than 400 known species, is the largest group and a recently established model to study whole-body regeneration. Nemertodermatida has 18 described species, and Xenoturbellida has just 6 species (5 of which were described after 2015). These simple, acoelomate bilaterians have few organs and a largely nonganglionated nervous system. Some lack a true digestive cavity, and all lack an anus and excretory organs. Their development is known only for a few species; all appear to have direct development, and the Acoelomorpha have a unique "duet cleavage" pattern (not reported for xenoturbellids). Important areas of future research for xenacoelomorphs are related to their phylogenetic position (some analyses still support a position within deuterostomes), evo-devo studies of regeneration and body patterning, and better understanding of development (especially in Xenoturbellida).

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CHAPTER 10

Protostomia, Spiralia, and the Phylum Dicyemida

This and the following 14 chapters cover an enormous clade of bilaterian animals called Protostomia, and the next 7 chapters treat a subclade of those known as the Spiralia (Box 10A). Early in the evolution of bilaterians the split into two major lineages, which have long been called Protostomia and Deuterostomia, occurred. These groups were named over a century ago, and they were long defined on the basis of embryological principles. In protostomes, the blastopore (the portion in the embryo that typically gives rise to endodermal tissues) was said to give rise to the mouth ("protostome" = mouth first). Typically, in deuterostomes, the blastopore gives rise to the adult anus, the mouth thus forming secondarily at a different location ("deuterostome" = mouth second).

Protostomes and Deuterostomes

As twenty-first-century molecular phylogenetic discoveries began reshuffling animal phyla among the protostome and deuterostome lineages, new views of embryological patterns also emerged. In Deuterostomia (a small group of around 100,000 species in just three phyla—Echinodermata, Hemichordata, and Chordata), the blastopore *does* consistently give rise to the anus, and the mouth forms secondarily. But among the Protostomia, gastrulation is now known to be much more variable than originally thought. In fact, we have learned that in protostomes, while the anus usually does form secondarily, the blastopore does not always give rise to the mouth, especially among animals in the large clade known as Spiralia (annelids, molluscs, nemerteans, and others). And even within Spiralia's sister clade Ecdysozoa, we now know that deuterostomy can occur. For example, both nematomorphs and priapulans appear to have deuterostomous development, with the blastopore giving rise to the anus (at the vegetal pole) and the mouth arising at the animal pole. Gene expression studies have shown that in *Priapulus caudatus*, typical metazoan foregut and hindgut gene expression accompanies this development, and the hindgut/posterior markers *brachyury* (*bra*) and *caudal* (*cdx*) are expressed as the anus emerges from the blastopore. Furthermore, continuing developmental work is revealing that many species of crustaceans also express a form of deuterostomy. And in Chaetognatha gastrulation occurs by invagination of the presumptive endoderm, leaving no blastocoel—the blastopore marks the eventual posterior end of the animal, and both mouth and anus form secondarily, thus also a deuterostomous-like development. In fact, evidence is accumulating that mouth formation from oral ectoderm (in the animal hemisphere), typical of deuterostomy, may be ancestral in both protostomes and deuterostomes, and perhaps in Bilateria itself.

BOX 10A Classification of Bilateria Used in This Book

BILATERIA

Phylum Xenacoelomorpha

NEPHROZOA

PROTOSTOMIA

Spiralia

Phylum Dicyemida (= Rhombozoa)

Gnathifera
Phylum Chaetognatha
Phylum Gnathostomulida
Phylum Rotifera
Phylum Micrognathozoa

Platytrochozoa
Phylum Entoprocta
Phylum Cycliophora

Lophotrochozoa
Phylum Mollusca
Phylum Nemertea
Phylum Annelida*

Lophophorata
Phylum Phoronida
Phylum Bryozoa
Phylum Brachiopoda

Rouphozoa
Phylum Gastrotricha
Phylum Platyhelminthes

Ecdysozoa

Scalidophora**
Phylum Kinorhyncha
Phylum Priapula
Phylum Loricifera

Nematoida
Phylum Nematoda
Phylum Nematomorpha

Panarthropoda
Phylum Tardigrada
Phylum Onychophora
Phylum Arthropoda
Suphylum Chelicerata

Mandibulata
Subphylum Myriapoda

Pancrustacea
Subphylum Crustacea***
Subphylum Hexapoda

DEUTEROSTOMIA
Phylum Chordata
Subphylum Cephalochordata
Subphylum Urochordata
Subphylum Vertebrata

Ambulcraria
Phylum Hemichordata
Phylum Echinodermata

*Annelida includes Sipuncula, Echiura, and Orthonectida
**Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
***Paraphyletic (excludes Hexapoda)

So, we see that although the names Protostomia and Deuterostomia are still used for the two clades of Bilateria, the names themselves are no longer perfectly descriptive—they are **legacy names**. It has been suggested that new names should be coined for these two large groups, but as yet there has been no agreement on what those names might be. The 23 phyla belonging to Protostomia include the largest—Arthropoda (over a million described living species) and Mollusca (nearly 80,000 described living species)—and the smallest animal phyla (Micrognathozoa and Cycliophora; one and two described species each, although several undescribed species are known to exist in these small phyla).

Today, the groups Protostomia and Deuterostomia constitute clades based mostly on molecular phylogenetic evidence, and morphological and developmental synapomorphies defining them remain rather ambiguous. A likely ancestral trait of the Protostomia, as it is now constituted, is a central nervous system with a dorsal cerebral ganglion that usually has circumesophageal connectives to a pair of ventral nerve cords. However, there are deviations in this nervous system pattern likely linked to other changes in body morphology that have evolved over the past 500+ million years, especially in sessile and burrowing animals. Probable synapomorphies of Deuterostomia are a trimeric body coelom condition and pharyngeal gill slits, at least primitively (trimery is lacking in the phylum Chordata, and gill slits are absent in extant echinoderms but may have been present in some extinct, stem-group echinoderms). Although still somewhat controversial, the position of the phylum Xenacoelomorpha (acoels, nemertodermatids, and *Xenoturbella*) appears to be basal within Bilateria, this group not aligning strongly with either protostomes or deuterostomes (Box 10A), although some studies have placed xenacoelomorphans within deuterostomes. Protostomes and deuterostomes are viewed as sister groups comprising a clade called Nephrozoa.

Spiralia and Ecdysozoa

Protostomes are composed of two subclades—Spiralia (15 phyla) and Ecdysozoa (8 phyla). Like Protostomia, these clades

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are based primarily on molecular phylogenetics. However, it is likely that spiral cleavage is an ancestral trait for the Spiralia even though it has been lost or modified in some phyla (e.g., the three lophophorate phyla). Spiral cleavage does not occur outside Spiralia, and it does occur in at least some members of the three main spiralian subclades: Gnathifera, Rouphozoa, and Lophotrochozoa. Although not all members of the clade Spiralia demonstrate clear spiral cleavage, we retain the term as a well-known legacy name. Spiral cleavage was described in Chapter 4, but to remind you—it is a highly stereotyped embryo cleavage pattern in which the 4d cell (the "mesentoblast") gives rise to most of the mesoderm of the adult individual. A caveat of gnathiferan development is that no one has yet been able to determine cell fates, and only a superficial report of spiralian development for a species of gnathostomulid is available. Many spiralians also generate some mesoderm from micromeres of the second or third quartet that are primarily responsible for ectoderm formation (thus it is called ectomesoderm) and this commonly gives rise to larval musculature. Also, in spiral cleavage the embryonic cell divisions shift between dextral and sinistral cleavages in an alternating chirality pattern of development. Spiralia is an ancient clade, and fossils from the Ediacaran Period Doushantuo Formation (China) have even been interpreted as spiral-cleaving embryos.

Some spiral-cleaving animals have a unique larval type, called the trochophore larva (e.g., Mollusca, Annelida, and possibly some others), and the clade name "Trochozoa" has been proposed for those phyla, although this clade gets very mixed support in molecular trees and appears not to be monophyletic. The phylogenetic relationships of the spiralian phyla remain to be sorted out, and so far their deep ancestry has defied clear resolution. However, several clades within Spiralia do seem to be well supported, and we recognize these (see Box 10A). Thus, we identify two main subclades of spiralians (excluding Dicyemida)—Gnathifera (4 phyla; see Chapter 11) and Platytrochozoa (10 phyla; covered in Chapters 12–17). Ecdysozoans are covered in Chapters 18–24.

The Phylum Dicyemida (= Rhombozoa)

Dicyemidans were first described by A. Krohn in Germany in 1839.[1] But it was not until 1876 that a careful study of these unusual creatures was published by the Belgian zoologist Edouard van Beneden. He was convinced that these odd symbionts represented a "link" between the protists and the Metazoa, and it was van Beneden who coined the name "Mesozoa" (= middle animals) to emphasize this point of view, although that name and concept have no phylogenetic basis. Stunkard (1982) considered the phylum (which he called Rhombozoa, to avoid confusion with the order Dicyemida) as a class of "Mesozoa" comprising the orders Dicyemida and Heterocyemida. Most workers today no longer use these two orders and, instead, recognize three families: Conocyemidae, Dicyemidae, and Kantharellidae.

Dicyemidans have a simple, solid body construction—there are no body cavities or differentiated organs. No symmetry exists. An outer layer of somatic/nutritive cells surrounds an inner reproductive cell. Species that have been examined lack a layered extracellular matrix (EMC) and basement membrane, although type IV collagen (localized intracellularly) has been shown by immunolabeling and further studies are needed. All are obligate symbionts in the renal sacs of cephalopod molluscs. Over 120 species have been described, from about 40 species of cephalopods. However, based on the number of known cephalopod species yet to be examined for these symbionts, it is likely that a great many dicyemidans remain undescribed. Infection rates of cephalopods are higher in temperate seas than in the tropics/subtropics. Most of the described dicyemidans live in benthic octopuses, but *Dicyemennea gracile* is a symbiont in cuttlefish of the genus *Sepia*.

The current protocols for recognizing species of dicyemidans, based on morphological traits, appear inadequate. Using molecular methods, Eshragh and Leander (2015) showed that multiple "species" of dicyemidans, from three species of cephalopods, were actually a single polymorphic species in each host. This suggests that the ~120 described morphospecies (based largely on the anatomy of the polar cap) could be a considerable overestimate, and most hosts may harbor only a single species of dicyemidan.

Recent molecular studies—including sequencing of 18S rRNA and other genes, the presence of the *Dox*C gene (which encodes a spiralian peptide), and patterns of Hox (and other genes) expression—all suggest that dicyemidans are probably highly reduced and specialized symbionts in the protostome clade Spiralia. Beyond that, however, their phylogenetic ties remain uncertain. It is quite possible that by the fifth edition of *Invertebrates*, we will have discovered that these odd little creatures are highly specialized symbionts belonging to another spiralian phylum.

Anatomy and Biology of Dicyemidans

Adult dicyemidans are very small, just 0.5 to 3 mm long (see Box 10B). They have from about 9 to 41 body

[1]We use the diminutives "dicyemidan" for the phylum name, and "dicyemid" for the family name.

BOX 10B Characteristics of the Phylum Dicyemida

1. Small (0.5–3 mm), poorly understood, obligate symbionts that live in the renal sacs of cephalopods (octopuses, squids, and cuttlefish); life outside cephalopod hosts is unknown
2. Body simple, asymmetrical, and with a solid construction; without body cavities or differentiated organs
3. Young dicyemidans swim in the host's urine by ciliary action, but when they mature they attach to the inner lining of the nephridia by their polar caps; feed by consuming particulate and molecular nutrients from the host's urine
4. An outer layer of somatic/nutritive cells surrounds a large inner reproductive cell (the axial cell), in which there are smaller cells called axoblasts that float in the cytoplasm
5. Two adult forms known: nematogens produce vermiform embryos asexually from an agamete in the axoblasts of the axial cell; sexually motivated vermiforms are rhombogens, which produce two distinct types of infusoriform embryos (sometimes called larvae) from fertilized eggs
6. Molecular studies suggest dicyemidans may be highly reduced and specialized symbionts in the clade Spiralia

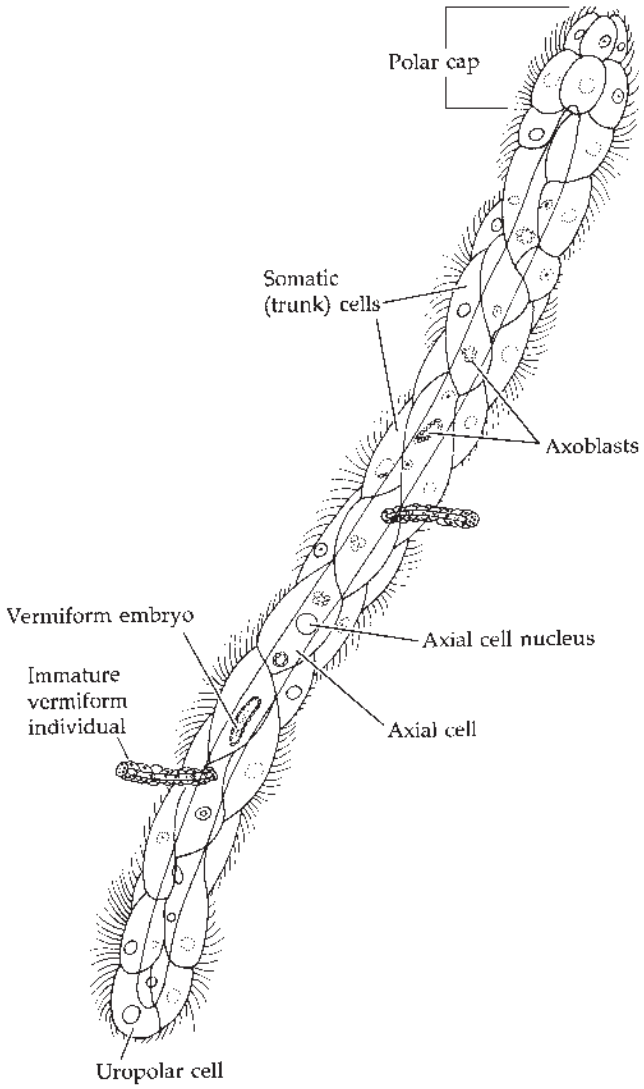

FIGURE 10.1 Nematogen of *Dicyema* (Dicyemida).

cells, depending on the species—one of the smallest cell counts among the Metazoa. As in other Bilateria, dicyemidans have been shown to have three types of cell-cell junctions: septate, adherens, and gap junctions. There are two adult forms, **nematogens** and **rhombogens** that have nearly the same organization but that produce two distinct types of embryos (which are sometimes called "larvae").[2] Nematogens produce **vermiform embryos** asexually from an agamete in the axoblast (see the Life Cycles section), whereas rhombogens sexually produce **infusoriform embryos** from fertilized eggs.

The body of a nematogen consists of an outer sheath of 8–40 ciliated **somatic cells**, the number of which has been constant for most, but not all, species that have been examined, and a single long, interior **axial cell** which is covered by the outer somatic cells (Figure 10.1).[3] The axial cell contains a large polypoid nucleus and intracellular stem cells called **axoblasts**. Eight or nine somatic cells at the anterior end form a distinctive **polar cap** (or **calotte**). Immediately behind the polar cap are two **parapolar cells**. The rest of the somatic cells are sometimes called "trunk cells"; the two posterior-most cells are the **uropolar cells**.

Young dicyemidans are motile and swim about in the host cephalopod's urine by ciliary action. The adults, however, attach to the inner lining of the nephridia by their polar caps. There is no conclusive evidence that these animals cause damage to their hosts, but when present in very high numbers they may interfere with the normal flow of fluids through the nephridia. They attach by inserting the polar cap into renal tubules or crypts of the host's kidney. Nematogens consume particulate and molecular nutrients from the host's urine by phagocytotic and pinocytotic action of their somatic cells. Once the adult has attached to the host, the somatic cilia might serve to keep fluids moving over the body, bringing nutrients

[2]Because the reported differences between rhombogens and nematogens are not consistently found, some workers prefer to simply call them sexual and asexual vermiform adults, respectively.

[3]Constancy in the number of cells (in a given organ, or in the entire body of an animal) is called "eutely," and it is a feature of certain microscopic or near-microscopic animals.

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in contact with the surface cells. Although in nature dicyemidans appear to be obligatorily associated with cephalopods, they have been successfully maintained in experimental nutrient media.

Life Cycles

What we know so far about dicyemidan life history is rather bizarre, and the stages of the dicyemidan life cycle that occur outside the host are still incompletely known. The host-dwelling portion of the life cycle includes both asexual and sexual processes, but without a regular alternation between them. Adult dicyemidans thus produce two kinds of offspring. The name "dicyemid" derives from the presence of these two different types of embryos during their life cycle. The nematogen stage produces the vermiform embryo formed asexually as axoblasts develop into **agamete cells**; these grow to become new worms (the nematogens and rhombogens) in the renal sac of the host. Vermiform stages consist of an axial cell and a single layer of 8 to 30 ciliated peripheral cells (a number that is constant for a species). The rhombogen stage produces the **infusoriform embryos**, which develop from fertilized eggs produced around hermaphroditic "gonads" called **infusorigens**, and these eventually escape the host to enter the sea. Infusoriforms consist of 37 to 39 cells, including 4 large internal cells known as urn cells, each containing a germinal cell. There is evidence that a high population density in the renal sac may cause the shift from asexual to sexual reproduction, the infusoriform embryos escaping from the renal sac in search of a new host. How they find their new hosts is unknown. Notably, in sexual reproduction, both fertilization and embryonic development occur within the worm's body.

Asexual reproduction is curious indeed. The cytoplasm of the single axial cell of the nematogen contains numerous tiny cells called **axoblasts**. Immature vermiform organisms are produced asexually by an embryogeny-like process of these individual axoblast cells within the parent axial cell (see Figures 10.2 and 10.3). The first division of an axoblast is unequal and produces a large presumptive axial cell and a small

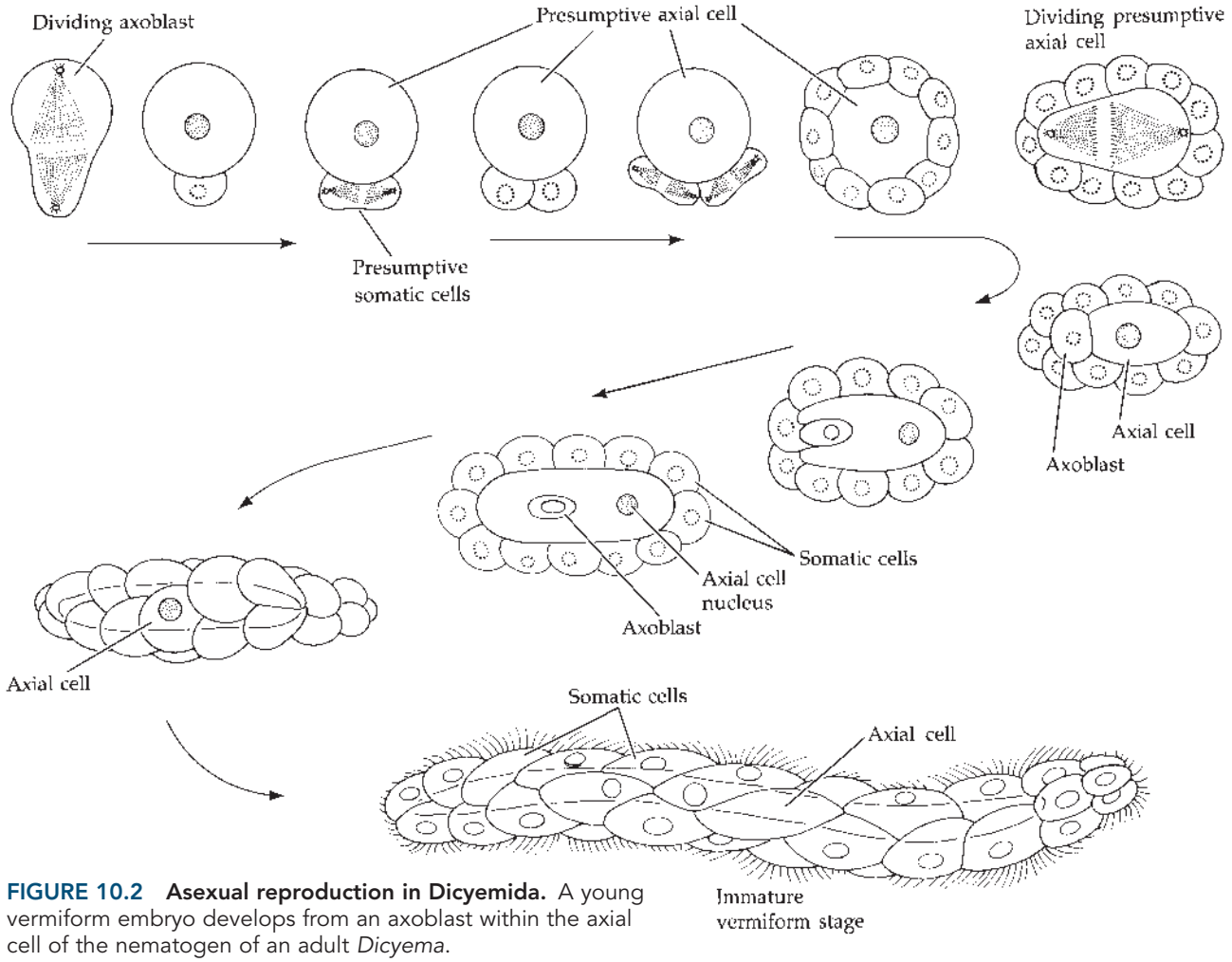

FIGURE 10.2 Asexual reproduction in Dicyemida. A young vermiform embryo develops from an axoblast within the axial cell of the nematogen of an adult *Dicyema*.

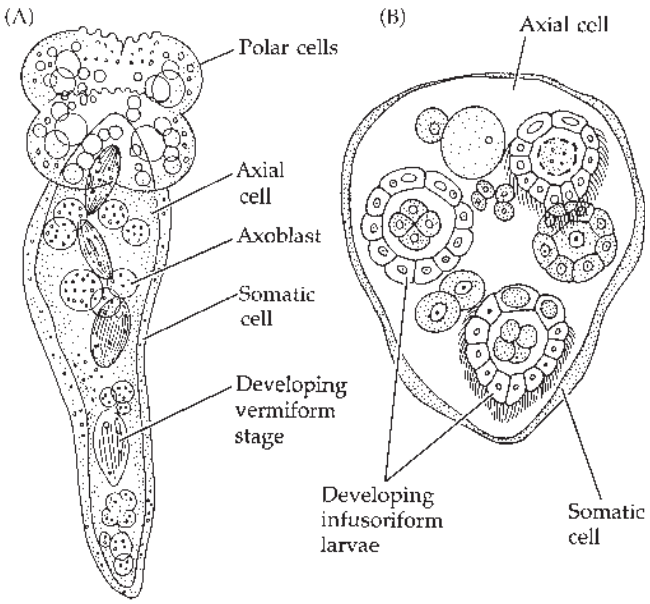

FIGURE 10.3 The dicyemidan *Conocyema*.
(A) Vermiform adult. (B) During the reproductive phase, infusoriform larvae are formed within the adult's axial cell (cross section).

presumptive somatic cell. The presumptive somatic cell divides repeatedly, and its daughter cells move by an epiboly-like process (rapid growth of animal pole ectodermal cells to from a sheetlike covering to the vegetal cells) to enclose the presumptive axial cell, which has not yet divided. When this inner cell finally does divide, it does so unequally, and the smaller daughter cell is then engulfed by the larger one! The larger cell becomes the progeny's axial cell proper with its single nucleus, and the smaller engulfed cell becomes the progenitor of all future axoblasts within that axial cell. The "embryo," which now consists of its own central axial cell surrounded by somatic cells, elongates, and the somatic cells develop cilia. The resulting structure is a miniature vermiform organism. The immature vermiform organism leaves the parent nematogen and swims about in the nephridial fluids. Eventually it attaches to the host and enters the adult stage of the life cycle.

Once the vermiform adults become sexually "motivated," they are called rhombogens, and their somatic cells usually enlarge as they become filled with yolky material (Figure 10.4 and chapter opener photo). The axoblast of a rhombogen develops into multicellular structures called **infusorigens**, each consisting of an outer layer of ova and an inner mass of sperm (Figure 10.4B). The infusorigens are retained within a vacuole of the parent's axial cell, and they are functionally hermaphroditic gonads. In each infusorigen, the centrally located sperm fertilize the peripherally arranged ova, each zygote then developing into a ciliated infusoriform larva (Figure 10.4C). This embryo has a fixed number of cells; the two anterior-most cells—called apical cells—contain high-density substances within their cytoplasm. The rest of the surface cells are ciliated and form a sheath around a ring of capsule cells, which in turn enclose four central cells. The number of infusorigens, and the embryos they produce, seems to be related to the size of the adult rhombogen. The infusoriform embryos escape from the parent vermiform adult and pass out of the host's body with the urine.

The development of several species has been studied, and there is no clear evidence of germ-layer formation

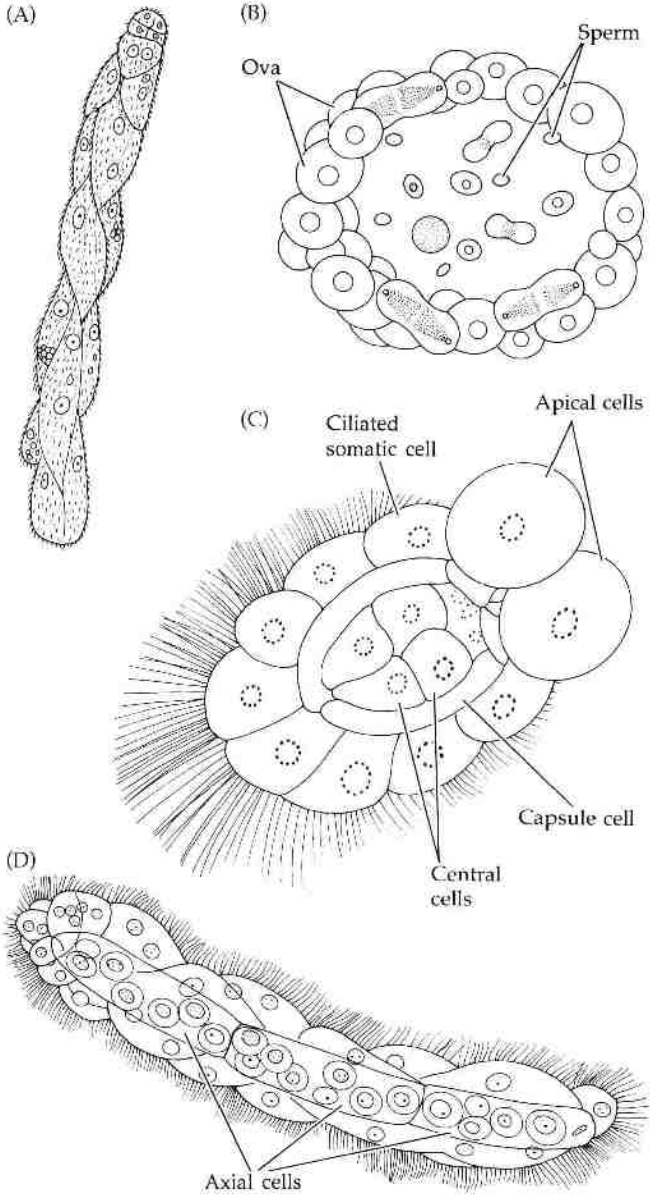

FIGURE 10.4 Sexual reproduction in Dicyemida.
(A) Adult, sexual (rhombogen) form. (B) Infusorigen of sperm and ova formed within the axial cell of the adult. (C) Infusoriform embryo produced by fertilization. (D) Stem nematogen with three axial cells.

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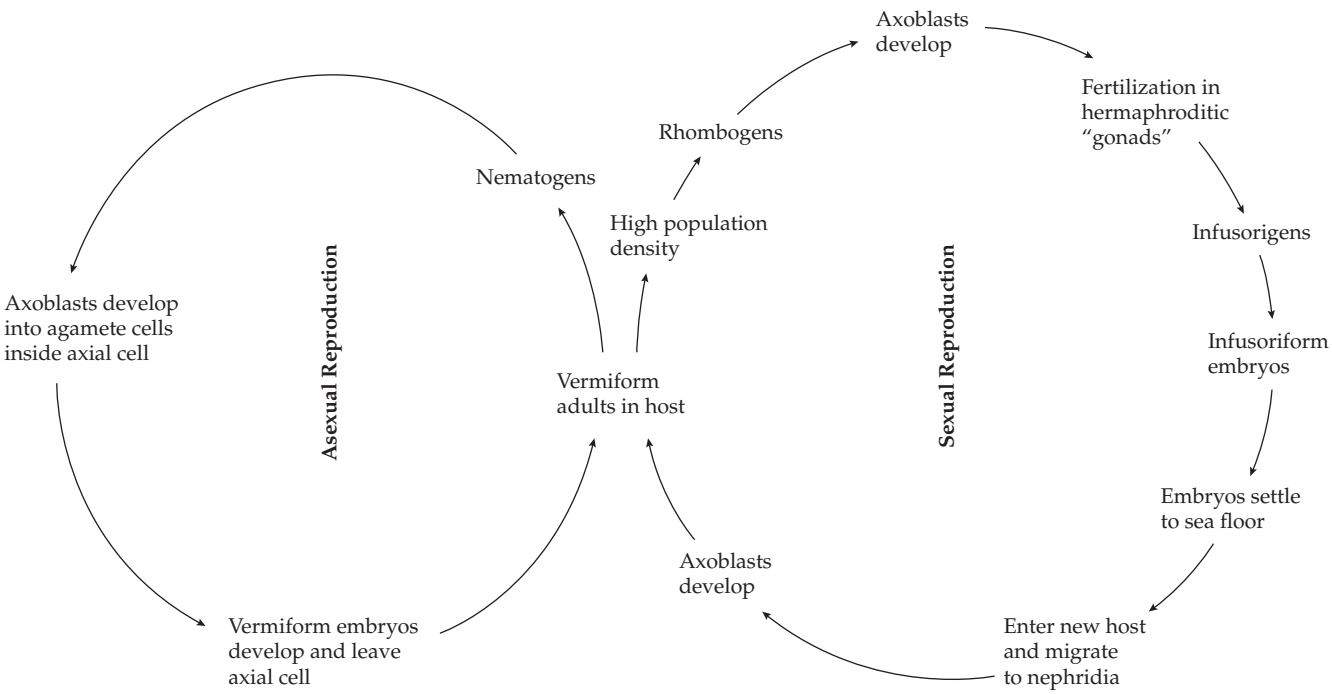

FIGURE 10.5 **Life cycle of a dicyemidan, illustrating the two pathways of sexual and asexual reproduction.**

in the development of the infusoriform embryo, with a rough distinction only as outer and inner cells. The outer cells occupy the dorsal and caudal surfaces of the embryo, and the inner cells are derived from the blastomeres of the vegetal hemisphere. The innermost germinal cells are derived from the cells that form the vegetal pole. The cleavage pattern of sexually produced embryos in *Dicyema japonicum* has been described as holoblastic and spiral, although it is not a typical kind of spiral cleavage. A cavity (the urn cavity) appears among the ventral internal cells, but this small space is interpreted to appear secondarily and not to be a blastocoel.

The events of the dicyemidan life cycle that occur outside the cephalopod host remain a mystery. Some workers have held to the view that the infusoriform embryo enters an intermediate host (presumably some benthic invertebrate), but most of the evidence to date suggests that this is not the case. While much remains to be learned, the following scenario seems plausible. After leaving the host, the infusoriform embryo sinks to the bottom of the ocean—the dense contents of the apical cells serving as ballast. The embryo, or some persisting part of the embryo (perhaps the innermost four cells), enters another cephalopod host. This infectious individual travels through the host, probably via the circulatory system, and enters the nephridia, where it becomes a so-called stem nematogen (Figure 10.4D). The stem nematogen is similar to the vermiform adult except that the former has three axial cells rather than one. Axoblasts within the axial cells of the stem nematogen give rise to more vermiform adults, just as the axoblasts within the adults described earlier did. The vermiform adults produce more individuals like themselves until the onset of sexual reproduction is triggered again, presumably by the high population density. This putative life cycle is schematically represented in Figure 10.5.

Chapter Summary

This chapter introduced you to large and important clades within the Bilateria (i.e., Protostomia and Spiralia) and to the enigmatic phylum Dicyemida (= Rhombozoa). In protostomes, while the anus usually forms secondarily, the blastopore does not always give rise to the mouth, especially among animals in the large clade known as Spiralia. Thus, the clade Protostomia is based primarily on molecular phylogenetic evidence, and morphological and developmental synapomorphies are rather ambiguous. A likely ancestral trait of the Protostomia is a central nervous system with a dorsal cerebral ganglion that usually has circumesophageal connectives to a pair of ventral nerve cords. However, there are deviations in this nervous system pattern likely linked to other changes in body morphology that have evolved over the past 500+ million years. Protostomes

(*Continued*)

Chapter Summary (*continued*)

are composed of two subclades—Spiralia (15 phyla) and Ecdysozoa (8 phyla). Like Protostomia, these clades are also based primarily on molecular phylogenetics, although several synapomorphies may be present in Ecdysozoa, especially in relation to the molting of the cuticle and the lack of locomotory cilia. However, it is likely that spiral cleavage is an ancestral trait for the Spiralia even though it has been lost or modified in many spiralian phyla (e.g., rotifers, chaetognaths, gastrotrichs, and the three lophophorate phyla). Important future research areas are the resolution of phylogenetic relationships within Protostomia and Spiralia.

The spiralian phylum Dicyemida has a simple, solid body construction, without symmetry, body cavities, or differentiated organs. An outer layer of somatic/nutritive cells surrounds an inner reproductive cell. All dicyemidans are obligate symbionts in the renal sacs of cephalopod molluscs, with over 120 species described. Future research should address the phylogenetic relationship of Dicyemida among the other spiralians and unravel the full life history of dicyemidans, especially outside the body of the host cephalopods.

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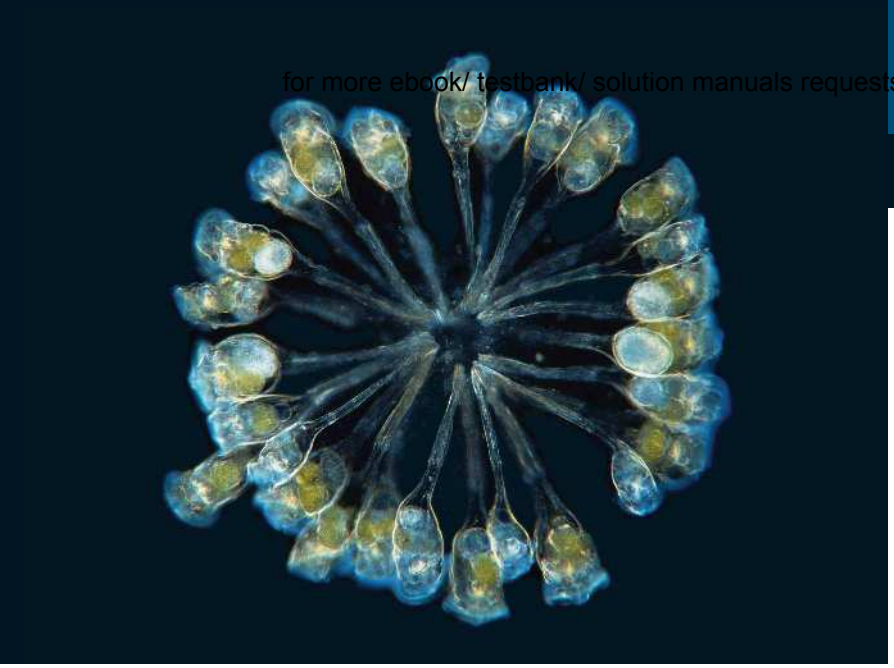

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CHAPTER 11

Gnathifera

The Phyla Gnathostomulida, Rotifera (including Acanthocephala), Micrognathozoa, and Chaetognatha

The spiralian protostome clade Gnathifera includes four phyla: Gnathostomulida, Rotifera (including the Acanthocephala), Micrognathozoa, and Chaetognatha. The name is derived from the Greek *gnathos*, "jaw," and the Latin *fera*, "to bear," and it refers to the presence of pharyngeal hard parts or "jaws." While jaws are present in most gnathiferan species, some derived lineages lack them, the assumption being they have been lost secondarily. Despite the small size of many (e.g., gnathostomulids, rotifers, and micrognathozoans), gnathiferans show a remarkable complexity of anatomy, especially in their jaw structures. Although the relationships of the four phyla among themselves are yet to be fully resolved, the composition of the jaws, built of translucent rods with an electron-dense core, and the jaws having pincers caudally articulating into unpaired pedicles (absent in chaetognaths), are unifying features of the clade. The organization of the muscular and nervous systems of gnathiferans is also very similar.

Until the mid-1990s, the Gnathostomulida and Rotifera were pooled together with other microscopic taxa in artificial groups such as "Aschelminthes" or "Nemathelminthes"—catchall categories that were more or less solely characterized by being microscopic taxa with uncertain phylogenetic positions. At that time the Acanthocephala was treated as a distinct phylum; but despite their macroscopic size and endoparasitic biology, they were already considered closely related to the Rotifera based on ultrastructural similarities in their integument. During the 1990s, a number of researchers began to

The sections on Gnathostomulida and Rotifera were revised by Martin Vinther Sørensen. The section on Micrognathozoa was revised by Katrine Worsaae and Reinhardt Møbjerg Kristensen. The section on Chaetognatha was revised by George Shinn.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

investigate the phylogenetic positions of the aschelminth phyla. In 1995, two important papers (by W. H. Ahlrichs, R. M. Rieger, and S. Tyler) suggested a sister-group relationship between Gnathostomulida and Rotifera, based on a proposed homology between the jaws in the two groups. The homology was supported by ultrastructural data from transmission electron microscopy that demonstrated jaws in both taxa that were composed of rodlike elements that in cross section appear as translucent areas with a central, electron-dense core. Ahlrichs referred to this grouping as Gnathifera, and he further suggested that the endoparasitic acanthocephalans were actually highly modified rotifers.

At the same time that Gnathifera was taking its shape, a new kind of animal was discovered in mosses from a cold spring in Greenland. It was a tiny, microscopic invertebrate that in some respects resembled a rotifer, and in other ways a gnathostomulid, but also possessed several characteristics that were not found in any other groups. Transmission electron microscopy showed that the ultrastructure of the jaws was nearly identical with that of Rotifera and Gnathostomulida. But the new creatures' jaws were even more complex and had more elements than those found in the two other gnathiferan phyla. In 2000, six years after its discovery, R. M. Kristensen and P. Funch named the animal *Limnognathia maerski* and assigned it to a new animal group, Micrognathozoa, which three years later was recognized as a third gnathiferan phylum.

Molecular phylogenetics strongly suggests Rotifera is the sister group to Micrognathozoa, and they also share similarities in the ultrastructure of their integuments. Both free-living rotifers and acanthocephalans have a syncytial epidermis in which the outer cuticle has been replaced by an intracellular protein lamina in the epidermal cells. Micrognathozoa has a regular nonsyncytial epidermis, but a similar intracellular protein lamina is found in its dorsal epidermal plates, and the presence of this lamina is considered synapomorphic for Micrognathozoa and Rotifera. In addition, the sister-group relationship of rotifers and micrognathozoans is supported by a large array of neuroanatomical characters and by the presence of a skeletal lamina in rotifers and in the dorsal epithelium of micrognathozoans.

Based on ultrastructural similarities in their integuments, the microscopic rotifers and the macroscopic acanthocephalans had long been considered as likely sister taxa. However, evidence from molecular studies shows that Acanthocephala is not the sister group of Rotifera, but actually evolved from within the Rotifera—presumably as a clade that became obligately endoparasitic and subsequently went through a series of dramatic morphological modifications and changes. Modern acanthocephalans are so modified and adapted to their endoparasitic lifestyle that it is hard to find comparative morphological characters that would place them inside Rotifera, but the molecular support is strong and includes studies based on selected target loci and transcriptomes, as well as the complete mitochondrial genomes. Indeed, the sister group of Acanthocephala appears to be Seisonidea, also parasitic, and the two in turn comprise the sister group to Bdelloidea.

The first record of an arrow worm was by the Dutch naturalist Martinus Slabber in 1775, but the name Chaetognatha was not proposed until 80 years later by the German zoologist Rudolf Leuckart (in 1854). The systematic position of the group has been hotly debated ever since. Arrow worms have been at times allied with molluscs, arthropods, and certain blastocoelomates (particularly nematodes). For many years chaetognaths were considered deuterostomes, based on developmental features and their tripartite body coelom. But their placement among the deuterostomes never seemed a fully comfortable match. Even the American zoologist Libbie Hyman, while treating them as deuterostomes, found it a less-than-perfect fit. Modern research is beginning to resolve some long-standing issues. For example, arrow worms are, without doubt, coelomate animals (other gnathiferans are acoelomate or blastocoelomate), and molecular phylogenetics has clearly shown them to be protostomes. The coelomate nature of arrow worms was revealed by early embryological studies, but it took transmission electron microscopy to demonstrate that the adult body cavities are completely lined by mesodermally derived tissues.

In the late 1990s morphological arguments were made that chaetognaths are gnathiferans, based partly upon the proposed homology between their movable grasping spines and the buccal apparatus of rotifers, gnathostomulids, and micrognathozoans. An analysis of Hox genes (in 2017) also identified similarities between Chaetognatha and Rotifera (although gnathostomulids and micrognathozoans were not included in that analysis). In 2019, two phylogenomic analyses using large data sets also suggested they are part of the Gnathifera clade, perhaps even the sister group to the remaining gnathiferans. In addition, it has been proposed that the high chitin content of the spines and teeth, and the structures of the chitinous cuticle of the chaetognath head could be homologous with the chitinous parts and membranes of the pharynx in gnathiferans. Although we include Chaetognatha in the clade Gnathifera, the exact position of this phylum is still not fully resolved, and we look forward to new information and ideas on their relationships over the coming years. Chaetognaths, of course, exhibit classical deuterostome embryological features such as formation of the mesoderm from the gut (enterocoely) and secondary opening of the mouth, although they are

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now regarded as members of the Protostomia. The sister group of Gnathifera remains unclear.

In 1911, the American paleontologist Charles Walcott described *Amiskwia sagittiformis* from the middle Cambrian Burgess Shale as a chaetognath. The 7–31 mm creature had a conspicuous head with tentacles, hard gnathiferan-like jaws with 8 to 10 teeth, an elongate trunk, and lateral and caudal fins. It was later claimed to be a nemertean worm or perhaps a mollusc, and then still later deemed "unassignable" to any modern phylum. Quite recently, *Amiskwia* was again reassigned to Chaetognatha, based in part upon its bilaterally arranged set of head structures that have been interpreted as jaws situated within an expanded pharyngeal complex (said to be homologous with those of gnathiferans). However, a reevaluation in 2019 examined Walcott's original 5 specimens and 21 previously unpublished specimens from the same locality and concluded that while *Amiskwia* is a gnathiferan, it may not be a chaetognath. Arguing against it being a crown chaetognath, *Amiskwia* possessed cephalic tentacles and lacked the external grasping spines diagnostic of modern chaetognaths. Although the precise assignment of *Amiskwia* remains elusive, it seems reasonably certain that it belongs to the clade Gnathifera, either as a stem chaetognath or as some other gnathiferan creature. A second species, *Amiskwia sinica*, has been described from the lower Cambrian of China. Importantly, these and other fossils show that lower and middle Cambrian fauna of >500 million years ago included large coelomate spiralians.

Phylum Gnathostomulida: The Gnathostomulids

The phylum Gnathostomulida (Greek, *gnathos*, "jaw"; *stoma*, "mouth") includes about 100 species of minute vermiform hermaphroditic animals (Figure 11.1). These meiofaunal creatures were first described by Peter Ax in 1956 as free-living platyhelminths (then referred to as turbellarians) but given their own phylum rank by Rupert Riedl in 1969. Gnathostomulids are found worldwide, interstitially in marine sands mixed with detritus, from the intertidal zone to depths of hundreds of meters. These interstitial worms vary in body length, from 320 µm in *Problognathia minima* and up to typically 2 mm in the long and slender filospermoids. The longest, *Haplognathia belizensis*, reaches a body length of 3.6 mm! The gnathostomulid body is usually divisible into head, trunk, and in some species a narrow tail region. Distinguishing features of this phylum include a unique jawed pharyngeal apparatus and monociliated epidermal cells (Box 11A). The currently described 100 species and 26 genera are divided into two orders.

GNATHOSTOMULIDA CLASSIFICATION

ORDER FILOSPERMOIDEA Body usually very elongate, with slender rostrum; jaws relatively simple; male parts without injectory penis; sperm filiform (with one 9+2 flagellum); female parts without vagina and bursa. (3 genera: *Cosmognathia*, *Haplognathia*, and *Pterognathia*)

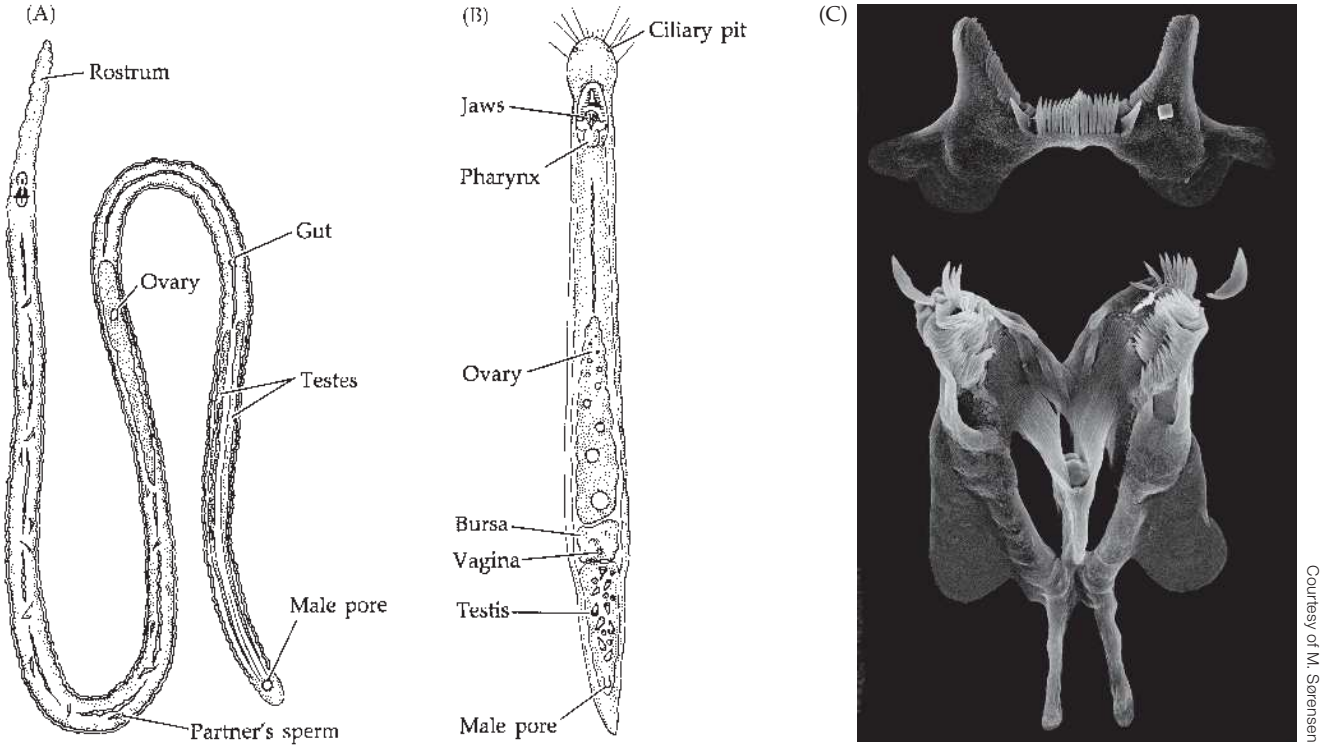

FIGURE 11.1 Representative Gnathostomulida. (A) *Haplognathia simplex*. (B) *Austrognatharia kirsteueri*. (C) Basal plate and jaws of *Gnathostomula armata*. (A,B after W. E. Sterrer. 1972. *Syst Zool* 21: 151–173.)

BOX 11A Characteristics of the Phylum Gnathostomulida

1. Triploblastic, bilateral, unsegmented, vermiform acoelomates
2. Epidermis monolayered; all epithelial cells monociliated
3. Gut incomplete (anus rudimentary, vestigial, or absent)
4. Pharynx with unique, complex jaw apparatus
5. Without circulatory system or special gas exchange structures
6. Excretion through protonephridia with monociliated terminal cells
7. Hermaphroditic
8. Cleavage spiral and development direct
9. Found in marine, interstitial environments

ORDER BURSOVAGINOIDEA Body usually not extremely elongate relative to width; head with shorter rostrum and often a constriction in the neck area; jaws complex; male parts with penis, with or without a stylet; sperm cells aflagellate, either dwarf cells or giant conuli; female parts with bursa and usually a vagina. (23 genera, including *Agnathiella*, *Austrognatharia*, *Gnathostomula*, and *Onychognathia*)

The Gnathostomulid Body Plan

Body Wall, Support, and Locomotion

Each outer epithelial cell bears a single cilium by which the animal moves in a gliding motion. This condition has received special attention, as it is not common among protostomes. Movement is aided by body contortions produced by the contraction of thin strands of subepidermal (cross-striated) muscle fibers. These actions, plus reversible ciliary beating, facilitate twisting, turning, and crawling among sand grains and allow limited swimming in some species. Mucous gland cells occur in the epidermis of at least some species. The body is supported by its more or less solid construction, with a loose mesenchyme filling the area between the internal organs.

Nutrition, Circulation, Excretion, and Gas Exchange

The mouth is located on the ventral surface at the "head-trunk" junction and leads inward to a complex muscular pharynx armed with pincerlike jaws and in some species an unpaired anterior basal plate (Figure 11.1). Curiously, the two known species of the genus *Agnathiella* have no jaws at all. Gnathostomulids ingest bacteria and fungi by snapping actions made by the jaws or by scraping with the basal plate. The pharynx connects with a simple, elongate, saclike gut. A permanent, functional anus is not present, but in a few gnathostomulids a tissue connection between the posterior end of the gut and the overlying epidermis has been observed. This enigmatic feature has been variously interpreted as either a temporary anal connection to the exterior, as the remnant of an anus that has been evolutionarily lost, or as an incipient anus that has yet to fully develop.

Gnathostomulids depend largely on diffusion for circulation and gas exchange. The excretory system is composed of serially arranged protonephridia that stretch from the pharyngeal region to the terminal end of the body. Like the epithelial cells, the protonephridial terminal cells are monociliated.

Nervous System

The nervous system is intraepidermal and unsegmented. It consists of a brain, a buccal ganglion, and up to four dorsal and five ventral longitudinal nerve cords, connected by up to three commissures. Various sensory organs, such as sensory ciliary pits and stiff sensoria formed by groups of joined cilia from monociliated cells, are concentrated in the head region. Gnathostomulid specialists have attached a formidable array of names to these structures, which are of major taxonomic significance.

Reproduction and Development

Gnathostomulids are hermaphrodites. The male reproductive system includes one or two testes generally located in the posterior part of the trunk and tail; the female system consists of a single large ovary (Figure 11.1). Members of the order Bursovaginoidea possess a vaginal orifice and a sperm-storage bursa, both associated with the female gonopore, and a penis in the male system; members of the order Filospermoidea lack these structures.

Mating has been only superficially studied in gnathostomulids. Although the method of sperm transfer is not certain, suggestions include filiform sperm of filospermoid gnathostomulids boring through the body wall. Among some bursovaginoid gnathostomulids, sperm is transferred directly to the mating partner's bursa by hypodermic impregnation via the sclerotized penis stylet. In any case, these animals appear to be gregarious, to rely on internal fertilization, and to deposit zygotes singly in their habitat. Cleavage is reported as spiral, and development is direct, but clear details on embryonic and juvenile development are scarce.

Phylum Rotifera: The Free-Living Rotifers

The phylum Rotifera (Latin *rota*, "wheel"; *fera*, "to bear") includes around 2,150 described species, most of which are microscopic (100 to 1,000 μm long) and

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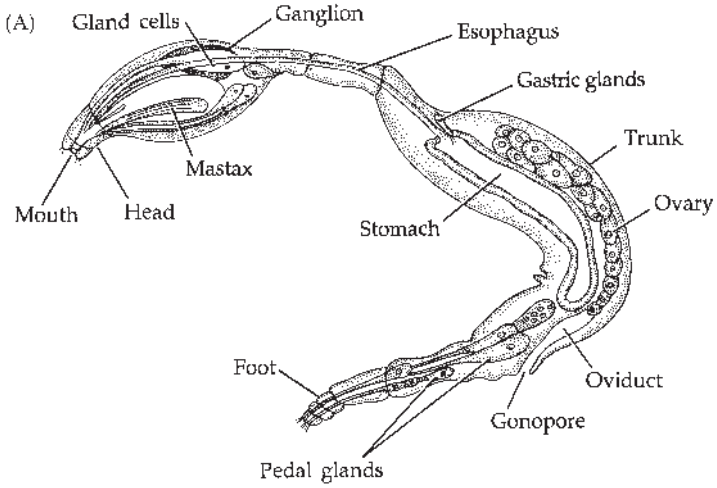
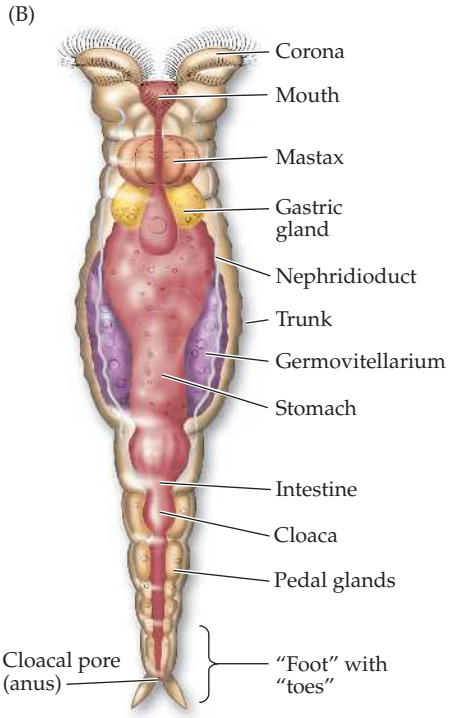
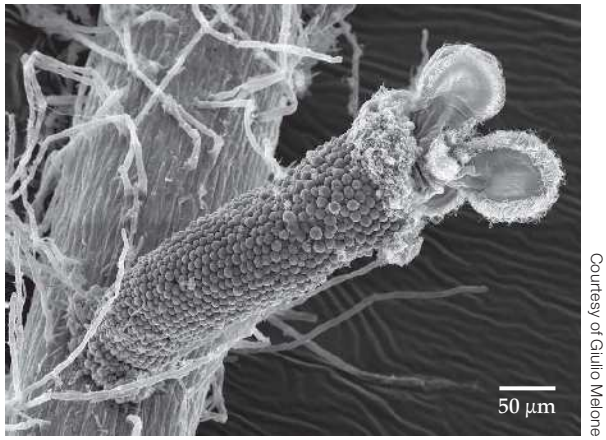
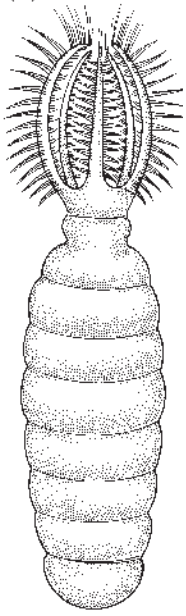
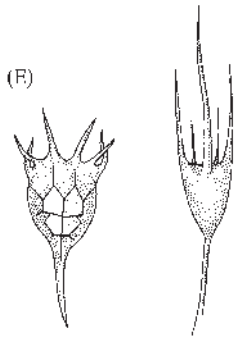










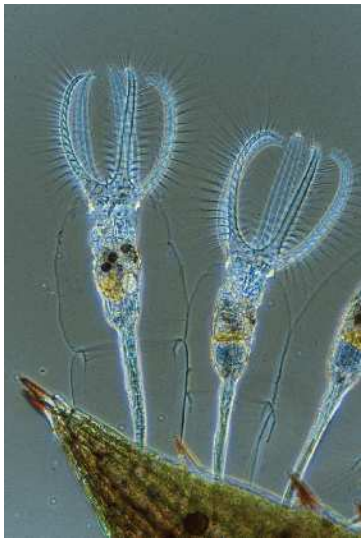


FIGURE 11.2 Representative rotifers. (A) *Paraseison annulatus* (subclass Seisonidea), a marine ectoparasitic rotifer from the gills of *Nebalia*. (B) *Philodina roseola* (subclass Bdelloidea). (C–F) Members of the subclass Monogononta. (C) SEM of a sessile rotifer (*Floscularia*) that lives inside a tube that it constructs from small pellets composed of bacteria and detritus. (D) *Stephanoceros*, one of the strange collothecacean rotifers with the corona modified as a trap. (E) The loricae of two loricate rotifers. (F) Live specimens of *Stephanoceros*.

free-living, and about 1,200 parasitic acanthocephalans. The macroscopic acanthocephalan worms represent a rotifer ingroup, but due to their considerable differences in biology and morphology, they will be discussed separately. Thus, in this first section the name Rotifera refers to the microscopic, free-living rotifers only. The name "Syndermata" was proposed some time ago for a clade of Rotifera + Acanthocephala, but with the current understanding that these are not sister groups (the latter arose as a clade from within the former), that name is no longer useful.

Rotifers were known to early microscopists, such as Antony van Leeuwenhoek in the late seventeenth century; at that time they were lumped with the protists as "animalcules" (mainly because of their small size). Besides the 2,000 or so known, morphologically recognizable species, complexes of cryptic species have been demonstrated for several morphospecies. For example, *Brachionus plicatilis* has been subject to intensive studies, and at least 22 putative cryptic species have been identified within this species complex. As a whole, rotifers remain poorly characterized systematically, and many named species have ambiguous descriptions and have not been rediscovered since their original discovery.

Despite their small size, rotifers are actually quite complex and display a variety of body forms (Figure 11.2). Most are solitary, but some sessile forms are colonial, a few of which secrete gelatinous casings into

which the individuals can retract. They are most common in fresh water, but many species are also known from marine or brackish habitats and from damp soil or the water film on mosses. A few species are even ecto- or endoparasites in other invertebrates. They often comprise an important component of the plankton of fresh and brackish waters.

The body comprises three general regions—the head, trunk, and foot. The head bears a ciliary organ called the **corona**. When active, the coronal cilia often give the impression of a pair of rotating wheels, hence the derivation of the phylum name; in fact, rotifers were historically called "wheel animalcules." Members of this phylum are further characterized by being blastocoelomate and having an integument without an outer cuticle, but instead with a supportive intracellular protein lamina. They usually show a tendency to eutely and have a complete gut, protonephridia, and often syncytial tissues or organs (Box 11B). The pharynx is modified as a **mastax** comprising sets of internal jaws called **trophi**. The morphology of the trophi is of considerable systematic importance and often the main character to identify species and genera.

A highly surprising discovery about rotifers was made in 2008, when it was found that bdelloid rotifers have incorporated large numbers of genes from diverse foreign sources into their genomes, including bacteria, fungi, and plants. These foreign genes have accumulated mainly in the telomeric regions at the ends of chromosomes, and at least most of them seem to retain their functional integrity. Bdelloids also are prone to infection by an aggressive fungus, *Rotirephthora angustispora*, that eats them from the inside out. Experiments have shown that the longer the rotifers remain dry and in a state of dormancy, the more likely they are to avoid infection by *R. angustispora*, suggesting that their adaptation for quiescence may also be an adaptation to avoid fungal predation.

BOX 11B Characteristics of the Phylum Rotifera

1. Triploblastic, bilateral, unsegmented blastocoelomates
2. Gut complete and regionally specialized
3. Pharynx modified as a mastax, containing jawlike elements called "trophi"
4. Anterior end bearing variable ciliated fields as a corona
5. Posterior end often bearing toes and adhesive glands
6. Epidermis syncytial, with fixed number of nuclei; secreting extracellular glycocalyx and intracellular skeletal lamina (the latter forming a lorica in some species)
7. With protonephridia, but no special circulatory or gas exchange structures
8. With unique retrocerebral organ
9. Males generally reduced or absent; parthenogenesis common
10. With modified spiral cleavage
11. Found in marine, freshwater, or semiterrestrial environments; sessile or free-swimming
12. Cryptobiosis present in many species

CLASSIFICATION OF PHYLUM ROTIFERA

CLASS HEMIROTIFERA

Endoparasites, ectoparasites, or free-living; this group is recognized only by molecular data.

SUBCLASS ACANTHOCEPHALA Macroscopic endoparasites; see the Phylum Rotifera, Subclass Acanthocephala section.

SUBCLASS BDELLOIDEA (Figure 11.2B) Free-living, found mostly in fresh water, moist soils, and foliage (also marine, and terrestrial); corona typically well developed; trophi ramate (grinding). (20 genera, all asexual, e.g., *Adineta*, *Embata*, *Habrotrocha*, *Philodina*, *Rotaria*, and *Zelinkiella*)

SUBCLASS SEISONIDEA (Figure 11.2A) Epizoic on the marine leptostracan crustacean *Nebalia*; corona reduced to bristles; trophi fulcrate (piercing); males fully developed and considered to have diploid chromosome numbers; sexual females produce only mictic ova. (2 genera: *Paraseison* and *Seison*)

CLASS EUROTIFERA

SUBCLASS MONOGONONTA (Figure 11.2C–F) Predominately freshwater, some are marine; swimmers, creepers, or sessile; corona and trophi variable; males typically short-lived, haploid, and reduced in size and complexity; sexual reproduction probably occurs at some point in the life history of all species; mictic and amictic ova produced in many species; single germovitellarium. (121 genera, e.g., *Asplanchna*, *Brachionus*, *Collotheca*, *Dicranophorus*, *Encentrum*, *Epiphanes*, *Euchlanis*, *Floscularia*, *Lecane*, *Notommata*, *Proales*, *Synchaeta*, *Testudinella*)

The Rotifer Body Plan

Body Wall, General External Anatomy, and the Corona

Most rotifers have a soft, gelatinous glycocalyx outside their epidermis, but unlike many other invertebrates, they have no external cuticle. Instead they have an intracellular protein lamina located inside the epidermis, for protection and stabilization of the body. This protein lamina may vary considerably in thickness and flexibility among the genera and families. Species with a very thin protein lamina are called "illoricate

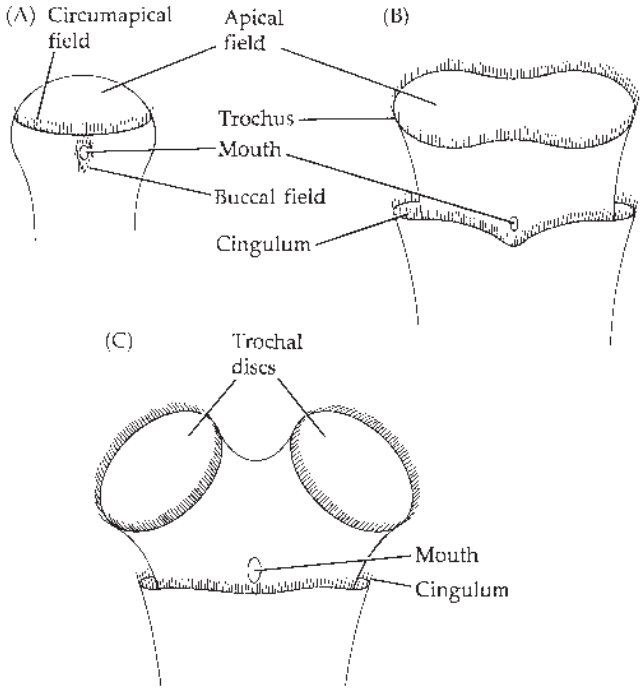


FIGURE 11.3 Modifications of the corona among selected rotifer types. (A) The presumed plesiomorphic condition has buccal and circumapical fields. (B) The circumapical field is separated into trochus and cingulum. The trochus is lobed, like that of *Floscularia*. (C) The trochus is separated into two trochal discs, as found in many bdelloid rotifers.

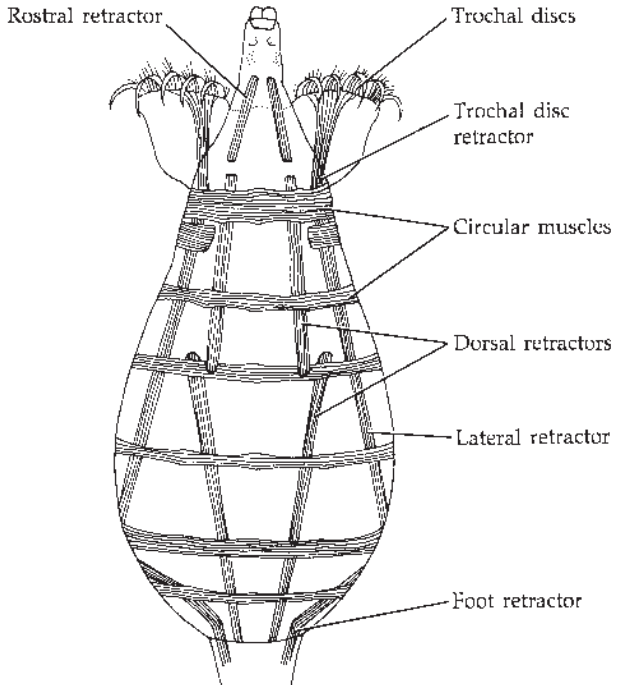


FIGURE 11.4 Major muscle bands of the bdelloid rotifer, *Rotaria* (dorsal view).

rotifers," and they often appear as very flexible and hyaline animals that contract completely when disturbed. In other species, the intracellular protein lamina is much thicker and forms a body armor, called a **lorica**, and these species are referred to as "loricate rotifers." Another special condition of the rotifer epidermis is the absence of walls between the epidermal cells, meaning that the epidermis is a syncytium with about 900 to 1,000 nuclei.

The body surface of many illoricate rotifers is annulated, allowing flexibility. The surface of loricate species often bears spines, tubercles, or other sculpturing (Figure 11.2E). Many rotifers bear single dorsal and paired lateral sensory antennae arising from various regions of the body. A **foot** is not present in all species, but when present it is often elongate, with cuticular annuli that permit a telescoping action. The distal portion of the foot often bears spines, or a pair of "toes" through which ducts from the pedal glands pass. The secretion from the pedal glands enables the rotifer to attach temporarily to the substratum. The foot is absent in some swimming forms (e.g., *Asplanchna*) and is modified for permanent attachment in sessile types (e.g., *Floscularia*).

The **corona** is the most characteristic external feature of rotifers. Its morphology varies greatly, and in some groups, the corona is an important taxonomic character. The presumed primitive condition is shown in Figure 11.3A. A well-developed patch of cilia surrounds the anteroventral mouth. This patch is the buccal field, or circumoral field, and it extends dorsally around the head as a ciliary ring called the circumapical field. The extreme anterior part of the head bordered by this ciliary ring is the apical field. The corona has evolved to a variety of modified forms in different rotifer taxa. In some species, the buccal field is quite reduced, and the circumapical field is separated into two ciliary rings, one slightly anterior to the other (Figure 11.3B). The anterior-most ring is called the trochus, the other the cingulum. In many bdelloid rotifers the trochus is a pair of well-defined anterolateral rings of cilia called trochal discs (Figure 11.4C), which may be retracted or extended for locomotion and feeding. It is the metachronal ciliary waves along these trochal discs that impart the impression of rotating wheels.

Many organs and tissues of rotifers display eutely: cell or nuclear number constancy. This condition is established during development, and there are no mitotic cell divisions in the body following ontogeny.

Body Cavity, Support, and Locomotion

Beneath the epidermis are various circular and longitudinal muscle bands (Figure 11.4); there are no sheets or layers of body wall muscles. The internal organs lie within a typically spacious, fluid-filled blastocoelom.

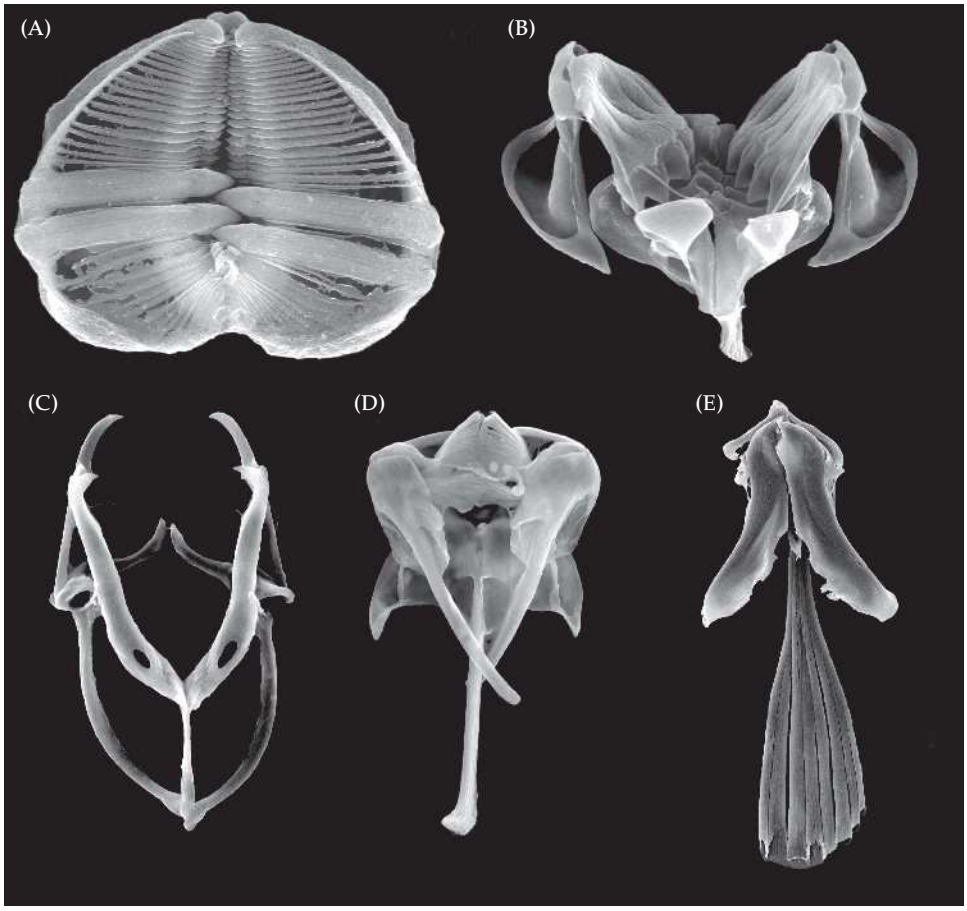
In the absence of a thick, muscular body wall, body support and shape are maintained by the intraepidermal skeletal lamina and the hydrostatic skeleton provided by the body cavity. In loricate species the integument is only flexible enough to allow slight changes in shape, so increases in hydrostatic pressure within the body cavity can be used to protrude body parts (e.g., foot, head, and corona). These parts are also protracted and retracted by various muscles (Figure 11.4), each consisting of only one or two cells.

Although a few rotifers are sessile, most are motile and quite active, moving about by swimming or creeping like an inchworm. Some are exclusively either swimmers or crawlers, but many are capable of both methods of locomotion. Swimming is accomplished by beating the coronal cilia, forcing water posteriorly along the body, and driving the animal forward, sometimes in a spiral path. When creeping, a rotifer attaches its foot with secretions from the pedal glands, then elongates its body and extends forward. It attaches the extended anterior end to the substratum, releases its foot, and draws its body forward by muscular contraction.

Feeding and Digestion

Rotifers display a variety of feeding methods, depending upon the structure of the corona (Figure 11.3), the mastax, and the trophi (Figure 11.5). Ciliary suspension feeders have well-developed coronal ciliation and a grinding mastax. These forms include the bdelloids, which have trochal discs and ramate trophi (Figure 11.5A), and a number of monogonont rotifers, which have a separate trochus and cingulum and a malleate trophus (Figure 11.5B). These forms typically feed on organic detritus or minute organisms. The feeding current is produced by the action of the cilia of the trochus (or trochal discs), which beat in a direction opposite to that of the cilia of the cingulum. Particles are drawn into a ciliated food groove that lies between these opposing ciliary bands and are carried to the buccal field and mouth.

Raptorial feeding is common in many species of Monogononta. Coronal ciliation in these rotifers is often reduced or used exclusively for locomotion. Raptorial feeders obtain food by grasping it with protrusible, pincerlike mastax jaws; most possess either forcipate



Courtesy of M. Sorensen

FIGURE 11.5 SEMs showing different rotifer trophi types. (A) *Dissotrocha aculeata* with the ramate trophus type, found in all bdelloids. (B) *Brachionus calyciflorus* with the malleate trophus type that characterizes several monogonont families. (C) *Encentrum astridae* with forcipate trophi, found in the monogonont family Dicranophoridae. (D) *Resticula nyssa* with its virgate trophi, typical for Notommatidae and several other monogonont families. (E) *Paraseison kisfaludyi*, fulcrate trophi of the ectoparasitic Seisonidea.

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trophi (nonrotating) (Figure 11.5C) or incudate trophi (rotating 90°–180° during protrusion). Raptorial rotifers feed mainly on small animals but are known to ingest plant material as well. They may ingest their prey whole and subsequently grind it to smaller particles within the mastax, or they may pierce the body of the plant, protist, or animal with the tips of the mastax jaws and suck fluid from the prey (Figure 11.5D).

Some monogonont rotifers have adopted a trapping method of predation. In such cases the corona usually bears spines or setae arranged as a funnel-shaped trap (Figure 11.2D,F). The mouth in these trappers is located more or less in the middle of the ring of spines (rather than in the more typical anteroventral position); thus, captured prey is drawn to it by contraction of the trap elements. The mastax in trapping rotifers is often reduced.

A few rotifers have adopted symbiotic lifestyles. As noted in the classification scheme, seisonids live on marine leptostracan crustaceans of the genus *Nebalia*. These rotifers (*Seison* and *Paraseison*) crawl around the base of the legs and gills of their host, feeding on detritus and on the host's brooded eggs. It has been suggested that species of the predatory *Paraseison* may use the anterior tip of the fulcrum of their fulcrate trophi (Figure 11.5E) to pinch the cuticle of the leptostracan host and feed on its hemolymph. Some bdelloids (e.g., *Embata*) also live on the gills of crustaceans, particularly amphipods and decapods, and *Zelinkiella synaptae* lives on the integument of certain sea cucumbers and terebellid annelids. There are isolated examples of endoparasitic rotifers inhabiting hosts such as *Volvox* (a colonial protist), freshwater algae, snail egg cases, and the body cavities of certain annelids and terrestrial slugs. Little is known about nutrition in most of these species.

The digestive tract of most rotifers is complete and more or less straight (Figure 11.6A). (The anus has been secondarily lost in a few species, and some have a moderately coiled gut.) The mouth leads inward to the pharynx (mastax) either directly or via a short, ciliated buccal tube. Depending on the feeding method and food sources, swallowing is accomplished by various means, including ciliary action of the buccal field and buccal tube, or a pistonlike pumping action of certain elements of the mastax apparatus. The mastax is ectodermal in origin. Opening into the gut lumen just posterior to the mastax are ducts of the salivary glands. There are usually two to seven such glands; they are presumed to secrete digestive enzymes and perhaps lubricants aiding the movement of the trophi.

A short esophagus connects the mastax and stomach. A pair of gastric glands opens into the posterior end of the esophagus; these glands apparently secrete digestive enzymes. The walls of the esophagus and gastric glands are often syncytial. The stomach is generally thick walled and may be cellular or syncytial, usually comprising a specific number of cells or nuclei in each species (Figure 11.6B). The intestine is short and leads to the anus, which is located dorsally near the posterior end of the trunk. Except for *Asplanchna*, which lacks a hindgut, an expanded cloaca connects the intestine and anus. The oviduct and usually the nephridioducts also empty into this cloaca.

Digestion probably begins in the lumen of the mastax and is completed extracellularly in the stomach, where absorption occurs. In one large and enigmatic group of bdelloids the stomach lacks a lumen. Although much remains to be learned about the digestive physiology of rotifers, some experimental work indicates that diet has multiple and important effects on various aspects of their biology, including the size and shape of individuals as well as some life cycle activities.

Circulation, Gas Exchange, Excretion, and Osmoregulation

Rotifers have no special organs for internal transport or for the exchange of gases between tissues and the environment. The blastocoelomic fluid provides

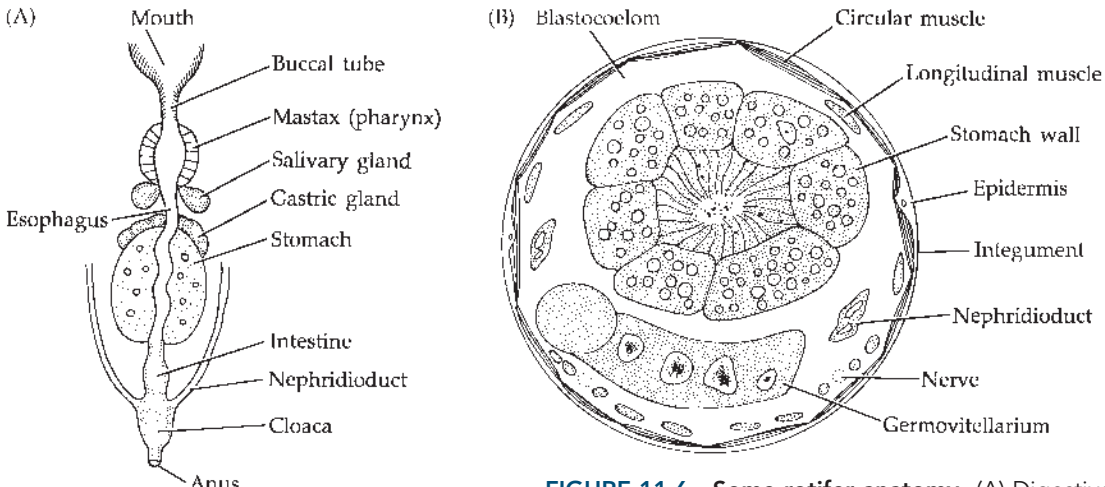

FIGURE 11.6 Some rotifer anatomy. (A) Digestive system of a rotifer. (B) Cross section through the trunk.

a medium for circulation within the body, which is aided by general movement and muscular activity. Small body size reduces diffusion distances and facilitates the transport and exchange of gases, nutrients, and wastes. These activities are further enhanced by the absence of linings and partitions within the body cavity, so the exchanges occur directly between the organ tissues and the body fluid. Gas exchange probably occurs over the general body surface wherever the integument is sufficiently thin.

Most rotifers possess one or several pairs of flame bulb protonephridia, located far forward in the body. A nephridioduct leads from each flame bulb to a collecting bladder, which in turn empties into the cloaca via a ventral pore. In some forms, especially the bdelloids, the ducts open directly into the cloaca, which is enlarged to act as a bladder (Figure 11.6A). The protonephridial system of rotifers is primarily osmoregulatory in function, and it is most active in freshwater forms. Excess water from the body cavity and probably from digestion is also pumped out via the anus by muscular contractions of the bladder. This "urine" is significantly hypotonic relative to the body fluids. It is likely that the protonephridia also remove nitrogenous excretory products from the body. This form of waste removal is probably supplemented by simple diffusion of wastes across permeable body wall surfaces.

Some rotifers (especially the freshwater and semiterrestrial bdelloids) are able to withstand extreme environmental stresses by entering a state of metabolic dormancy. They have been experimentally desiccated and kept in a dormant condition for as long as four years—reviving upon the addition of water. Some have survived freezing in liquid helium at –272°C and other severe stresses dreamed up by biologists.

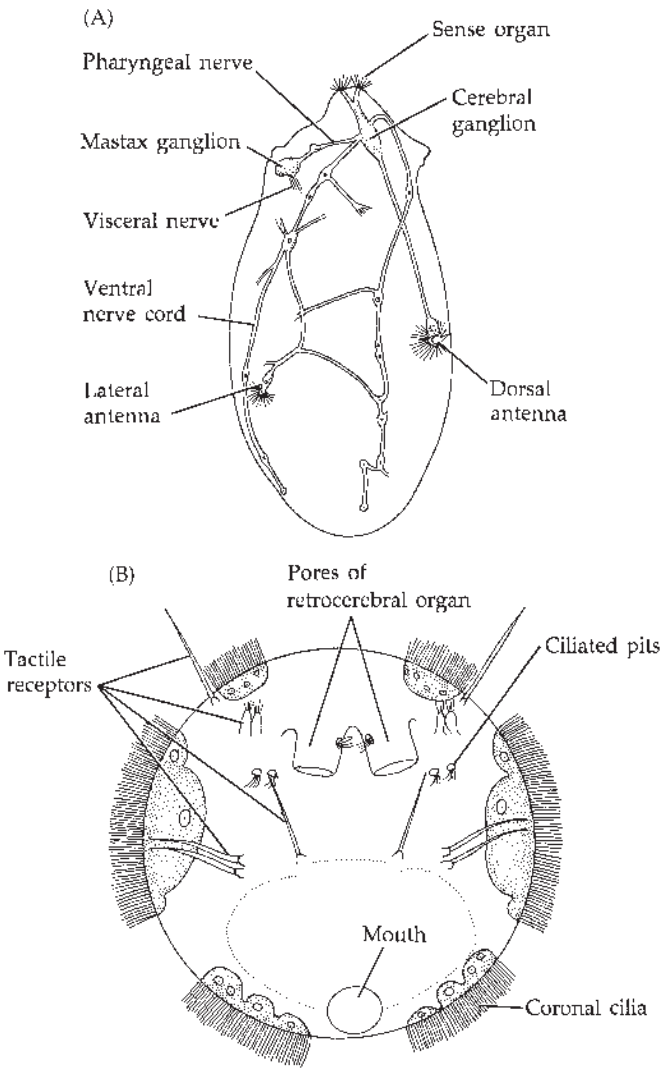

FIGURE 11.7 More rotifer anatomy. (A) The nervous system of *Asplanchna*. (B) The coronal area of *Euchlanis* (apical view). Note the various sense organs.

Nervous System and Sense Organs

The cerebral ganglion of rotifers is located dorsal to the mastax, in the neck region of the body. Several nerve tracts arise from the cerebral ganglion, some of which bear additional small ganglionic swellings (Figure 11.7A). There are usually two major longitudinal nerves, either both ventrolateral or one dorsal and one ventral.

The coronal area generally bears a variety of touch-sensitive bristles or spines and often a pair of ciliated pits thought to be chemoreceptors (Figure 11.7B). The dorsal and lateral antennae are probably tactile. Some rotifers bear sensory organs, which are arranged as a cluster of micropapillae encircling a pore. These organs may be tactile or chemosensory. Most of the errant rotifers possess at least one simple ocellus embedded in the cerebral ganglion. In some, this cerebral ocellus is accompanied by one or two pairs of lateral ocelli on the coronal surface, and sometimes by a pair of apical ocelli in the apical field. The lateral and apical ocelli are multicellular epidermal patches of photosensitive cells. In 1977 Pierre Clément described possible baro- or chemoreceptors in the body cavity that may help regulate internal pressure or fluid composition.

Associated with the cerebral ganglion is the so-called **retrocerebral organ**. This curious glandular structure gives rise to ducts that lead to the body surface in the apical field (Figure 11.7B). Though it was once thought to be sensory in function, more recent work suggests that it may secrete mucus to aid in crawling.

Reproduction and Development

Parthenogenesis is probably the most common method of reproduction among rotifers. Other forms of asexual reproduction are unknown, and most groups show only very weak powers of regeneration. Most rotifers are gonochoristic. However, other than the Seisonidea,

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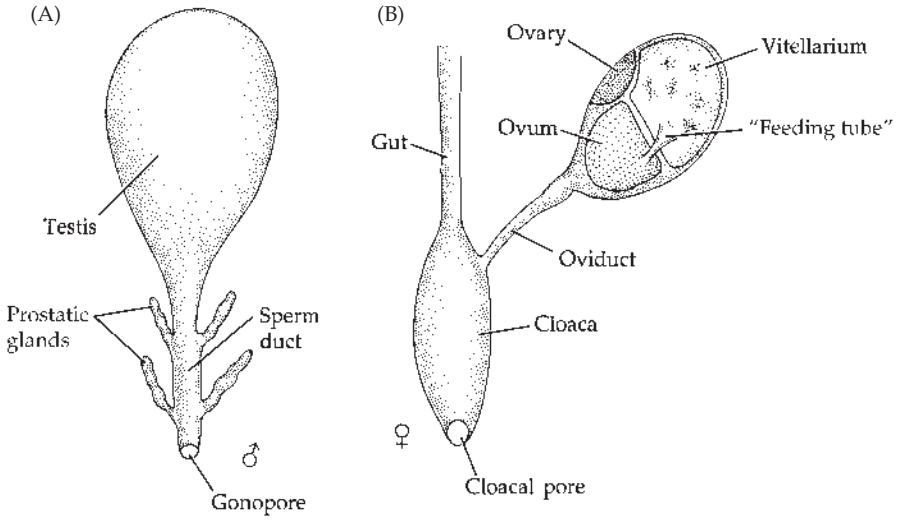


FIGURE 11.8 Reproductive systems from a generalized monogonont rotifer. (A) Male. (B) Female.

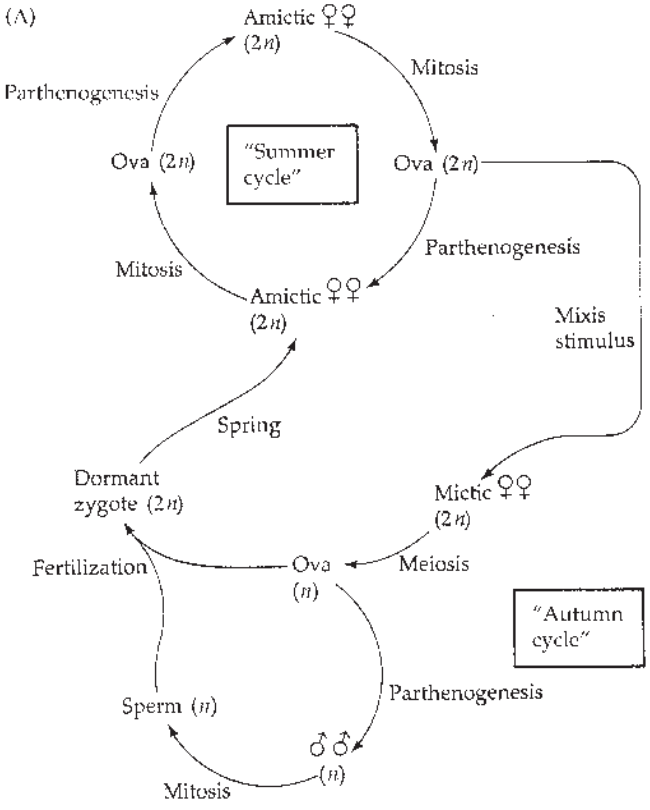
males either are reduced in abundance, size, and complexity and have haploid chromosome numbers (Monogononta) or do not exist (Bdelloidea). If you find a rotifer, the chances are good that it is a female.

The male reproductive system (Figure 11.8A) includes a single testis (paired in Seisonidea), a sperm duct, and a posterior gonopore whose wall is usually folded to produce a copulatory organ. Prostatic glands are sometimes present in the wall of the sperm duct. The males are short-lived and possess a reduced gut unconnected to the reproductive tract.

The female system includes paired (Bdelloidea) or single (Monogononta) syncytial germovitellaria (Figure 11.8B). Eggs are produced in the ovary and receive yolk directly from the vitellarium before passing along the oviduct to the cloaca; in those forms that have lost the intestinal portion of the gut (e.g., *Asplanchna*), the oviduct passes directly to the outside via a gonopore. There are no yolk glands in Seisonidea.

In rotifers with a male form, copulation occurs either by insertion of the male copulatory organ into the cloacal area of the female or by hypodermic impregnation. In the latter case, males attach to females at various points on the body and apparently inject sperm directly into the blastocoelom (through the body wall). The sperm somehow find their way to the female reproductive tract, where fertilization takes place. The number of eggs produced by an individual female is determined by the original, fixed number of ovarian nuclei—usually 20 or fewer, depending on the species. Once fertilized, the ova produce a series of encapsulating membranes and are then either attached to the substratum or carried externally or internally by the brooding female.

Parthenogenesis is generally the rule among bdelloids, but it is also a common and usually seasonal occurrence in monogononts, where it tends to alternate with sexual reproduction. This cycle (Figure 11.9A) is an adaptation to freshwater habitats that are subject to severe seasonal changes. During favorable conditions, females reproduce parthenogenetically through the production of mitotically derived diploid ova (amictic ova). These eggs develop into more females without fertilization.



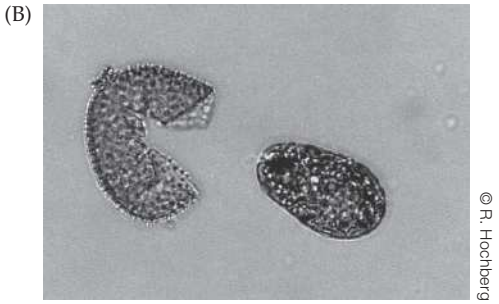


FIGURE 11.9 Life cycle of a monogonont rotifer. (A) Mictic/amictic alternation in the life cycle of a monogonont rotifer. (B) Micrograph of an amictic female hatching from an overwintering phase.

However, when ova from amictic females are subjected to particular environmental conditions (so-called mixis stimuli), they develop into mictic females, which then produce mictic (haploid) ova by meiosis. The exact stimulus apparently varies among different species and may include such factors as changes in day length, temperature, or food resources or increases in population density. Although these cycles are commonly termed summer and autumn cycles, this is a bit misleading because mixis can also occur during warm weather and many populations have several periods of mixis each year. Mictic ova require fertilization by male gametes to develop a new female individual, but if no males are present, the unfertilized mictic ova will instead develop into haploid males, which produce sperm by mitosis. These sperm fertilize other mictic ova, producing diploid, thick-walled, resting zygotes. The resting zygotic form is extremely resistant to low temperatures, desiccation, and other adverse environmental conditions. When favorable conditions return, the zygotes develop and hatch as amictic females (Figure 11.9B), completing the cycle.

Only a few studies have been conducted on the embryology of rotifers (see especially Pray 1965). In spite of the paucity of data, and some conflicting interpretations in the literature, it is generally thought that rotifers have modified spiral cleavage. However, detailed analyses of cell lineages are still needed to determine if the typical spiral pattern persists past the first couple of cell divisions, especially with regard to the origin of the mesoderm. The isolecithal ova undergo unequal holoblastic early cleavage to produce a stereoblastula. Gastrulation is by epiboly of the presumptive ectoderm and involution of the endoderm and mesoderm; the gastrula gradually hollows to produce the blastocoel, which persists as the adult body cavity. The mouth forms in the area of the blastopore. Definitive nuclear numbers are reached early in development for those organs and tissues displaying eutely.

Errant rotifers undergo direct development, hatching as mature or nearly mature individuals. Sessile forms pass through a short dispersal phase, sometimes called a larva, which resembles a typical swimming rotifer. The "larva" eventually settles and attaches to the substratum. In all cases, there is a total absence of cell division during postembryonic life (i.e., they are eutelic).

Many rotifers exhibit developmental polymorphism, a phenomenon also seen in some protists, arachnids, and insects. This is the expression of alternative morphotypes under different ecological conditions by organisms of a given genetic constitution (the differentiation of certain castes in social insects is one of the most remarkable examples of developmental polymorphism). In all such animals studied to date, the alternative adult morphotypes appear to be products of flexible developmental pathways, triggered by environmental cues and often mediated by internal mechanisms such as hormonal activities. In one well-studied genus of rotifers (*Asplanchna*), the environmental stimulus regulating which of several adult morphologies is produced is the presence of a specific molecular form of vitamin E, α-tocopherol. *Asplanchna* obtains tocopherol from its diet of algae or other plant material or when it preys on other herbivores (animals do not synthesize tocopherol). The chemical acts directly on the rotifer's developing tissues, where it stimulates differential growth of the syncytial hypodermis after cell division has ceased. Predator-induced morphologies also occur among rotifers. *Keratella slacki* eggs, in the presence of the predator *Asplanchna* (both are rotifers), are stimulated to develop into larger-bodied adults with a very long anterior spine, thus rendering them more difficult to eat.

Phylum Rotifera, Subclass Acanthocephala: The Acanthocephalans

As adults, the 1,200 or so described species of acanthocephalans are obligate intestinal parasites in vertebrates, particularly in birds and freshwater fishes. Larval development takes place in various arthropod intermediate hosts. The name Acanthocephala (Greek *acanthias*, "prickly"; *cephalo*, "head") derives from the presence of recurved hooks located on an eversible proboscis at the anterior end. The rest of the body forms a cylindrical or flattened trunk, often bearing rings of small spines. Most acanthocephalans are less than 20 cm long, although a

BOX 11C Characteristics of the Subclass Acanthocephala (Phylum Rotifera)

1. Triploblastic, bilateral, unsegmented blastocoelomates
2. Gut absent
3. Anterior end with hook-bearing proboscis
4. Tegument and muscles contain a unique system of channels called the lacunar system
5. Protonephridia absent except in a few species
6. With unique system of ligaments and ligament sacs partially partitioning the body cavity
7. With unique hydraulic structures called lemnisci that facilitate extension of proboscis
8. Gonochoristic
9. With modified spiral cleavage
10. All are obligate parasites in guts of vertebrates; many have complex life cycles with a so-called acanthor larva.

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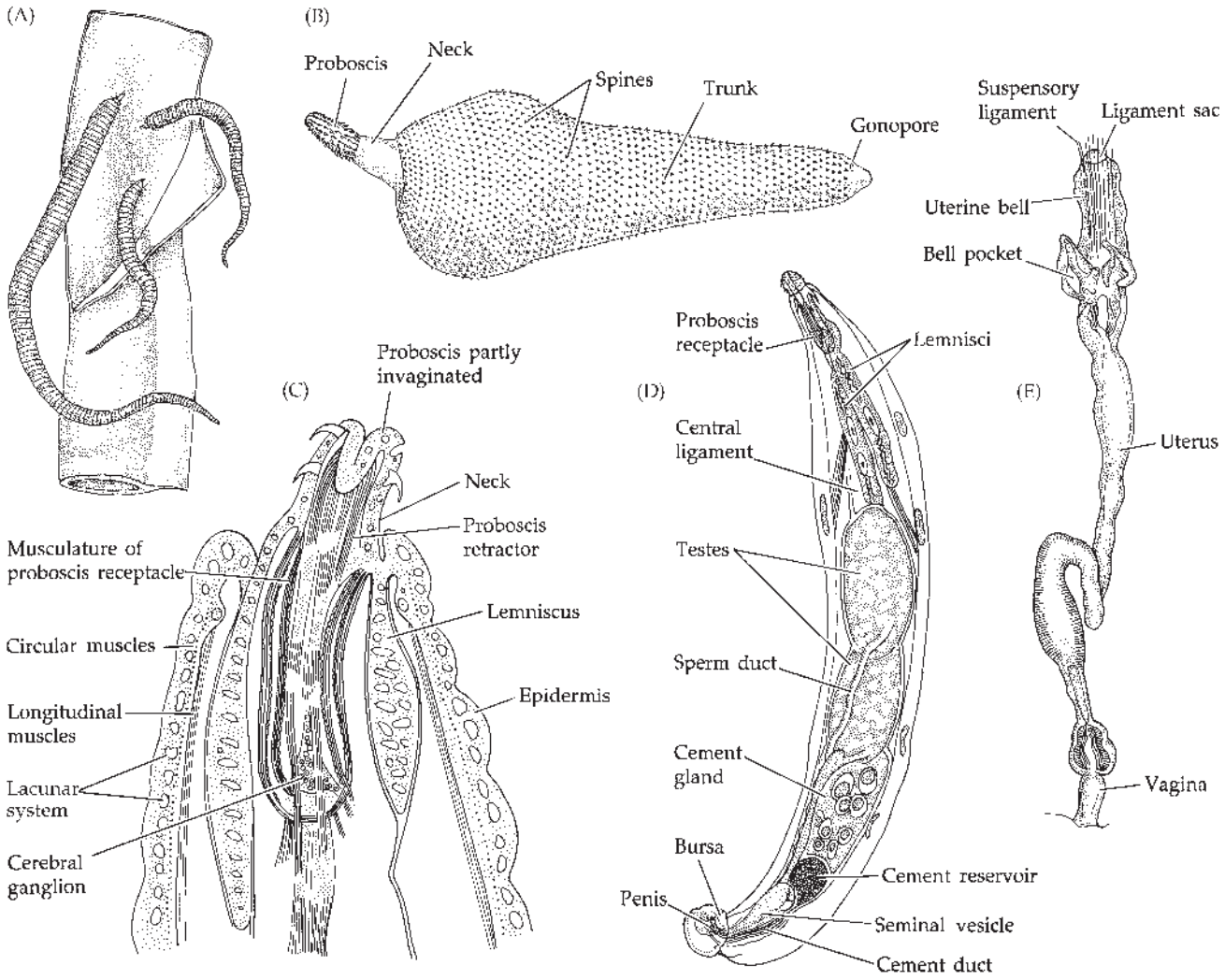

FIGURE 11.10 Representative acanthocephalans. (A) *Macracanthorhynchus hirudinaceus*, an archiacanthocephalan, attached to the intestinal wall of a pig. (B) *Corynosoma*, a palaeacanthocephalan found in aquatic birds and seals. (C) Longitudinal section through the anterior end of *Acanthocephalus* (class Palaeacanthocephala). (D) An adult male eoacanthocephalan (*Pallisentis fractus*). (E) The isolated female reproductive system of *Bolbosoma*. (E after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

few species exceed 60 cm in length; females are generally larger than males. The digestive tract has been completely lost, and except for the reproductive organs, there is significant structural and functional reduction of most other systems, a condition related to the parasitic lifestyles of these worms (Box 11C). The persisting organs lie within an open blastocoelom, partially partitioned by mesentery-like ligaments.

The acanthocephalans are usually divided into three groups based on the arrangement of proboscis hooks, the nature of the epidermal nuclei, spination patterns on the trunk, and the nature of the reproductive organs: Palaeacanthocephala (e.g., *Polymorphus, Corynosoma, Plagiorhynchus, Acanthocephalus*), Archiacanthocephala (e.g., *Moniliformis*), and Eoacanthocephala (e.g., *Neoechinorhynchus, Octospiniferoides*) (see Figure 11.10).

The Acanthocephalan Body Plan

Body Wall, Support, Attachment, and Nutrition

Adult acanthocephalans attach to their host's intestinal wall by their proboscis hooks, which are retractable into pockets, like the claws of a cat (Figure 11.10). In nearly all species, the proboscis itself is retractable into a deep proboscis receptacle, enabling the body to be pulled close to the host's intestinal mucosa. Nutrients provided by the host are absorbed through the parasite's body wall, and a gut is absent. The outer body wall is a multilayered,

syncytial, living tegument, which overlies sheets of circular and longitudinal muscles. The tegument includes layers of dense fibers as well as what appear to be sheets of plasma membrane, and an intracellular protein lamina, such as the one found in free-living rotifers. The tegument is perforated by numerous canals that connect to a complex set of unique circulatory channels called the **lacunar system** (Figure 11.10C). The tegumental channels near the body surface may facilitate pinocytosis of nutrients from the host. The body wall organization is such that each species has a distinct external appearance; some even appear to be segmented, but they are not.

At the junction of the proboscis and trunk, the epidermis extends inward as a pair of hydraulic sacs (**lemnisci**) that facilitate extension of the proboscis, as in free-living bdelloid rotifers; the proboscis is withdrawn by retractor muscles. The lemnisci are continuous with each other and with a ring-shaped canal near the anterior end of the body, whereas their distal ends float free in the blastocoelom. This arrangement may help to circulate nutrients and oxygen from the body to the proboscis.

One or two large sacs lined with connective tissue arise from the rear wall of the proboscis receptacle and extend posteriorly in the body. These structures support the reproductive organs and divide the body into dorsal and ventral **ligament sacs** in the archiacanthocephalans and eoacanthocephalans, or they produce a single ligament sac down the center of the body cavity in the palaeacanthocephalans (Figure 11.10D,E). Within the walls of these sacs are strands of fibrous tissue—the ligaments—that may represent remnants of the gut. The space between these internal organs is blastocoelomic.

The body is supported by the fibrous tegument and the hydrostatic qualities of the blastocoelom and lacunar system. The muscles and ligament sacs add some structural integrity to this support system, and canals of the lacunar system penetrate most of the muscles.

Circulation, Gas Exchange, and Excretion

Exchanges of nutrients, gases, and waste products occur by diffusion across the body wall, although some Archiacanthocephala possess a pair of protonephridia and a small bladder. Internal transport is by diffusion within the body cavity and by the lacunar system, the latter functioning as a unique sort of circulatory system, which permeates most body tissues. The lacunar fluid is moved about by action of the body wall muscles.

Nervous System

As in many obligate endoparasites, the nervous system and the sense organs of acanthocephalans are greatly reduced. A cerebral ganglion lies within the proboscis receptacle (Figure 11.10C) and gives rise to nerves to the body wall muscles, the proboscis, and the genital regions. Males possess a pair of genital ganglia. The proboscis bears several structures that are presumed to be tactile receptors, and small sensory pores occur at the tip and base of the proboscis. Males have what appear to be sense organs in the genital area, especially on the penis.

Reproduction and Development

Acanthocephalans are gonochoristic, and females are generally somewhat larger than males. In both sexes, the reproductive system is associated with the ligament sacs (Figure 11.10E). In males, paired testes (usually arranged in tandem) lie within a ligament sac and are drained by sperm ducts to a common seminal vesicle. Entering the seminal vesicle or the sperm ducts are six or eight cement glands, whose secretions serve to plug the female genital pore following copulation. When nephridia are present, they also drain into this system. The seminal vesicle leads to an eversible penis, which lies within a genital bursa connected to the gonopore. This gonopore is often called a cloacal pore because the bursa appears to be a remnant of the hindgut.

In females, a single mass of ovarian tissue forms within a ligament sac. Clumps of immature ova are released from this transient ovary and enter the body cavity, where they mature and are eventually fertilized. The female reproductive system comprises a gonopore, a vagina, and an elongate uterus that terminates internally in a complex open funnel called the **uterine bell** (Figure 11.10E). During mating the male everts the copulatory bursa and attaches it to the female gonopore. The penis is inserted into the vagina, sperm are transferred, and the vagina is neatly capped with cement. Sperm then travel up the female system, enter the body cavity through the uterine bell, and fertilize the eggs.

Much of the early development of acanthocephalans takes place within the body cavity of the female. Cleavage is holoblastic, unequal, and likened to a highly modified spiral pattern. A stereoblastula is produced, at which time the cell membranes break down to yield a syncytial condition. Eventually, a shelled **acanthor larva** is formed (Figure 11.11). The embryo leaves the mother's body at this (or an earlier) stage. Remarkably, the uterine bell "sorts" through the developing embryos by manipulating them with its muscular funnel; it accepts only the appropriate embryos into the uterus. Embryos in earlier stages are rejected and pushed back into the body cavity, where they continue development. The selected embryos pass through the uterus and out the genital pore and are eventually released with the host's feces.

Once outside the definitive host, the developing acanthocephalan must be ingested by an arthropod intermediate host—usually an insect or a crustacean—to continue its life cycle. The acanthor larva penetrates the gut wall of the intermediate host and enters the body cavity, where it develops into an **acanthella** and then into an

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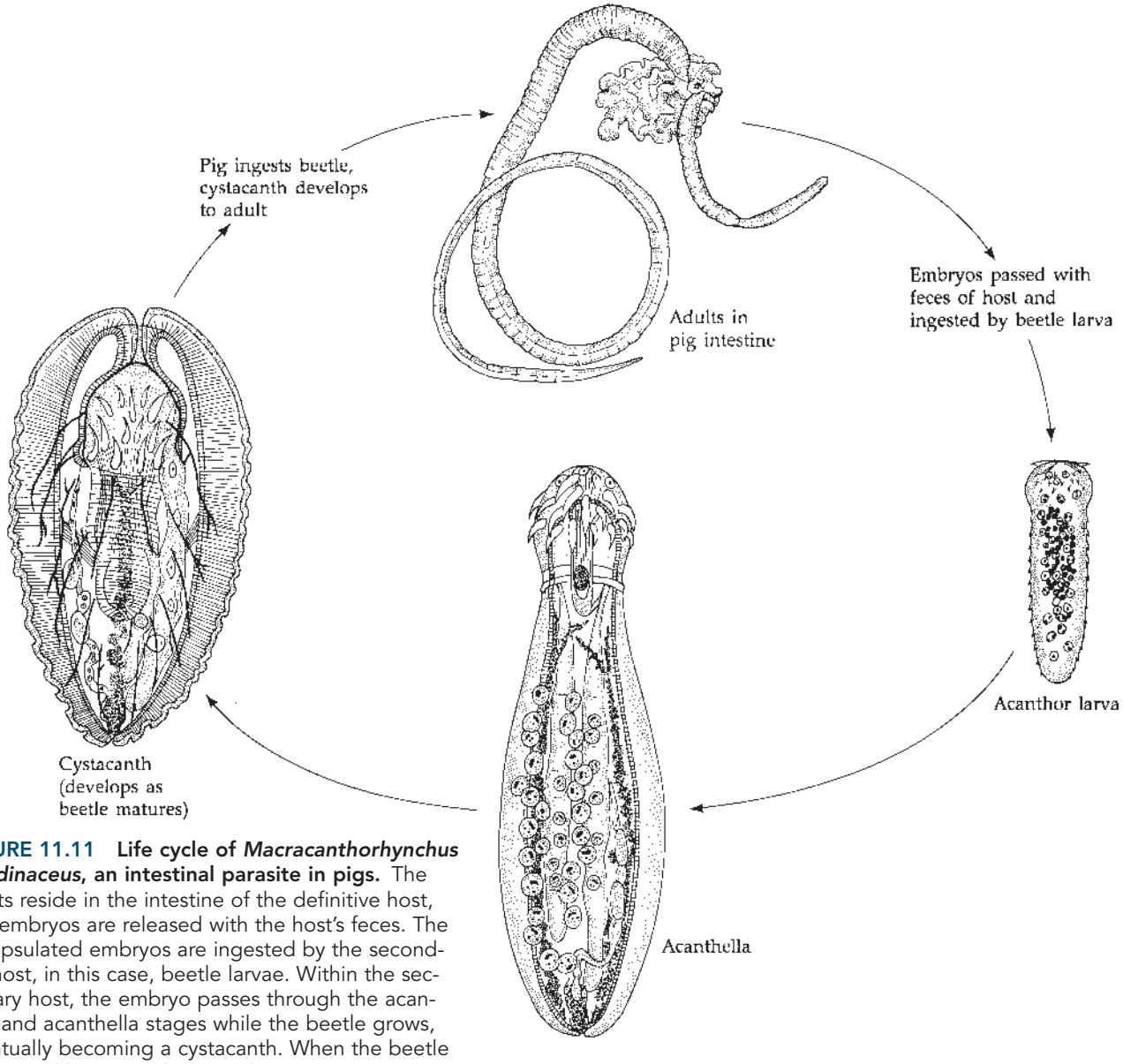

FIGURE 11.11 Life cycle of *Macracanthorhynchus hirudinaceus*, an intestinal parasite in pigs. The adults reside in the intestine of the definitive host, and embryos are released with the host's feces. The encapsulated embryos are ingested by the secondary host, in this case, beetle larvae. Within the secondary host, the embryo passes through the acanthor and acanthella stages while the beetle grows, eventually becoming a cystacanth. When the beetle is ingested by a pig, the juvenile matures into an adult, thereby completing the cycle.

encapsulated form called a **cystacanth** (Figure 11.11). When the intermediate host is eaten by an appropriate definitive host, the cystacanth attaches to the intestinal wall of the host and matures into an adult.

Phylum Micrognathozoa: The Micrognathozoans

A new microscopic animal, *Limnognathia maerski*, was described in 2000 by Reinhardt Kristensen and Peter Funch from a cold spring at Disko Island, West Greenland. Due to the numerous unique features of this new microscopic animal, a new monotypic class, Micrognathozoa (Greek, *micro*, "small"; *gnathos*, "jaw"; *zoa*, "animal"), was erected. Although *L. maerski* shows a superficial resemblance to microscopic annelids, its affiliation with Gnathostomulida and Rotifera was quickly established based on ultrastructural similarities of the epidermis and jaws. Jawlike structures are also found in other protostome taxa, such as in the kalyptorhynch turbellarians with their proboscises, in dorvilleid annelids, and in aplacophoran molluscs, but studies of their ultrastructure show that none of these jaws are homologous with those of *L. maerski*. Early molecular phylogenetic studies showed that Micrognathozoa did not nest within either of the two other gnathiferan phyla (Gnathostomulida and Rotifera), but next to them. For this reason, Micrognathozoa was given phylum status (Giribet et al. 2004). A later phylogenetic analysis based on transcriptomic data (Laumer et al. 2015) placed Micrognathozoa as the sister group to Rotifera (including Acanthocephala), with these

two comprising the sister clade to Gnathostomulida. Micrognathozoa still includes only the single described species from Greenland, but two later records of morphologically similar micrognathozoans from freshwater creeks in widely separated geographical areas (southern Indian Ocean and Great Britain) will most likely prove to be distinct species when DNA analyses have been completed. In the southern Indian Ocean, on Île de la Possession (Crozet Islands), micrognathozoans were found in low densities in both stagnant and running waters during the subantarctic summer (De Smet 2002), whereas in the United Kingdom only a few animals have been found from a stream in southern Wales (and only in winter) and a single animal was found on a sand grain of river sediment in Lambourn Parish, Berkshire (J. Schmid-Araya and P. E. Schmid pers. comm.). Finally, Giribet and Edgecombe (2020) reported on micrognathozoan environmental DNA in several peat bogs of the Pyrenees (O. Wangersteen unpubl. data). Micrognathozoa is thus the only animal phylum known strictly from freshwater habitats.

The Micrognathozoan Body Plan

Limnognathia maerski is an acoelomate animal ranging from about 80 μm to 150 μm in adult length (juveniles measuring 85–107 μm in length). The adult body can be divided into three main regions: a head, an accordion-like thorax, and an abdomen (Figures 11.12 and 11.13); the head contains the prominent jaw apparatus (Box 11D).

Epidermis, Ciliation, and Body Wall Musculature

Despite their small size, micrognathozoans have a complex support system and body musculature. *Limnognathia maerski* has dorsal and lateral **epidermal plates** formed by an intracellular matrix as in rotifers (including acanthocephalans) (Figures 11.12 and 11.13). Ventral plates are lacking, but the "naked" epidermis has a thin extracellular glycocalyx layer and a true cuticular oral plate The animal lacks syncytia, a key character of Rotifera (and Acanthocephala); however, it possesses a unique form of gap junctions showing transverse electron dense bands in a zipper-like pattern (we call these **zip-junctions**) between the dorsal epidermal cells.

The pattern of ventral multiciliated cells is characteristic of Micrognathozoa and has shown to be somewhat more complicated than illustrated in Figure 11.12 (so see also Figure 11.14). These cells comprise on the head a semicircular anterior field and also a posterior arched, ciliary field surrounding the mouth anterolaterally, as well as one anterior and three posterolateral pairs of **ciliophores** (synchronously beating multiciliated cells) surrounding the pharyngeal bulb. The midventral ciliation of the thorax and abdomen consist of about 17 transverse rows of two to four ciliophores, with the four last rows together constituting a posterior adhesive ciliary pad. The ventral paired ciliophores form the locomotory organ and are characterized by very long ciliary roots, originally mistaken for cross-striated muscles. These cells are highly similar to ciliophores found in the interstitial microscopic annelids *Diurodrilus* and *Neotenotrocha*. The posterior ciliary pad is very different from the adhesive toes of rotifers, gastrotrichs, and annelids, and the structure may be a unique synapomorphy for Micrognathozoa.

As in many marine interstitial animals (e.g., gnathostomulids, gastrotrichs, microscopic annelids), special forms of tactile bristles or sensoria are found on the body. A typical tactile bristle may consist of a single sensory cell, the **collar receptor**, with a single cilium in the middle surrounded by eight or nine microvilli that form the "collar" (see apicalia and dorsalia in Figure 11.12). Other sensory cells may have two or three cilia (see frontalia, lateralia and caudalia in Figure 11.12). The sensory cell clusters that form the two **apical ciliary tufts** (which are not collar receptors) are also multiciliary cells. Two large, posterior glands were recently revealed by immunostaining (Figures 11.12 and 11.14), which by their simple configuration and homogenous content resemble mucus-secreting glands. They might have an

BOX 11D Characteristics of the Phylum Micrognathozoa

1. Triploblastic, bilateral, unsegmented, acoelomate
2. Epidermis with supporting dorsal and lateral plates (intracellular matrix)
3. Without a syncytial epidermis
4. Ventral ciliation consisting of preoral ciliary field and paired ciliophores (synchronously beating multiciliated cells) around mouth and along midline of thorax and abdomen
5. Sensory organs in the form of stiff ciliated cells supported by microvilli and nonciliated internal eyes (phaosomes)
6. Posterior end with ciliated pad and one pair of glands
7. Mouth opening ventral, gut incomplete (the dorsal anus being temporary)
8. Pharyngeal apparatus containing complex jaw apparatus with four sets of jawlike elements and several sets of striated muscles largely related to the fibularium and the main jaws
9. Two pairs of protonephridia with monociliated terminal cells and paired connecting ducts
10. Without circulatory system or special gas exchange structures
11. Males unknown; probably parthenogenetic
12. Two female gonads in close contact with the midgut

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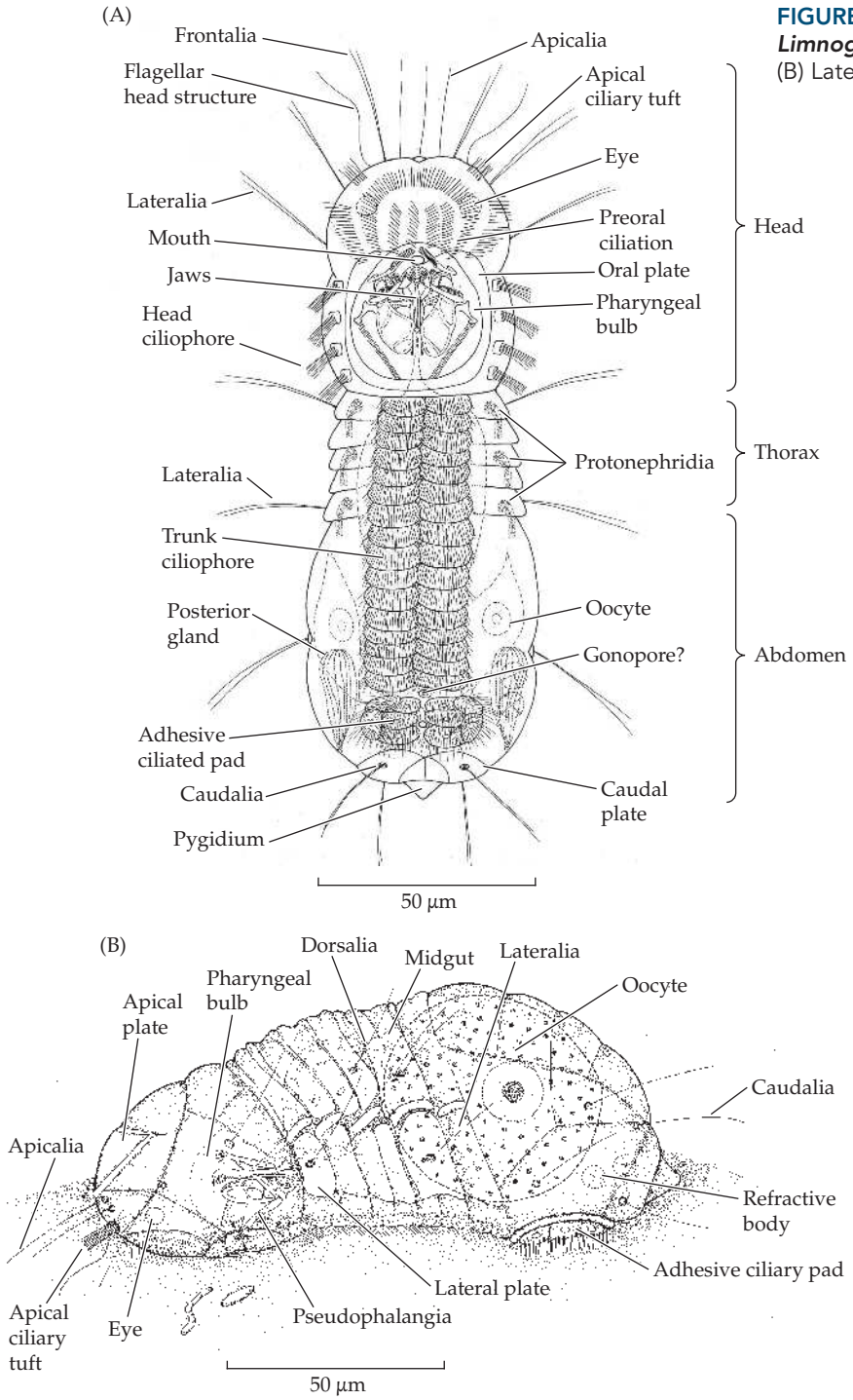


FIGURE 11.12 Micrognathozoa: *Limnognathia maerski.* (A) Ventral view. (B) Lateral view.

adhesive function, together with the ciliary pad, but they do not resemble the more complex adhesive duo gland system found in the posterior end of gastrotrichs and the interstitial annelid *Diurodrilus*. Otherwise, no epidermal glands are known from micrognathozoans.

Limnognathia maerski has an elaborate body wall musculature, comprising 7 main pairs of longitudinal muscles extending from head to abdomen, and 13 pairs of oblique dorsoventral muscles localized in the thoracic and the abdominal regions (Figure 11.15). The musculature further comprises several minor posterior muscles and fine anterior forehead muscle, as well as the prominent pharyngeal muscular apparatus (Figure 11.16B). Cross-striated muscles are found in both the body wall and the jaw musculature. The three main ventral longitudinal pairs and one dorsal pair of muscles (green and blue muscles, Figure 11.15) span the entire length of the body, and some fibers even branch off to continue anteriorly into the head and posteriorly into the abdomen, forming a delicate muscular fencelike

FIGURE 11.13 Micrognathozoa: *Limnognathia maerski*, light micrographs. (A) Adult female with mature egg (length 0.14 mm). (B) Juvenile with relatively large thorax/smaller abdomen and immature oocyte (length 0.09 mm).

structure. These muscles seemingly aid longitudinal contraction and ventral bending of the body. The 13 oblique dorsoventral muscles may function together with the longitudinal muscles as supporting semicircular body wall musculature. Their close approximation to the gut further suggests they may act as gut musculature, thus possibly compensating for the lack of outer or inner circular musculature in Micrognathozoa.

Locomotion

Micrognathozoans swim in a characteristic slow spiral motion when moving freely in the water column. It is a slow movement, very different from that of rotifers. From video recordings, it seems that the trunk ciliophores are used both in swimming and in epibenthic crawling or gliding motions on the substrate. Gliding is accomplished by the rows of motile ciliophores, each with multiple cilia beating in unison, in the same way as is seen in the annelid *Diurodrilus*. However, the preoral ciliary field does not seem to be involved in either swimming or gliding. *Limnognathia maerski* has never been observed moving backward (as is common among gnathostomulids), not even when they reverse the beating of their long cilia. In addition, an escape motion has been observed where contraction of trunk muscles creates rapid jerky movements.

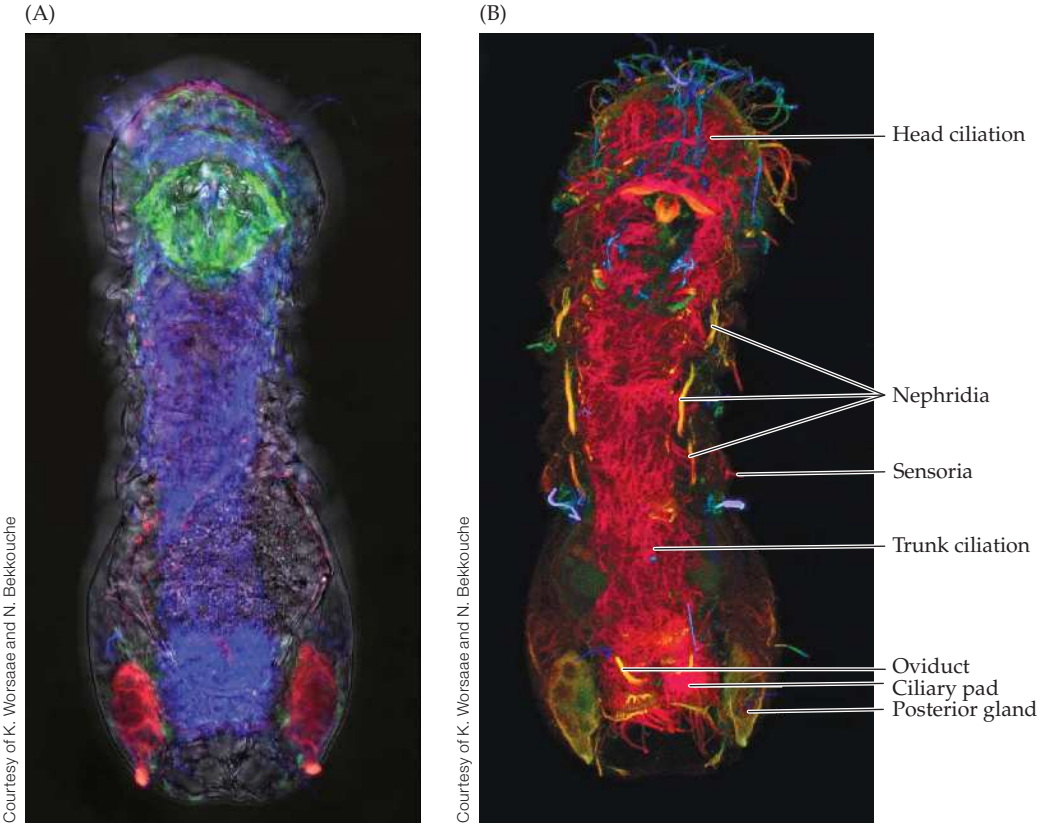
Pharyngeal Apparatus, Feeding, and Digestion

The mouth opens ventrally on the anterior margin of the cuticular, nonciliated oral plate and leads into the pharyngeal cavity, followed by a short esophagus dorsal to the paired jaw apparatus, then continues into the undifferentiated, nonciliated gut. The temporary anus is located dorsally and opens only periodically, as also seen in all gnathostomulids and in some gastrotrichs.

The pharyngeal apparatus, less than 30 μm wide, shows a complexity unseen in any other microscopic taxon, comprising numerous hard jaw parts and intricate musculature (Figure 11.16), as well as a buccal ganglion. The jaw parts comprise four main sets of sclerotized, denticulate, hard elements (sclerites): the large paired **fibularium**, the **main jaws**, the **ventral jaws**, and the **dorsal jaws**. The largest sclerite in each jaw is the fibularium, and it plays a central role in supporting the pharynx. Several subparts of the main sclerites have been described, including the anterior region of the ventral jaws called the **pseudophalangia**. So far, little is known about the functionality of this complex apparatus or the possible independent movement of all these parts, and only the pseudophalangia has been observed protruding from the mouth in fast snapping movements, possibly grasping food. The pharyngeal musculature is similarly complex and includes a major **ventral muscle plate** supporting (and moving) the entire jaw apparatus, as well as several other paired and unpaired striated muscles (Figure 11.16B). The ventral muscle plate is formed by 8–10 longitudinal cross-striated muscle fibers (purple muscles, Figure 11.16B) underlying the fibularium and enveloping the jaws laterally and caudally. This large muscle is unique to the Micrognathozoa, being absent in other gnathiferan phyla. The many paired and unpaired muscles seem mainly related to the fibularium and the main jaws, moving the jaws as well as supplying some of the minor jaw elements such as the accessory sclerites and the pharyngeal lamellae and allowing for the extrusion of the ventral jaws. The feeding biology of micrognathozoans is not well known. The animals are found on mosses or in the sediments, and video recordings have shown the animal eating bacteria on the surfaces of mosses and sand grains.

Circulation, Gas Exchange, and Excretion

Micrognathozoans are acoelomates and thus lack a circulatory system, and gas exchange takes place by diffusion across the epidermis. The paired nephridial system is in each lateroventral side composed of an anterior and a posterior, thoracic nephridium (with 4 and 2 terminal cells, respectively), possibly both opening into the intermediate collecting tubule (Figure 11.12A). The terminal cells are monociliated, in contrast to the multiciliated terminal cells of Rotifera but similar to those found in Gnathostomulida.



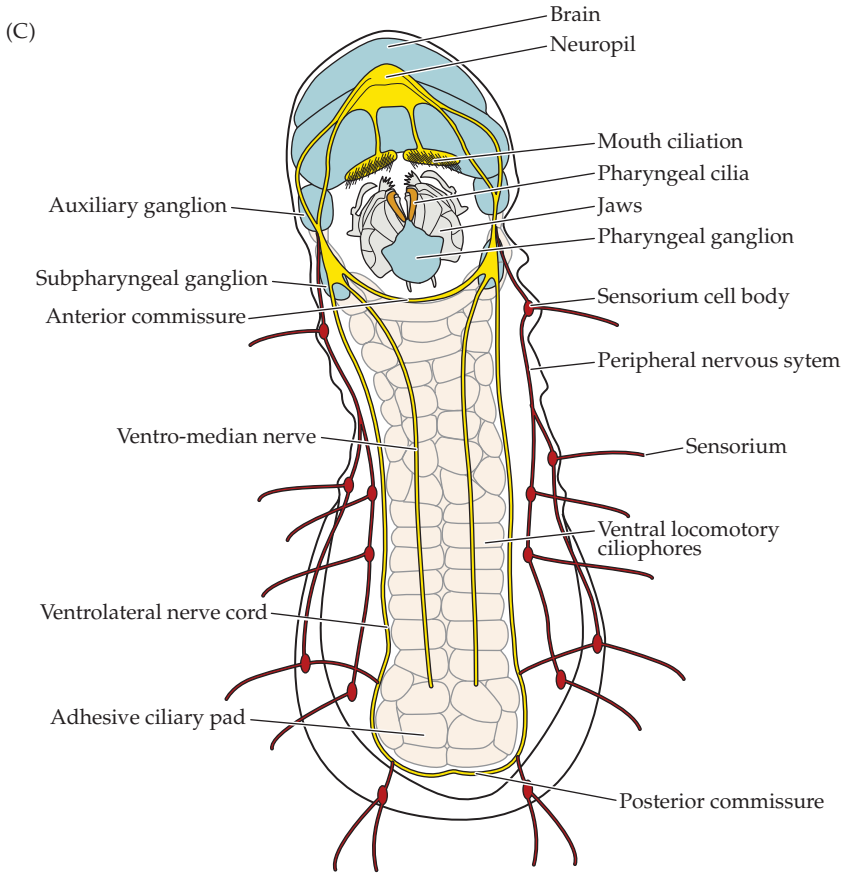
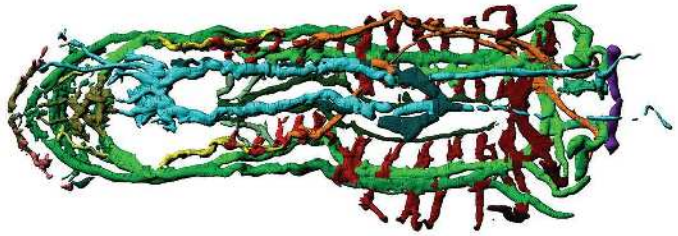


FIGURE 11.14 Micrognathozoa: *Limnognathia maerski* neural and ciliated structures. (A–B) Confocal laser scanning microscopy images of *Limnognathia maerski*, maximum-intensity projection of Z-stacks. (A) Antibody staining showing ventral ciliation in blue, pharyngeal musculature in green, posterior glands in red, transmitted light image as background. (B) Depth-coded projection of anti-acetylated α-tubulin immunoreactivity showing the ventral ciliation (red) and the ciliated nephridial ducts and one pair of posterior oviducts beneath the ciliary field (yellow). (C) Schematic illustration of the central nervous system outlined in yellow with ganglia in blue, sensory cilia and peripheral nerves in red, and ciliophore cells in tan.



Courtesy of K. Worsaae and N. Bekkouche

FIGURE 11.15 Micrognathozoa: *Limnognathia maerski* isosurface reconstruction of body wall musculature from confocal microscopy of phalloidin staining. Reconstruction showing 13 oblique dorsoventral pairs of muscles (red) and 7 main pairs of longitudinal muscles: 3 ventral (green), 2 lateral (yellow and orange), and 2 dorsal pairs (blue) as well as additional minor muscles.

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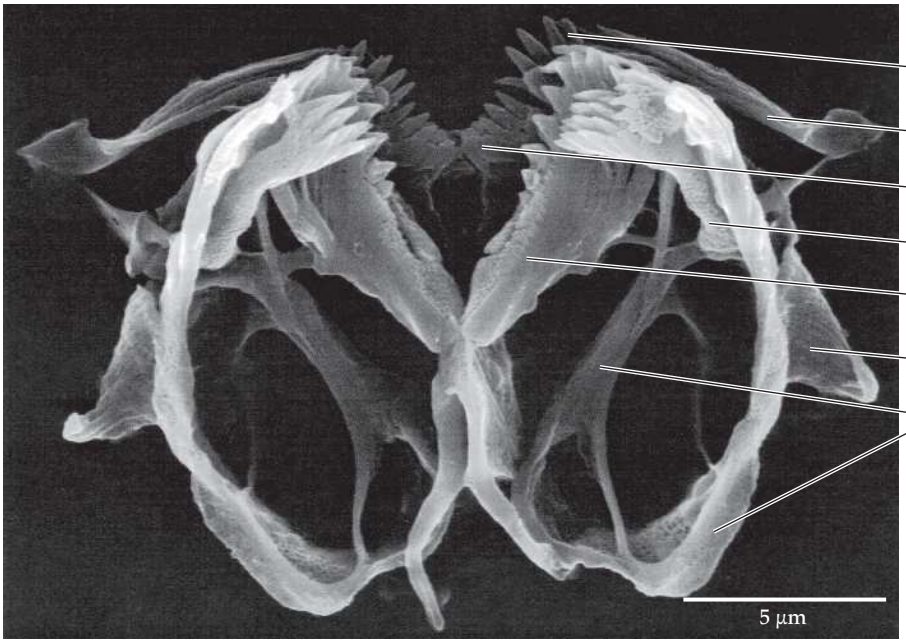

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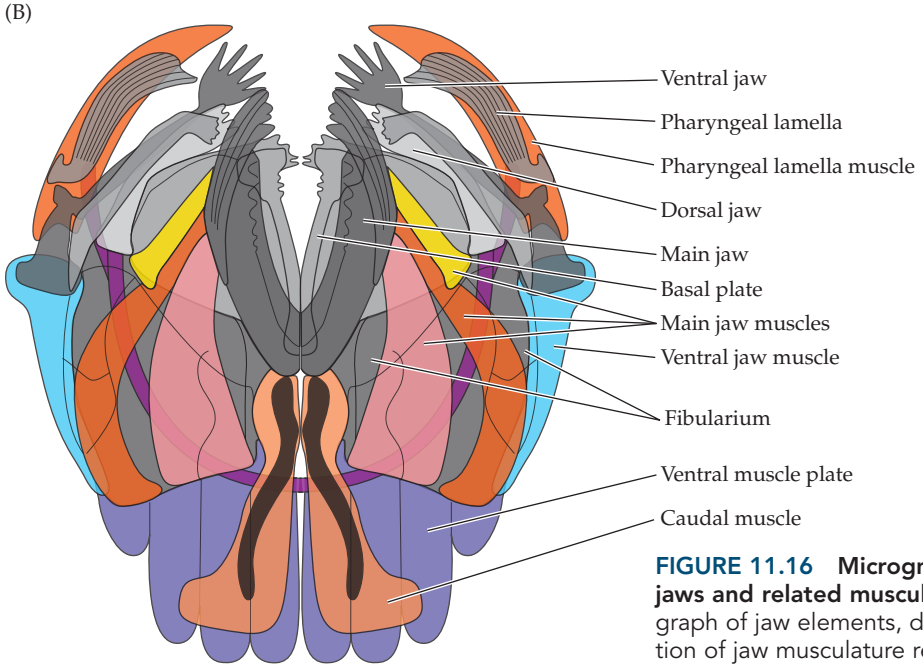

FIGURE 11.16 Micrognathozoa: *Limnognathia maerski* jaws and related musculature. (A) Scanning electron micrograph of jaw elements, dorsal view. (B) Schematic reconstruction of jaw musculature related to specific jaw elements.

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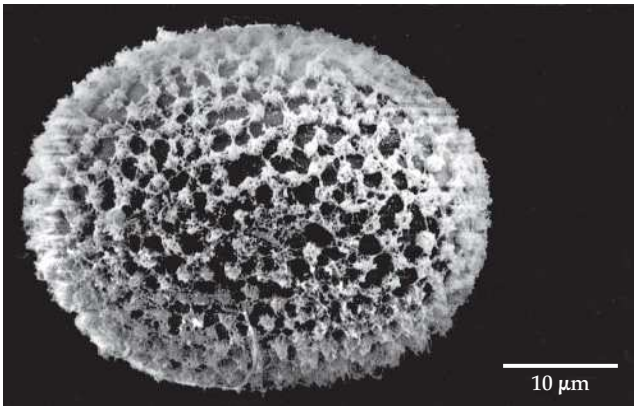
Nervous System and Sense Organs

Micrognathozoa possess a simple nervous system consisting of an anterior, slightly bilobed, dorsal brain and two pairs of ventral longitudinal nerves, connected by paired subpharyngeal commissural ganglia and a terminal commissure (Figure 11.14C). A large buccal assembly of somata (possible ganglion) is found caudal to the pharyngeal apparatus, which may control the movement of jaw elements. The numerous nucleated, minute cells found in the ganglia and musculature of the pharynx are in line with the suggested small size of the Micrognathozoa genome. Peripheral nerves extend from the cords, connecting to the sensory cilia (Figure 11.14B,C). Some of these cilia are clearly monociliated collar receptors (one cilium surrounded by eight to nine microvilli), whereas others are more complex with several sensory cells involved. The terms used for the sensory structures are, from anterior to posterior, apicalia, frontalia, lateralia, dorsalia, and caudalia (Figure 11.12). In the anterior end of the animal, a pair of lateral hyaline vesicles is present. They may be unpigmented, inner eyes of the annelid type, the so-called phaosomes, and like these they contain a dense layer of microvilli, but no ciliary structures.

Reproduction and Development

Only the female reproductive system has been found, suggesting that *Limnognathia maerski* is parthenogenetic. The reproductive system is anatomically simple, and it seems that the two ovaries obtain nutrition directly from the midgut, a feature also reported from freshwater chaetonotoid gastrotrichs. A pair of caudal, ciliated oviducts open midventrally (Figure 11.14B), possibly through the midventral pore found in the midst of the posterior ciliated pad. Though collecting has been done year-round in Greenland, the species is only found during the short summer. Two egg types have been found, as in limnic gastrotrichs and rotifers, where the smooth egg may be a quick-developing summer egg, and the strongly sculptured winter egg (Figure 11.17) may be a resting egg, not developing during the 10-month-long Arctic winter.



Courtesy of R. M. Kristensen and K. Worsaae

FIGURE 11.17 Micrognathozoa: scanning electron micrograph of *Limnognathia maerski* sculptured winter egg.

Phylum Chaetognatha

The chaetognaths (literally, "bristle jaws"), or arrow worms, comprise a small phylum of about 150 species of marine, mainly planktonic, voraciously predatory invertebrates (Figures 11.18 and 11.19). They are of moderate size, ranging from about 0.5 to 12 cm in length. Arrow worms are distributed throughout the world's oceans and occur in some estuaries; they are ecologically important as consumers of copepods and other small zooplankton. Arrow worms often occur in very high numbers and sometimes dominate the biomass in midwater plankton tows. Some species (e.g., *Spadella*) are epibenthic in shallow water. Special collection methods, such as use of submersibles, are turning up new species at great ocean depths, and many of these live just off the deep ocean floor (e.g., *Heterokrohnia* and *Archeterokrohnia*). At least two deep-water species, *Caecosagitta macrocephala* and *Eukrohnia fowleri*, are bioluminescent, releasing luminous particles that form glowing clouds in the water (although their luciferin-and-luciferase-based luminescent organs are located in different parts of the body). Definitive fossil chaetognaths with preserved soft tissues and grasping spines have been described from the middle Cambrian Burgess Shale of Canada (*Capinatator praetermissus*) and early Cambrian Chengjiang biota of China, about 520 million years ago (e.g., *Eognathacantha ercainella, Protosagitta spinosa, Ankalodous sericus*), and it is likely that Cambrian protoconodonts are grasping spines of arrow worms. Most of what we know about the biology of these delicate organisms is based on just a few nearshore species that can be collected without damage and kept alive in laboratory settings.

Comparative morphologists have not yet identified any unambiguous synapomorphies that unite chaetognaths with other protostome phyla, but molecular work, being phylogenetic analysis of genomic data or comparative analysis of Hox genes, places chaetognaths with the members of Gnathifera. Many unique features reveal the phylum status of arrow worms, including the movable cuticular grasping spines on

From E. V. Thuesen et al. 2010. *Biol Bull* 219: 100–111. Courtesy of E. Thuesen and S. Haddock

FIGURE 11.18 *Eukrohnia fowleri* (family Eukrohniidae). This stunning photograph by Eric Thuesen shows the deep-water chaetognath carrying its developing embryos in two temporary gelatinous pouches on either side of the body.

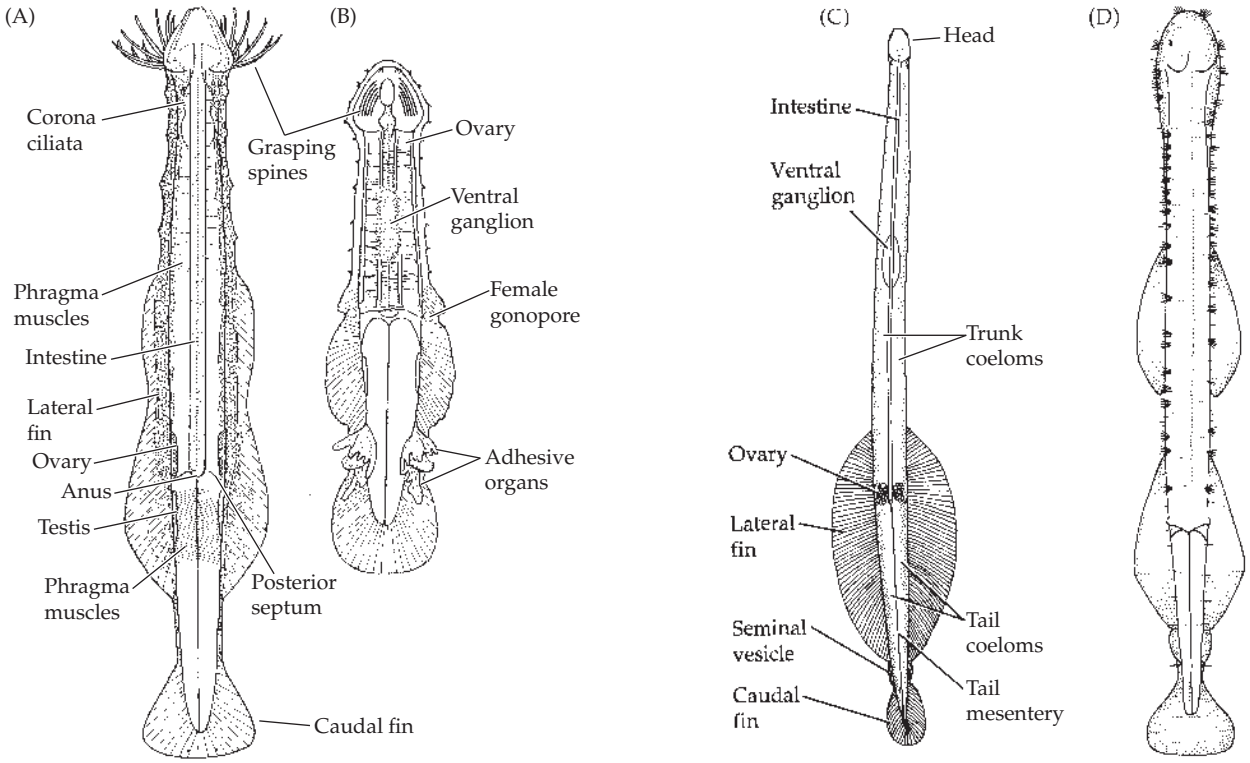


FIGURE 11.19 General anatomy of chaetognaths. (A) *Heterokrohnia involucrum* (dorsal view). (B) The benthic chaetognath *Paraspadella gotoi* (ventral view). (C) *Krohnitta subtilis* (dorsal view). (D) Outline of *Ferosagitta hispida*, showing ciliary receptors arranged longitudinally on the body. (E) Anatomy of the head of *Sagitta*. (F) Anatomy of *Sagitta* (cross section), showing the trunk on the left and tail on the right. (G) The nervous system of a generalized chaetognath. (H) Arrangement of eye units in a chaetognath. (I) Reproductive systems in *Sagitta*. (E after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

the head, a multilayered epidermis over most of the body, horizontal fins on the sides and posterior end, and closed seminal vesicles on the tail. Major characteristics of the phylum are listed in Box 11E.

Morphological uniformity within the phylum has resulted in few features that can be used to determine systematic relationships within the group. For many years, two orders were recognized: Phragmophora included all arrow worms having transverse "phragma" muscles, and Aphragmophora included all arrow worms lacking these muscles. The Phragmophora is now thought to be paraphyletic with respect to a monophyletic Aphragmophora. Presence of transverse muscles in both the trunk and tail is generally considered to be a plesiomorphic trait. A comprehensive cladistic analysis (Gasmi et al. 2014) based on both molecular and morphological characters recognized five well-resolved families. The first two families listed here represent a monophyletic group, as do the last three families, but neither of these groups has been given a name. In benthic and deep-sea species, the trunk and tail tend to be similar in length; in pelagic species the trunk tends to be conspicuously longer than the tail. Unless stated otherwise, the families are characterized by one pair of lateral fins and two paired rows of teeth.

CLASSIFICATION OF PHYLUM CHAETOGNATHA

FAMILY HETEROKROHNIIDAE Mostly deep-sea species, some presumably living on or close to the seafloor. Phragma muscles in both trunk and tail (*Archeterokrohnia*, *Heterokrohnia*, *Xenokrohnia*) or just the trunk (*Bathyspadella*). 23 species.

FAMILY EUKROHNIIDAE Pelagic, phragma muscles restricted to anterior trunk; one paired row of posterior teeth. 11 species, in the single genus *Eukrohnia*.

FAMILY SPADELLIDAE Epibenthic in shallow water; small; phragma muscles throughout much of trunk but absent from tail (e.g., *Paraspadella*, *Spadella*). 30 species.

FAMILY KROHNITTIDAE Pelagic, lack phragma muscles, one paired row of anterior teeth. One pair of lateral fins. 4 species, in the single genus *Krohnitta*.

FAMILY SAGITTIDAE Pelagic, a few nearshore species are facultatively epibenthic; lack phragma muscles. Two pairs of lateral fins except in *Pterosagitta* (e.g., *Caecosagitta*, *Ferosagitta*, *Parasagitta*, *Pterosagitta*, *Sagitta*). 60 species in 13 genera.

Three genera (*Bathybelos, Krohnittella, Pterokrohnia*), each belonging to its own family, are known from just

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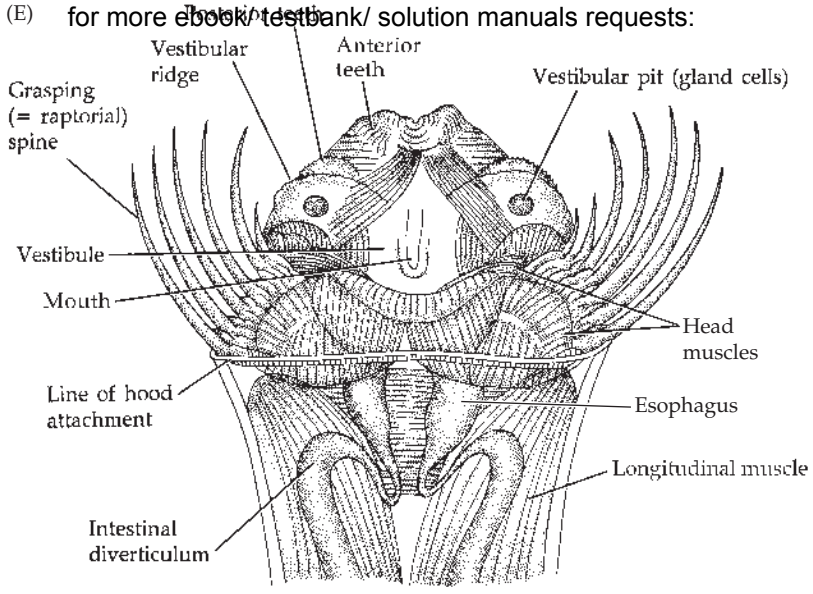

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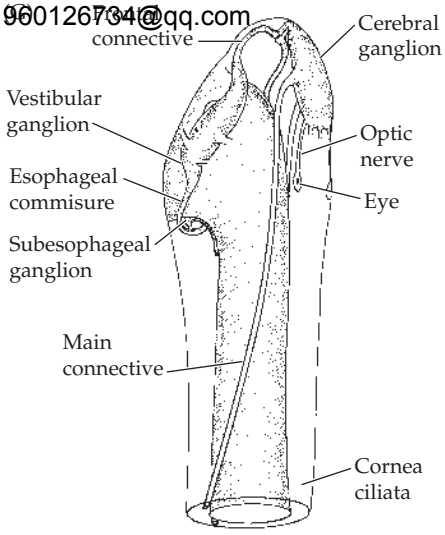

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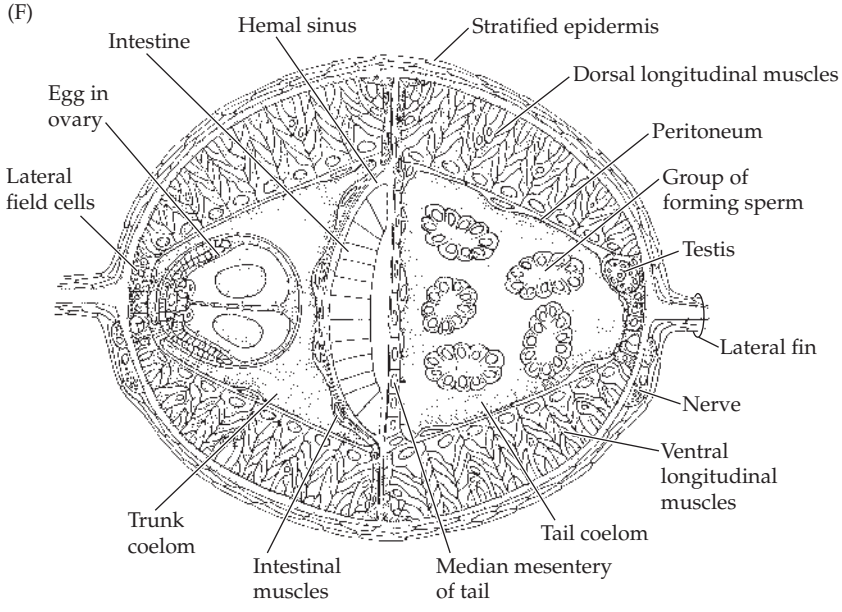

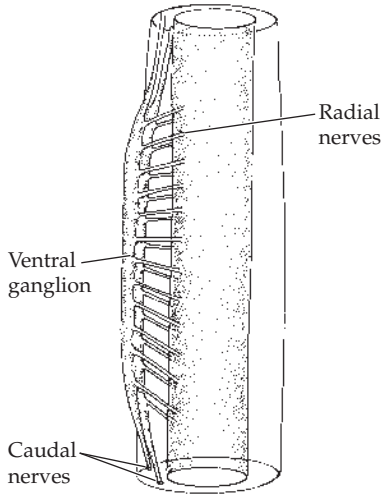

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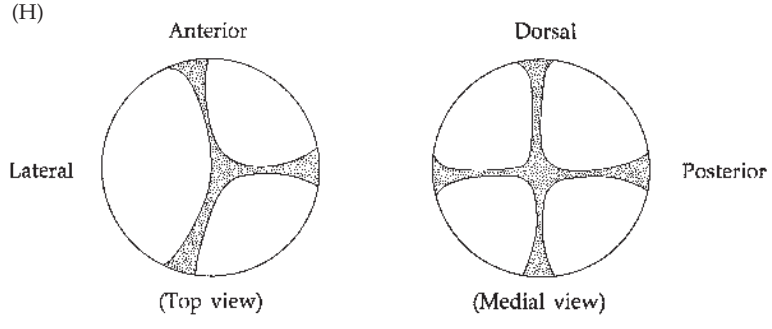

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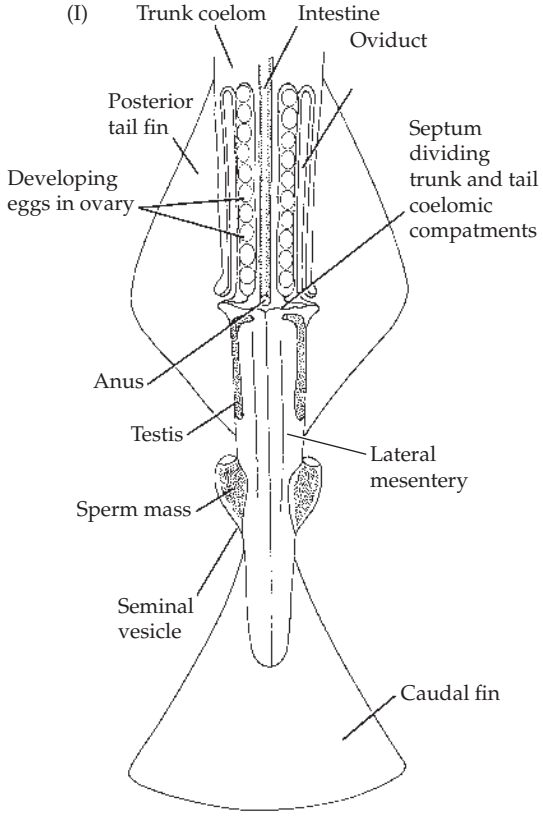

BOX 11E Characteristics of the Phylum Chaetognatha

1. Bilaterally symmetrical protostomes, with streamlined, elongate, trimeric body comprising head, trunk, and tail region; single head coelom, and paired trunk and tail coeloms separated by transverse septa
2. Epidermis mostly stratified, with cuticle on ventral side of head; body with lateral and caudal fins, supported by "rays" consisting of elongate cytoskeleton-rich epidermal cells; nonmolting
3. Mouth surrounded by sets of long moveable grasping spines and short teeth used in prey capture; mouth set in ventral vestibule; anterolateral fold of body wall forms retractable hood that can enclose grasping spines
4. With striated longitudinal muscles, arranged in quadrants; weak circular musculature consists of myoepithelial cells
5. No discrete gas exchange or excretory systems
6. Hemal system restricted to trunk, consisting of narrow peri-intestinal sinuses and larger sinuses in dorsal mesentery and posterior septum
7. Complete gut; anus ventral, at trunk-tail junction
8. Centralized nervous system with large dorsal (cerebral) and ventral (subenteric) ganglia connected by circumenteric connectives; ciliary receptors for detection of waterborne disturbances; anterior ciliary loop (= corona ciliata) of uncertain function (but possibly chemosensory). With inverted pigment-cup ocelli
9. Hermaphroditic, with internal fertilization and direct development. Cleavage equal, holoblastic, and apparently modified spiral. Mesoderm and body cavities form by heterocoely. Despite blastopore denoting posterior end of body, both mouth and anus forming secondarily, subsequent to closure of the blastopore
10. Strictly marine; raptorial carnivores; largely planktonic, but some benthic species known

one or a few poorly preserved specimens and are of uncertain phylogenetic status. *Bathybelos* is especially intriguing because the single known specimen, collected from 2,500 m deep in the Gulf of Mexico, was described as having many unusual features, including a unique dorsal ganglion on the very long head and no ventral ganglion.

The Chaetognath Body Plan

Externally, arrow worms are streamlined, with virtually perfect bilateral symmetry. Internally, transverse septa divide the coelomate body into a head, a trunk, and a tail. The head bears a ventrally placed mouth, set in a depression called the **vestibule**. The entire head region is elegantly adapted to a predatory lifestyle. Lateral to the mouth are long movable **grasping spines**, or "hooks," and in front of the mouth are short **cuticular teeth**—both used in prey capture and ingestion (Figures 11.19E and 11.20). The dorsolateral margins of the head possess a muscularized fold of the body wall called the **hood**. Except during prey capture, this is drawn ventrally around the sides of the head, thereby enclosing the grasping spines and streamlining the head. A pair of small, pigmented photoreceptors lie dorsally on the head. Also dorsally is a distinctive ring of innervated ciliated cells, the **corona ciliata**, which likely functions in chemoreception. The trunk bears one or two pairs of horizontal **lateral fins**, and the tail bears a single **tail fin**. Chaetognath fins are simple epidermal folds enclosing a thick sheet of supportive extracellular matrix; certain elongate epidermal cells form fin rays. The body surface has many multicellular **ciliary receptors**, which bear short rows of nonmotile cilia serving as mechanoreceptors for detecting disturbances in the water. The trunk contains the intestine, which terminates ventrally at the trunk-tail junction, and two ovaries. The female gonopores are located laterally at the posterior end of the trunk. The male reproductive system occupies the tail, which is commonly filled with masses of differentiating sperm. Paired seminal vesicles protrude laterally, between the lateral and caudal fins.

The chaetognath body plan couples structural simplicity with a high degree of specialization. We tend to view the specialized features of arrow worms as adaptations to a planktonic predatory lifestyle, but with nowhere to hide, pelagic arrow worms must also be adept at avoiding their own predators. Most chaetognaths are as transparent as glass and spend much of their time suspended motionlessly in the water—both features that minimize detection by visual predators such as fish. A chaetognath's sensitivity to waterborne disturbances is equally useful for detecting both prey and approaching predators, and the ability to move quickly enables both prey capture and escape from potential predators.

Body Wall, Support, and Movement

Over most of the body, the epidermis is a stratified epithelium. Flattened surface cells produce a thin layer of secretion over the body, much as in fish. Underlying epidermal cells are filled with cytoskeletal tonofilaments (supportive cytoskeletal microfilaments). The epidermis on the ventral and lateral parts of the head consist of a single layer of cuticularized cells. The cuticle is not molted. On all parts of the body, a thick basement membrane joins the epidermis to underlying tissues. Striated longitudinal muscle dominates the body wall of the trunk and tail (Figure 11.19F). On each side of the midline is a large group of dorsal longitudinal muscle and ventral longitudinal muscle (Figure 11.19F). These

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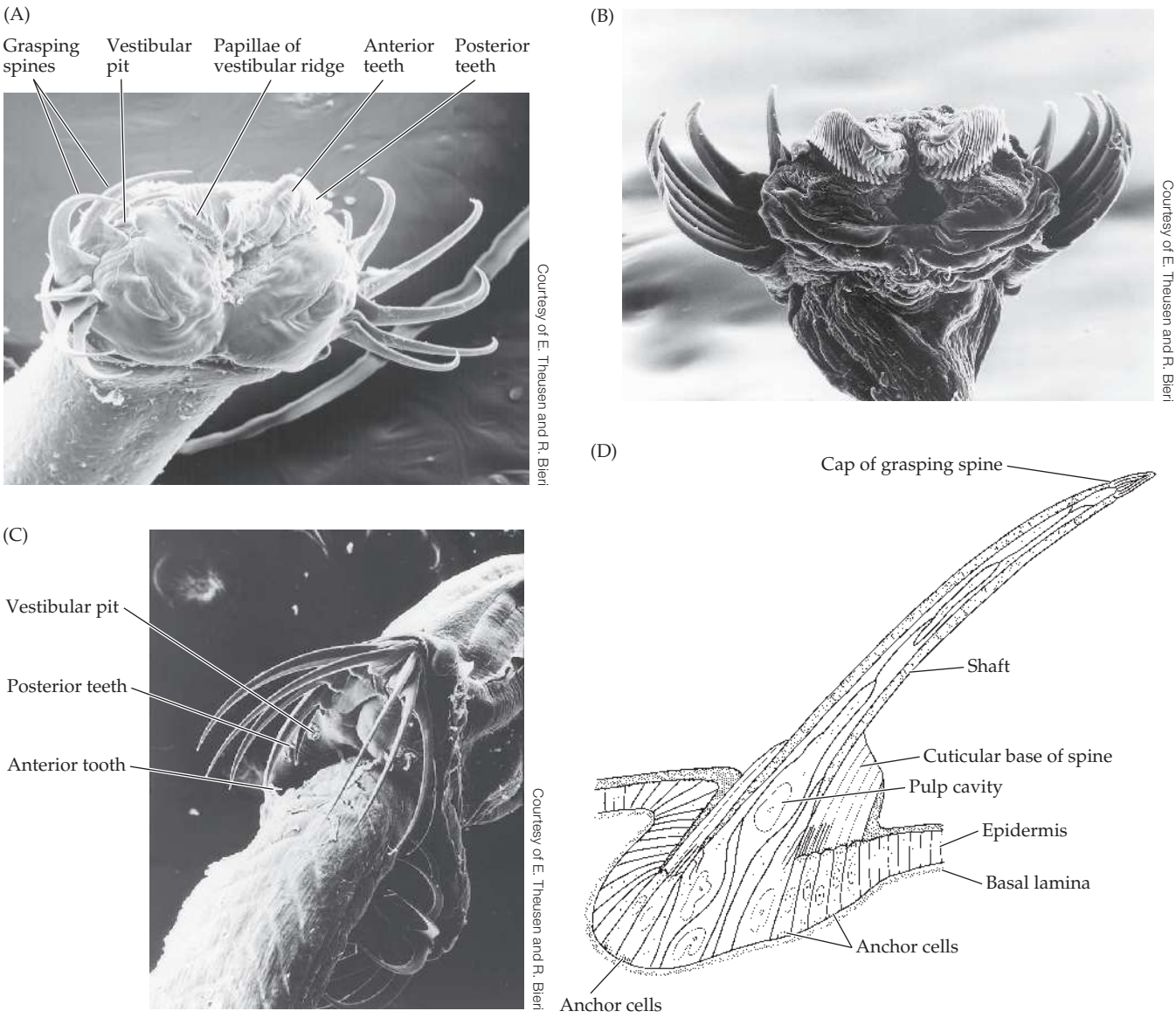

FIGURE 11.20 (A,B) Heads of chaetognaths. (A) *Zonosagitta pulchra*. Note the well-developed raptorial structures. (B) *Zonosagitta bedoti*, from the eastern Pacific. The hooks are clearly visible on either side of the head surrounding the large number (17–20) of long, narrow, posterior teeth. The shorter anterior teeth lie just above the mouth. The vestibular ridge with its pores is partially visible behind the left set of posterior teeth. (C) The chaetognath in this photo, *Flaccisagitta hexaptera*, has partially swallowed a fish larva (probably an anchovy). A single anterior tooth projects down below the second hook on the left side of the photo, and two posterior teeth can be seen between the first and second hooks. The circular organ just below the first hook is the vestibular pit. (D) Diagram of a grasping spine of *Parasagitta elegans*.

are separated from the body cavities by a thin layer of squamous peritoneum (noncontractile peritoneal cells). In addition, a weak circular musculature exists in the form of myoepithelial "lateral field cells" and dorsomedial and ventromedial cells. In some, sheets of transverse **phragma** muscle extend obliquely from the lateral body wall to the ventral midline (Figure 11.19A); their functions remain unknown. In all arrow worms, the head musculature is complex (Figure 11.19E).

The body cavities are true coeloms. The single head cavity is reduced by the elaborate cephalic musculature. In the trunk and tail, longitudinal mesenteries separate the coelomic space into left and right compartments, and in the tail incomplete lateral mesenteries partially subdivide each tail compartment (Figure 11.19F). The coelomic fluid is colorless in life, but it stains intensely, which suggests an abundance of dissolved organic molecules. Circulation of coelomic fluids in both trunk and tail is caused by ciliated cells in the lateral body wall. Coelomocytes are apparently lacking.

Body support in chaetognaths is provided by the hydrostatic quality of the coelom, crossed helical

arrangement of collagen fibers in the basement membrane, and tonus of the body wall musculature. Locomotion of both pelagic and epibenthic species involves forward darting motions caused by rapid alternating contractions of the dorsal- and ventral-longitudinal muscles. The fins are not used as propelling surfaces but are placed so that they slice through the water and serve as stabilizers. In pelagic species, brief swimming bursts alternate with quiescent periods, when the animals may slowly sink. This "hop-sink swimming," common among small planktonic invertebrates, probably constitutes a prey search behavior, and perhaps a depth stabilization measure (the fins also increase resistance to sinking between swimming bursts). Because swimming tends to be upward, it also helps the animals maintain a vertical position in the water column. Species that make pronounced diurnal vertical migrations—up at night and down during the day—are presumably capable of extended bouts of swimming. Some species of arrow worms are neutrally buoyant due to hypertrophied intestinal cells or vacuolated epidermal cells that contain fluids less dense than seawater.

Feeding and Digestion

Chaetognaths prey upon a variety of small pelagic animals, especially copepods. They can consume prey that are nearly as large as themselves, including small fish and other arrow worms! The complex musculature of the head operates the grasping spines and retraction of the hood during feeding. Both planktonic and benthic species are ambush predators, using ciliary receptors scattered over the body to detect movements of nearby prey. A chaetognath can determine both the direction and distance of potential prey at close range (even in the dark). Prey are ingested whole. The release of luminescent clouds in deep-sea species might serve to startle potential prey into movement, which can then be detected by the chaetognaths to facilitate predation. The luminescent cloud might also provide a means of escaping from predators.

Benthic forms, such as *Spadella*, feed while affixed to a substratum by adhesive secretions. As prey swim within reach, the anterior end is raised, and grasping spines are flared. The prey is captured by a quick downward flex of the head while the rest of the body remains firmly attached. The grasping spines close around and manipulate the prey, orienting it for ingestion. Planktonic chaetognaths feed on prey approaching the body from all sides. Laterally positioned prey are captured by rapid flexure of the body, and a short forward hop can be executed to grab prey located in front.

The grasping spines on the left and right sides can be moved simultaneously or alternately, resulting in a surprising degree of dexterity during manipulation of prey. When rigid prey such as small crustaceans are captured, the chaetognath positions the victim longitudinally for swallowing. The spines and teeth contain α-chitin, hardened at their tips by silicon in the two species so far examined closely. While superficially resembling setae of arthropods or chaetae of annelids, each tooth and grasping spine is a complex structure produced by a group of specialized epidermal cells. The grasping spines of some species bear serrations. Teeth are commonly cuspidate, a shape that may aid in the penetration of prey, including the exoskeletons of small crustaceans. A neurotoxin, tetrodotoxin, has been isolated from the heads of some species and may be used to quell prey. The toxin would presumably be incorporated into the sticky secretions produced by the pharynx and vestibular glands. It has been hypothesized that symbiotic bacteria produce the tetrodotoxin, but symbiotic bacteria have not been found during ultrastructural studies of the head or gut of arrow worms.

The gut is a relatively simple straight tube extending from the mouth in the vestibule to the ventral anus at the trunk-tail junction (Figure 11.19A,C,I). The mouth leads into a short pharynx and esophagus, both of which are equipped with gland cells. Swallowing is accomplished by well-developed esophageal muscles. The gut narrows where it passes through the head-trunk septum, and it extends posteriorly as a long intestine. A short rectum joins the posterior intestine to the anus. Most digestion occurs extracellularly in the posterior intestine and can be extremely rapid. Orange carotenoid pigments derived from the prey are incorporated into the otherwise transparent tissues of some deep-water chaetognaths.

Circulation, Gas Exchange, and Excretion

A simple hemal system exists in at least some chaetognaths, but it is easily overlooked because the blood is colorless and transparent. The hemal system consists of thin sinuses situated between the intestinal epithelium and surrounding myoepithelial peritoneum. Larger hemal sinuses exist in the dorsal mesentery, trunk-tail septum, ovaries, and body wall near the ventral ganglion. Transport through the hemal system is probably driven by the intestinal musculature. Even when the gut is empty, posteriorly directed peristalsis alternates with anteriorly directed peristalsis. The nutritive demands of various tissues in the tail are probably met by ultrafiltration across the tail side of the posterior septum, from the hemal sinus in the trunk-tail septum to the tail coelom. Gas exchange and excretion are apparently by diffusion through the body wall.

Nervous System and Sense Organs

Of paramount importance to the success of chaetognaths as active predators are features of the nervous system and associated sensory receptors. As we have

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seen in other groups, a body plan that emphasizes cephalization is usually an integral factor in adapting to a predatory lifestyle. The central nervous system of chaetognaths includes a large dorsal cerebral ganglion in the head. From this, paired nerves extend posterodorsally to the eyes and corona ciliata, and small anteriorly directed frontal connectives lead to paired esophageal ganglia and, ultimately, innervate the head muscles and gut, forming a sort of loop. Larger paired circumesophageal main connectives extend posteroventrally to join a large ventral ganglion (also called the **ventral nerve center**) located in the trunk epidermis (Figure 11.19G). From the ventral ganglion, numerous peripheral nerves radiate to all parts of the trunk and tail, branching to form an elaborate intraepidermal nerve plexus having both sensory and motor functions. Via the main connectives and these peripheral nerves, the ventral ganglion receives sensory input from the head and from ciliary receptors on the body. It controls swimming and other behaviors caused by the body wall musculature of the trunk and tail.

Ciliary receptors are short straight rows of nonmotile cilia that project from the body surface. They are stereotypically arranged and oriented either parallel (sometimes called "ciliary fences") or transversely (sometimes called "ciliary tufts") relative to the long axis of the body, such that the entire body functions as an "antenna" for reception of nearby disturbances. The ciliary receptors detect hydrodynamic stimuli and react to close-range mechanosensory input, thus are important for both prey detection and input leading to swimming behavior. Each receptor contains 50–300 cells. Although chemoreceptors have yet to be positively identified in chaetognaths, they almost certainly exist. Candidates include the aforementioned corona ciliata, the pore-bearing vestibular ridges located just behind the teeth, and other tiny pores flanking the mouth.

Most arrow worms possess a pair of eyes on the dorsal surface of the head. Typically, each eye has a large central pigment cell, indented to form seven cups containing the light-sensitive parts of the photoreceptor cells, which are ciliary (not rhabdomeric) (Figure 11.19H). We can infer from their structure that chaetognaths have a nearly uninterrupted visual field enabling them to orient to light direction and intensity. The eyes of deep-water arrow worms are variously modified in ways that presumably increase sensitivity to light. For example, in certain species of *Eukrohnia*, the photoreceptor cells are directed outward, and each is capped by a transparent "lens." The eyes probably do not form images but are used for orientation during vertical migration.

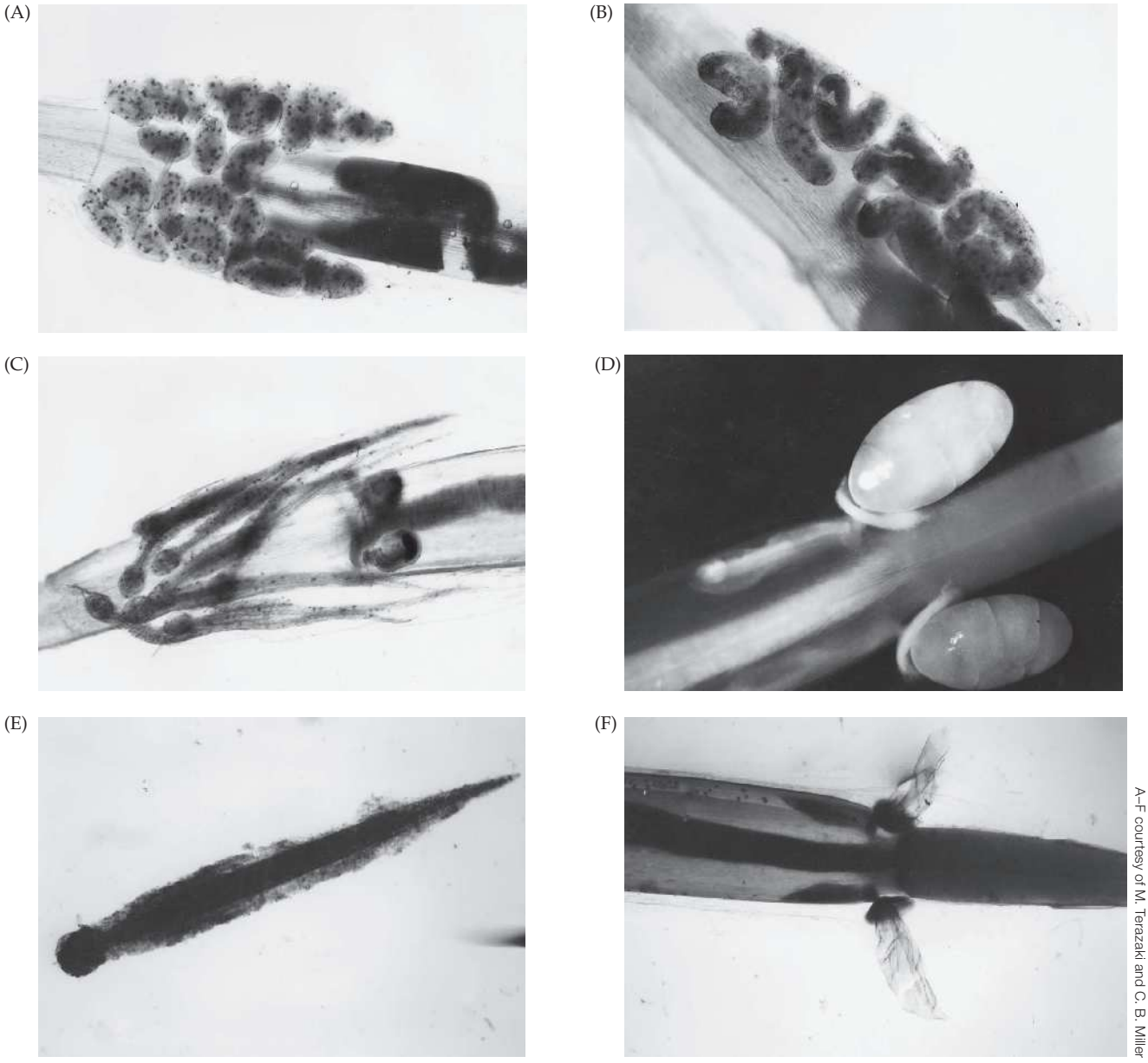
Reproduction and Development

Arrow worms are hermaphroditic, with paired ovaries in the trunk and paired testes in the tail (Figure 11.19I). Groups of spermatogonia are released from the testes to the tail coeloms, where they circulate as the sperm mature. The filiform sperm are picked up by open ciliated funnels and conveyed down the sperm ducts to a pair of seminal vesicles, which bulge from the sides of the tail. In some species, gland cells secrete a spermatophore wall around the enclosed sperm. When filled with sperm, the seminal vesicles are conspicuously white. Release of sperm involves rupture of the seminal vesicles during mating. This can lead to self-fertilization in some species but happens during mating in most species. Each ovary bears along its side an oviduct that leads to a genital pore just in front of the trunk-tail septum. Eggs develop within the ovaries where they are bathed in a nutritive fluid derived from the posterior hemal sinus. Fertilization occurs prior to ovulation as sperm received during mating pass from the oviduct through specialized accessory fertilization cells to the attached eggs. Immediately after fertilization, zygotes move into the oviduct for release to the environment.

Mating has been most extensively studied in some benthic spadellids (e.g., *Spadella cephaloptera*, *Paraspadella gotoi*) and the neritic *Ferosagitta hispida*. After a rather elaborate mating "dance," sperm from a seminal receptacle are deposited as a mass onto the mate's body. In *Paraspadella gotoi*, the sperm mass is precisely placed at the female gonopore, but in the others sperm masses are attached more anteriorly, and columns of sperm stream over the epidermis of the recipient to enter the female gonopores. Benthic chaetognaths (e.g., *Spadella*) tend to deposit fertilized eggs on algae or other suitable substrata. Planktonic species typically shed floating embryos to the sea. *Pterosagitta draco* encloses the embryos in a large floating gelatinous mass, and species of *Eukrohnia* carry developing embryos in gelatinous masses, one on either side of the body near the tail, until the young are ready to swim (Figure 11.18 and Figure 11.21). *Ferosagitta hispida* descends and attaches developing eggs to stationary benthic objects. When food is abundant, new batches of sperm and eggs can be produced in daily succession.

Development is direct, lacking any larval stage or metamorphosis. The transparent eggs contain little yolk, and cleavage is holoblastic and equal. Both classical and modern studies have suggested a modified spiral pattern of cleavage, with unmistakable animal and vegetal cross-furrow cells, but this is easily overlooked because animal-pole cells ("micromeres") and vegetal-pole cells ("macromeres") are similar in size, and cleavage of arrow worms has been incorrectly described in the past as being radial. However, while a spiralian-like tetrahedral four-cell embryo is derived via a levotropic blastomere displacement in the second cleavage, subsequent cleavage stages have not yet been documented, and further research is needed to understand the nature of cleavage in these animals. The coeloblastula consists of pyramidal cells arranged around a small blastocoel (Figure 11.22).

Gastrulation (germ layer formation) occurs by invagination of the presumptive endoderm, leaving no blastocoel. The blastopore marks the eventual posterior end of the animal—both mouth and anus form secondarily, thus giving chaetognaths a deuterostome-like developmental pattern. Starting at the future anterior end, vertical epithelial folds of endoderm grow posteriorly through the archenteron, separating the future lateral coelomic cavities from the medial gut cavity (Figure 11.22). Early formation of the head-trunk septum results in the early isolation of the head coeloms. As development continues, embryos elongate and the body cavities become compressed, but the surrounding mesodermal cells retain their epithelial morphology. The coeloms re-expand later in development and then persist as true coeloms into adulthood. Interestingly, all organs and tissues of mesodermal origin, including body wall musculature, intestinal musculature, and somatic reproductive tissues, derive entirely from the peritoneum of the embryonic coeloms. It seems that coelom and mesoderm formation in chaetognaths is neither fully enterocoelous nor schizocoelous; some have called this a modified enterocoely, whereas Kapp (2000) proposed the name **heterocoely** for the unique mode of coelom formation in this group.



A–F courtesy of M. Terazaki and C. B. Miller

FIGURE 11.21 The chaetognath *Eukrohnia*, with temporary gelatinous marsupia housing the developing embryos. (A–C) *Eukrohnia bathypelagica* carrying developing embryos and young in the marsupium. (D) *Eukrohnia fowleri* carrying fertilized eggs in posterior marsupial sacs. (E) Young *Eukrohnia fowleri* just after hatching. (F) *Eukrohnia fowleri* carrying the empty marsupial sacs from which the young have already escaped.

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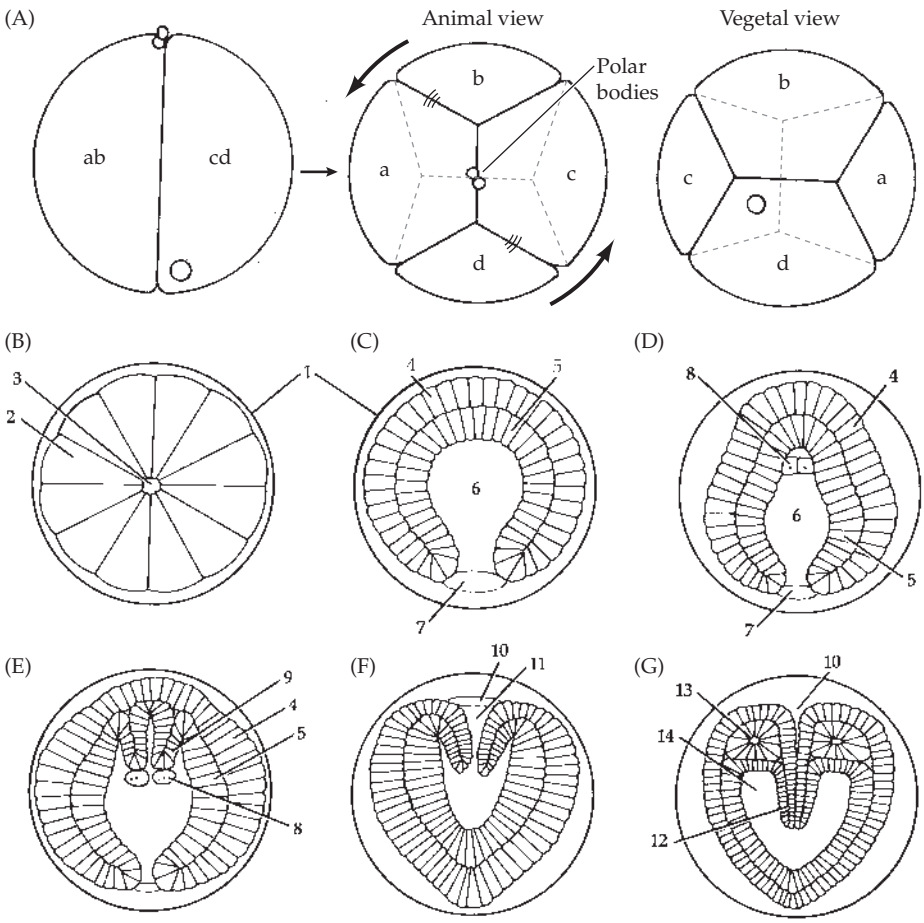

FIGURE 11.22 Early chaetognath development. (A) Two- and four-celled embryo of *Paraspadella gotoi*, showing the spiral arrangement of blastomeres. (B) Early blastula. (C) Gastrula. (D) Later gastrula. (E) Production of mesodermal folds from archenteron. (F) Blastopore closure and secondary mouth opening with the formation of a stomodeum. (G) Formation of coelomic pouches.

Development from zygote release to hatching as a juvenile chaetognath is rapid, about 48 hours. Parental investment per embryo is small, the eggs contain little yolk, and they are abandoned soon after fertilization, except in a number of brooding forms (Figures 11.18 and 11.21). The rapid development to a feeding juvenile is essential to the success of this life history strategy.

Chapter Summary

This chapter introduced you to the clade Gnathifera, which contains four phyla: Gnathostomulida, Rotifera, Micrognathozoa, and Chaetognatha. The name "Gnathifera" is derived from the presence of complex, hardened, pharyngeal jaws used for feeding in these four groups. Although differing in details, the jaws in these four phyla are thought to be homologous. Gnathostomulids and chaetognaths are strictly marine; micrognathozoans and most rotifers inhabit fresh waters. The parasitic and highly modified acanthocephalans, once assigned to their own phylum, are now recognized as a clade within Rotifera. Phylogenetic studies strongly support a sister-group relationship between Micrognathozoa and Rotifera, but the relationships of the other gnathiferans have yet to be fully resolved. Gnathostomulids comprise about 100 species of microscopic, vermiform, meiofaunal, hermaphroditic animals. Rotifers include about 2,150 species of mostly microscopic, free-living creatures, plus another 1,200 species of parasitic acanthocephalans that inhabit the guts of various vertebrates (especially birds and freshwater fishes). Free-living rotifers are common in fresh waters, but also occur in brackish and marine environments. Micrognathozoa, the only animal phylum known strictly from freshwater habitats, consists of a single described, microscopic (80 μm to 150 μm adult length) creature from a cold spring in Greenland. Records of micrognathozoans from freshwater creeks in the Indian Ocean region (Crozet Islands), England, and the Pyrenees (Spain) may prove to be distinct species. The chaetognaths, or arrow worms, are a small phylum of about 130 species of marine, mainly planktonic (although a number of benthic species are known), gelatinous animals that reach up to 12 cm in length. Outfitted with powerful jaws, arrow worms are voracious predators and important in oceanic planktonic food webs.

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Courtesy of M. Faasse

CHAPTER 12

Platytrochozoa and Two Enigmatic Phyla

Entoprocta and Cycliophora

The great protostome clade known as Spiralia contains 15 phyla, 14 of which belong to the two lineages Gnathifera and Platytrochozoa, while the phylogenetic relationship of the phylum Dicyemida remains unclear. The larger clade Platytrochozoa encompasses ten phyla, eight of which belong to the well-supported clades Lophotrochozoa and Rouphozoa (see Chapters 8, 13, and 17). But two platytrochozoan groups remain difficult to place among their spiralian kin: Entoprocta and Cycliophora. This chapter treats these two enigmatic phyla.

Unlike the Gnathifera, which show a relatively conserved body plan, the Platytrochozoa phyla are highly variable, and divergences such as blind versus through guts or the presence versus absence of primary and secondary body cavities seem to have evolved multiple times.

Entoprocts have been known since the nineteenth century, but cycliophorans were not discovered until the 1960s and not described until 1995. Both are small marine phyla, although two freshwater entoproct species are known. Entoprocts resemble minute cnidarian polyps and are often colonial, whereas cycliophorans are solitary microscopic symbionts on the mouthparts of lobsters. Neither is encountered frequently enough to have acquired a generally accepted vernacular name. Although species in these two phyla do not resemble one another superficially, you will recognize some fundamental anatomical similarities as you read about them here. Some morphological work (and early molecular phylogenies) supported a grouping of Entoprocta + Cycliophora + Bryozoa (the "Polyzoa"), but phylogenetic studies over the past decade have removed the bryozoans from this group, leaving just the entoprocts and cycliophorans as a possible sister group buried somewhere deep in the Spiralia lineage.

The section on Entoprocta was revised by Claus Nielsen.

Classification of The Animal Kingdom (Metazoa)

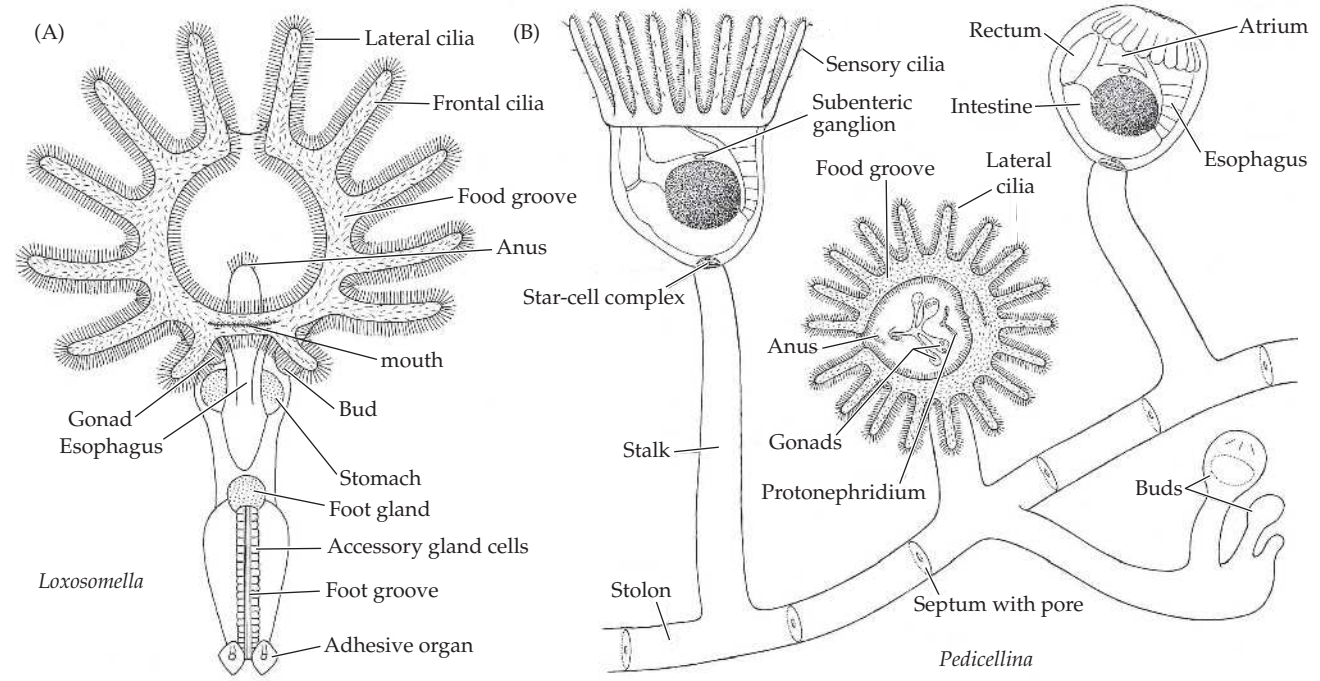
PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

Phylum Entoprocta: The Entoprocts

The phylum Entoprocta (Greek *entos*, "inside"; *proktos*, "anus"), or Kamptozoa (Greek *kamptos*, "bent"), includes about 200 described species of small, sessile, solitary or colonial creatures that superficially resemble cnidarian hydroids (Figure 12.1; Box 12A). All but two species are marine (the freshwater colonial *Urnatella gracilis* and *Loxosomatoides sirindhornae*). Colonial forms live attached to various substrata, including algae, shells, and rock surfaces. Many solitary species are commensal on a variety of hosts—especially sponges (Figure 12.1C), sipunculans, and other annelids—and are typically associated with just one or a few host species. Entoprocts are not uncommon in shallow water; most live shallower than 200 m in the sea, but some species are known from depths as great as 5,220 m. They are often mistaken for tiny cnidarian polyps or otherwise overlooked by the casual tide pool observer because of their small size, but a quick examination through a hand lens reveals both their beauty and their true nature. Certain benthic flatworms and molluscs are known to feed on entoprocts.

The individual zooids of entoprocts are goblet shaped but clearly bilateral, and the crown of feeding tentacles in most of the colonial species is almost circular. Each zooid consists of a cuplike body, the **calyx**, from which arises an almost closed horseshoe of ciliated tentacles (Figure 12.1). The tentacles encircle a concavity, called the **atrium** or vestibule, in which both the protonephridia and the gonoducts open. The



(C)

Courtesy of G. Paulay

(D)

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(E)

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mouth and anus both lie inside the tentacle crown, the mouth being situated on the rim carrying the tentacle crown, and the anus opening on a small anal cone in the atrium (hence the name Entoprocta). The calyx is carried on a stalk, which in solitary forms attaches to the substratum, either directly or via a complicated foot. In colonial forms the stalk attaches to branched stolons or an enlarged basal plate. The phylum is commonly divided into four families. Some specialists recognize orders on the basis of the presence or absence of a septum between the stalk and calyx, or on solitary versus colonial habits. Recent molecular studies, albeit with limited data, have supported a division into two classes: Solitaria (for Loxosomatidae) and Coloniales (for the remaining three families, in which the stalks attach to a common basal plate or to branched stolons).

The phylogenetic position of the entoprocts has been much discussed. Originally, they were treated as bryozoans, but when the larval protonephridium was discovered in 1877 (by Berthold Hatschek), they were placed in the Scolecida, with affinities to the Rotifera. Also, unlike Bryozoa and other lophophorates, entoprocts have spiral cleavage. In the 1920s, R. B. Clark discovered that they lack a coelom, and they were then placed somewhere in

BOX 12A Characteristics of the Phylum Entoprocta

1. Triploblastic, bilateral, unsegmented, probably acoelomate
2. Sessile, solitary, or colonial (with stalks borne on stolons)
3. Cup-shaped calyx body carried on a stalk and housing a U-shaped gut
4. Calyx with a horseshoe-shaped band of ciliated tentacles that surround the mouth, anus, gonoducts, and protonephridia; mouth situated at base of the frontal tentacles and anus at the opposite side of the atrium
5. Hermaphroditic or gonochoristic
6. Cleavage spiral
7. Some with trochophore larvae
8. Nearly all species shallow-water marine animals (two known freshwater species and a few that inhabit brackish waters) attached to stones or algae; many of the solitary species as commensals of annelids, sponges, and other water-current-producing invertebrates

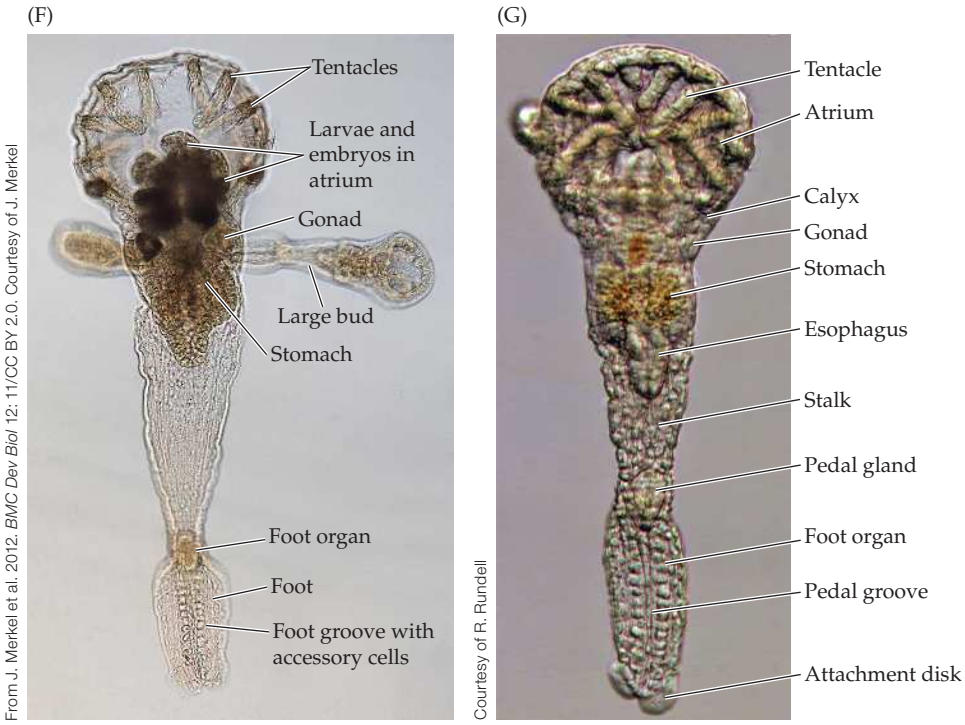

FIGURE 12.1 Entoprocts. (A,B) Diagrams of a solitary (*Loxosomella*) and a colonial (*Pedicellina*) entoproct. (C) Dense growth of an unidentified *Loxosomella* on a sponge; many calyces can be seen rising from their stalks. (D) Two zooids of *Pedicellina cernua*, each showing its calyx and stalk. (E) Zooids of an undescribed Australian species of *Barentsia*. (F) *Loxosomella vancouverensis* from San Juan Island, Washington, with embryos, larvae, and buds. (G) Labeled micrograph of the meiofaunal species *L. vancouverensis*, from British Columbia (Canada). Described in 2012, this is the first free-living entoproct, and only the third entoproct species, reported from the west coast of North America. The other two known west coast species are both symbionts on the mantis shrimp *Pseudosquilla ensigera*. *Loxosomella vancouverensis* is just 440 µm long and has 14 tentacles and two attachment discs at the base of the foot organ. The foot adheres to the substrate (sand grains and shell bits) but can detach and reattach.

the large group Spiralia. Their position among the Spiralia remains enigmatic, but recent work suggests they may be closely allied to Cycliophora.

Crown-group (modern) entoproct fossils are known only from specimens of *Barentsia* in the Late Jurassic of the United Kingdom. An entoproct-looking fossil from the Cambrian Chengjiang biota, *Cotyledion tylodes*, has been descried and has the typical body divisions of a calyx, stalk, and "holdfast."

ENTOPROCT CLASSIFICATION

FAMILY LOXOSOMATIDAE Solitary; without a septum between stalk and calyx; usually commensal on other invertebrates; some are capable of limited movement on a suckered base or a complicated foot; muscles continuous from stalk to calyx (see Figure 12.1A,C). (e.g., *Loxosoma*, *Loxosomella*)

FAMILY LOXOKALYPODIDAE Colonial; without a septum between stalk and calyx; a few zooids attached to a basal plate; muscles continuous from stalk to calyx; ectocommensal on the annelid *Glycera nana* in the northeastern Pacific. Monotypic: *Loxokalypus socialis*

FAMILY PEDICELLINIDAE Colonial; with incomplete stalk-calyx septum; with star-cell complex; muscles extend for the length of the stalk but are not continuous with those of calyx; stalk undifferentiated (see Figure 12.1B,D). (e.g., *Loxosomatoides*, *Myosoma*, *Pedicellina*)

FAMILY BARENTSIIDAE Colonial; with incomplete stalk-calyx septum; with star-cell complex; stalk differentiated into wide, muscular nodes and narrow, nonmuscular rods (see Figure 12.1E). (e.g., *Barentsia*, *Urnatella*)

The Entoproct Body Plan

Body Wall, Support, and Movement

The calyx (body) and stalk are covered by a thin cuticle that does not extend over the ciliated portion of the tentacles or the atrium. Some have described the fine structure of the cuticle as more similar to annelids than it is to either Bryozoa or Cycliophora. The stiff parts of the stalk of barentsiids have a thick cuticle, and cuticular dorsal "shields" are characteristic of some colonial species. The stalk often contains chitin. The epidermis is cellular. All entoprocts have a tentacle musculature with larger outer muscles and thinner inner muscles. These muscles move the tentacles and curl them up when the tentacle crown is retracted; a ring muscle just below the tentacle base constricts the atrium over the retracted tentacles. Other muscle bands compress the calyx to extend the tentacles. Contractions of longitudinal and oblique muscles in the basal part of the calyx and in the stalk make characteristic nodding movements of the zooid possible and also enable more complicated movements of the stalk. The myoanatomy of the so-called entoproct "creeping larva" shows similarities to the foot of some molluscs, as do the paired sets of dorsoventral muscles that intercross ventrally above the foot. Most authors suggest there is no persistent body cavity, and the area between the gut and body wall is filled with mesenchyme (Figure 12.2D). However, others have provided evidence for a primary body cavity separated from all surrounding tissues by a basal lamina, which underlies the ectodermal and endodermal epithelia and covers the excretory system, gonads, muscle cells, and nerves that cross the body cavity, thus suggesting that small remnants of a primary body cavity are retained as a hemocoel—this constituting the basis of the Lacunifera hypothesis that unites Entoprocta with Mollusca. And, at least one recent molecular analysis found a mollusc-entoproct clade.

Feeding and Digestion

Entoprocts are ciliary suspension feeders. They collect food particles, mostly phytoplankton, from currents produced by the lateral cilia on the tentacles (Figure 12.2A,C). The water currents pass between the tentacles and away from the atrium. Food particles are collected on the downstream side of the ciliary band by the "catch-up method" in which the compound lateral cilia—several cilia working together as one unit—cut through the water to contact the particle and push it to the frontal band of separate cilia on the frontal side of the tentacle (Figure 12.2B). The particles are then transported along the tentacle to the horseshoe-shaped ciliary band along the food groove on the atrial ridge and to the mouth (Figure 12.2C).

Food particles are moved into the gut by cilia lining the buccal tube and by muscular contractions of the esophagus (Figure 12.2D). The esophagus leads to a spacious stomach, from which a short intestine extends to the rectum located within the anal cone. Food is moved through the gut by cilia. The stomach lining secretes digestive enzymes and mucus, which are mixed with the food by a tumbling action caused by the ciliary currents. Digestion and absorption occur within the stomach and intestine, where food is held for a time by an intestinal-rectal sphincter muscle.

Circulation, Gas Exchange, and Excretion

The gut also apparently serves as an excretory passage. Cells in the ventral stomach wall accumulate brownish spheres and release them into the stomach lumen, from which they are discharged through the anus. Adult entoprocts also possess a pair of flame bulb protonephridia located between the stomach and the atrium epithelium (Figure 12.1B). The freshwater species *Urnatella gracilis* has additional, more complex protonephridia both in the body and in the joints of the stalk. The protonephridia drain to a short common nephridioduct that leads to a pore on the surface of the atrium. A similar condition is found in another

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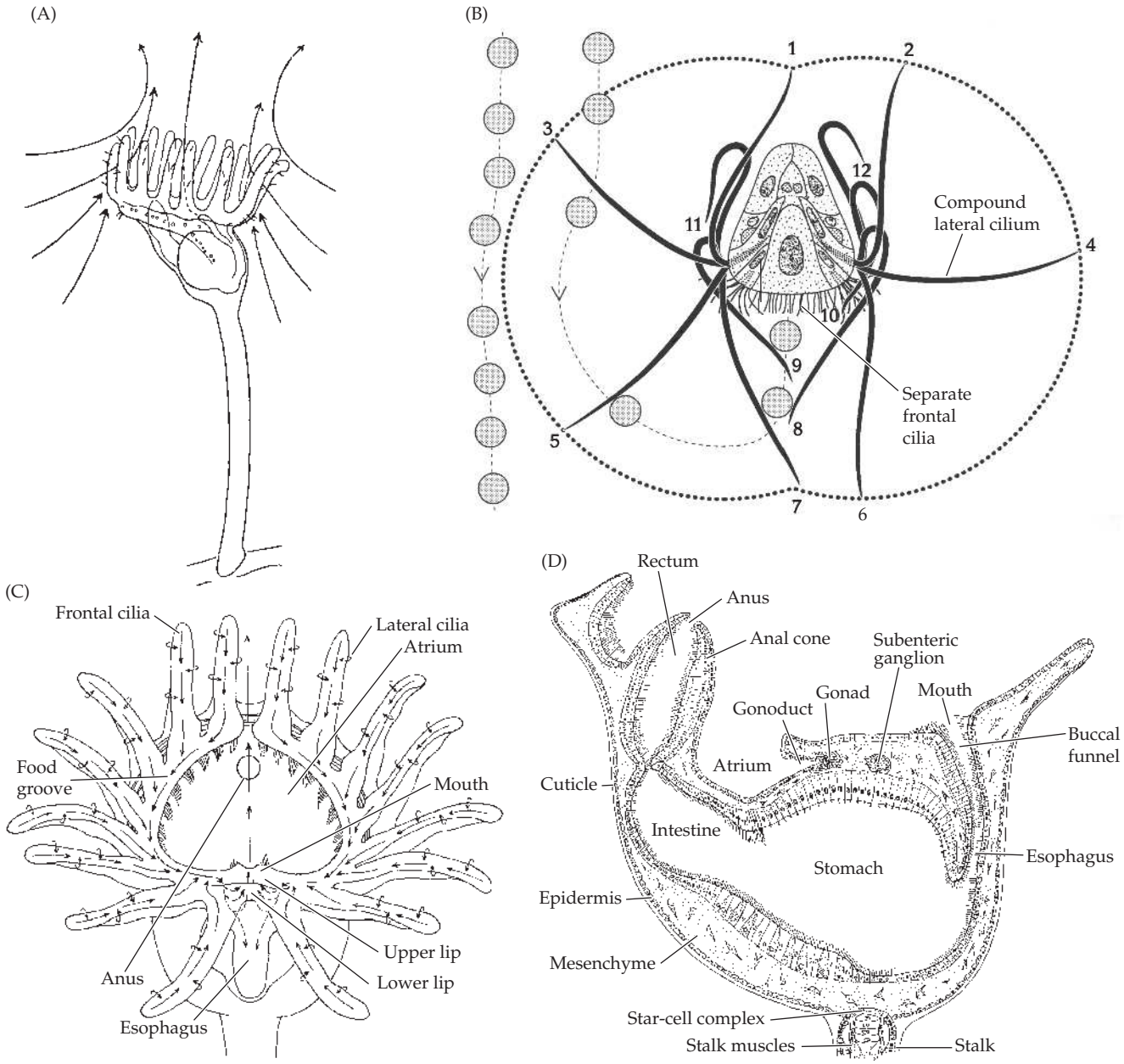


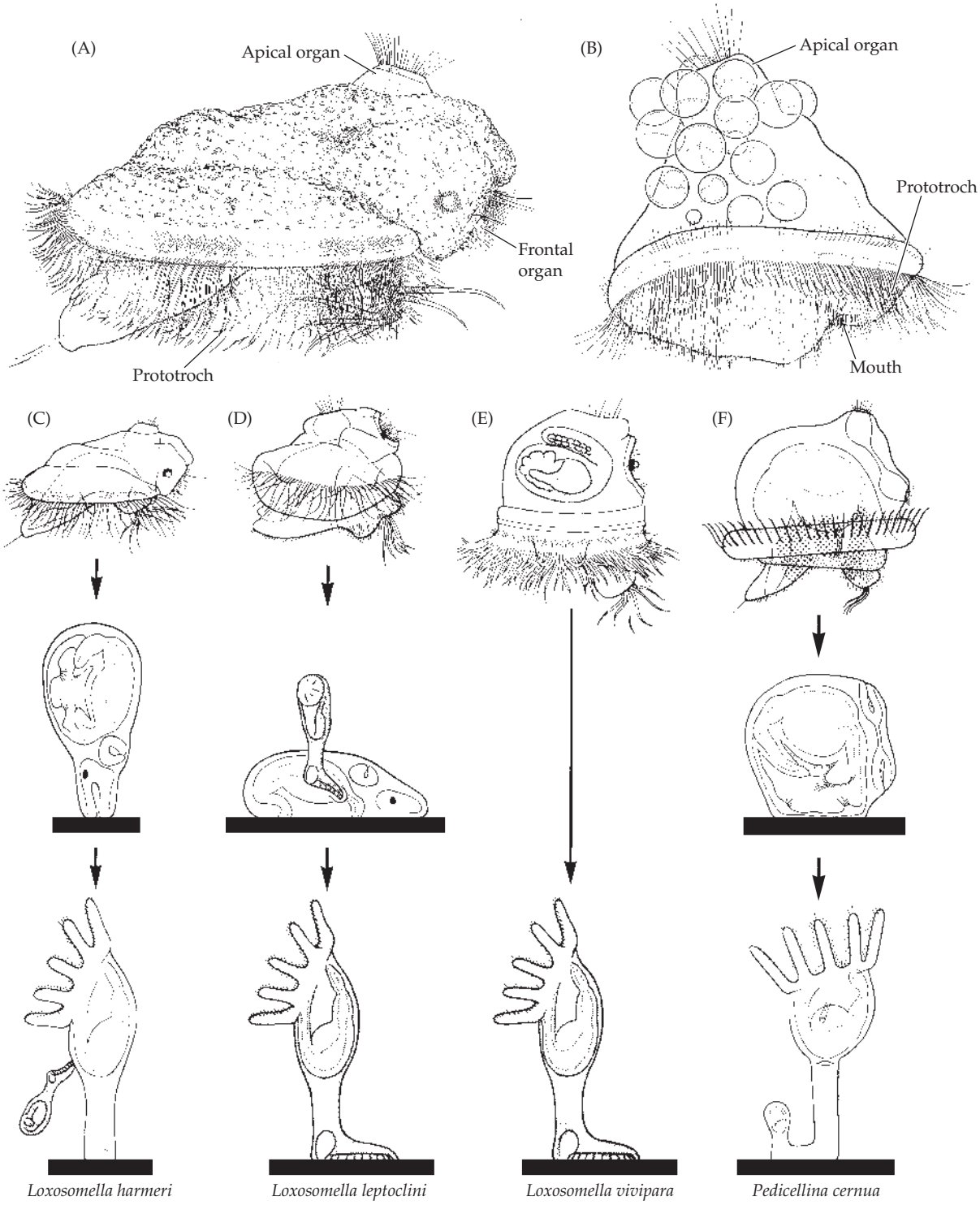
FIGURE 12.2 Entoproct feeding and digestion. (A) Water currents of the tentacle crown of *Loxosomella leptoclini* set up by the lateral cilia. (B) Downstream-collecting by the catch-up principle. A cross section through a tentacle with the movements of the large compound lateral cilia illustrated through successive steps (numbered 1–12) of a cilium on each side. The compound cilium catches up with the gray particle and pushes it to the frontal band of small separate cilia. (C) Ciliary feeding currents of the tentacle crown of a *Loxosomella*. Particles caught by the lateral cilia are transported along the frontal side of the tentacle to the food groove and further to the mouth. (D) Diagram of a median section of the calyx of a *Barentsia*.

unrelated freshwater species, *Loxosomatoides sirindhornae*. In most species, protonephridia appear to be present also in the larvae.

Internal transport is largely through the expansive gut; diffusion distances through the mesenchyme are small between its lumen and the body wall. Colonial entoprocts have a so-called **star-cell organ** located near the stalk-calyx junction (Figure 12.2D). This structure is thought to function as a heart by pulsating and pumping fluid from the calyx to the stalk. Gas exchange probably occurs over much of the body surface, particularly at the cuticle-free tentacles and atrium.

Nervous System

As is often the case in sessile invertebrates, the nervous system is greatly reduced. A single dumbbell-shaped ganglionic mass, called the subenteric ganglion, lies between the stomach and atrial surface (Figures 12.1B and 12.2D). The subenteric ganglion gives rise to several



pairs of nerves to the tentacles, calyx wall, and stalk. Unicellular tactile receptors are concentrated on the tentacles and scattered over much of the body surface. Ciliated papillae form lateral sense organs in some loxosomatids.

Reproduction and Development

Colony growth occurs by budding from the tips of the stolons (Figure 12.1B–E) or in some barentsiids from joints of the stalk. Solitary forms asexually produce buds on the calyx in the region of the esophagus, and these eventually separate from the parent (Figure 12.3C).

Most, perhaps all, loxosomatids are hermaphroditic and many are protandric. Those that are thought to have separate sexes may also be protandric, but with a long time between the male and female phases. Colonial forms may have hermaphroditic or gonochoristic zooids, and colonies may contain one or both sexes. One or two pairs of gonads lie just beneath the surface of the atrium. Short gonoducts lead from the gonads to

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◀ **FIGURE 12.3 Entoproct larvae and metamorphoses.** (A) Lecithotrophic larva of *Loxosomella harmeri*. (B) Planktotrophic larva of *Loxosoma pectinaricola*. (C–F) Settling and metamorphosis. (C) The larva settles with the frontal organ and becomes a juvenile (*Loxosomella harmeri*). (D) The larva settles and develops one or two buds that detach as juveniles; the larval body disintegrates (*Loxosomella leptoclini*). (E) The large internal bud disrupts the larval body and settles as a juvenile (*Loxosomella vivipara*). (F) The larva settles with the area just above the prototroch, and the gut rotates 180° with the mouth in front; the atrium reopens in the juvenile (*Pedicellina cernua*).

a common pore opening to the atrium (which serves as a brood chamber) (Figure 12.2D).

Sperm apparently are released into the water and then enter the female reproductive tract, with fertilization occurring in the ovaries or oviducts. As the zygote moves along the oviduct, cement glands secrete a tough surrounding membrane with a stalk by which the embryos are attached to the wall of the atrium/brood chamber. In a few species, the embryos are nourished by cells of the maternal atrium.

Cleavage in entoprocts is asynchronous, holoblastic, and clearly spiral. Nonsynchronous divisions produce five "quartets" of micromeres at about the 56-cell stage. Cell fates are similar to those in typical protostome development, including the derivation of mesoderm from the 4d mesentoblast. A coeloblastula forms and gastrulates by invagination. A larva develops that, in some species, resembles a typical planktotrophic trochophore (a basic larval type among protostomes), with a spiralian-like apical organ and proto- and metatroch bands used in swimming and downstream-collecting of food particles (Figure 12.3B). A few loxosomatids produce small eggs, and the larvae apparently spend a considerable period feeding in the plankton. Most of the loxosomatids and all the colonial species produce larger eggs; the fully differentiated larvae break the egg envelope and begin feeding. After release from the mother, these larvae have a short free period, and some of them do not feed (Figure 12.3A). Settling and metamorphosis show much variation. Some species of *Loxosomella* settle with a frontal organ, and the larval gut is retained in the adult (Figure 12.3C). Other loxosomatids develop external (Figure 12.3D) or internal (Figure 12.3E) buds from the episphere (the region above the prototroch) of the larva, and the larval body disintegrates. The larvae of the colonial species settle by cells just above the retracted prototroch and undergo a remarkable unequal growth of the body mass to rotate the gut so that the ventral, atrial surface points away from the substratum (Figure 12.3F).

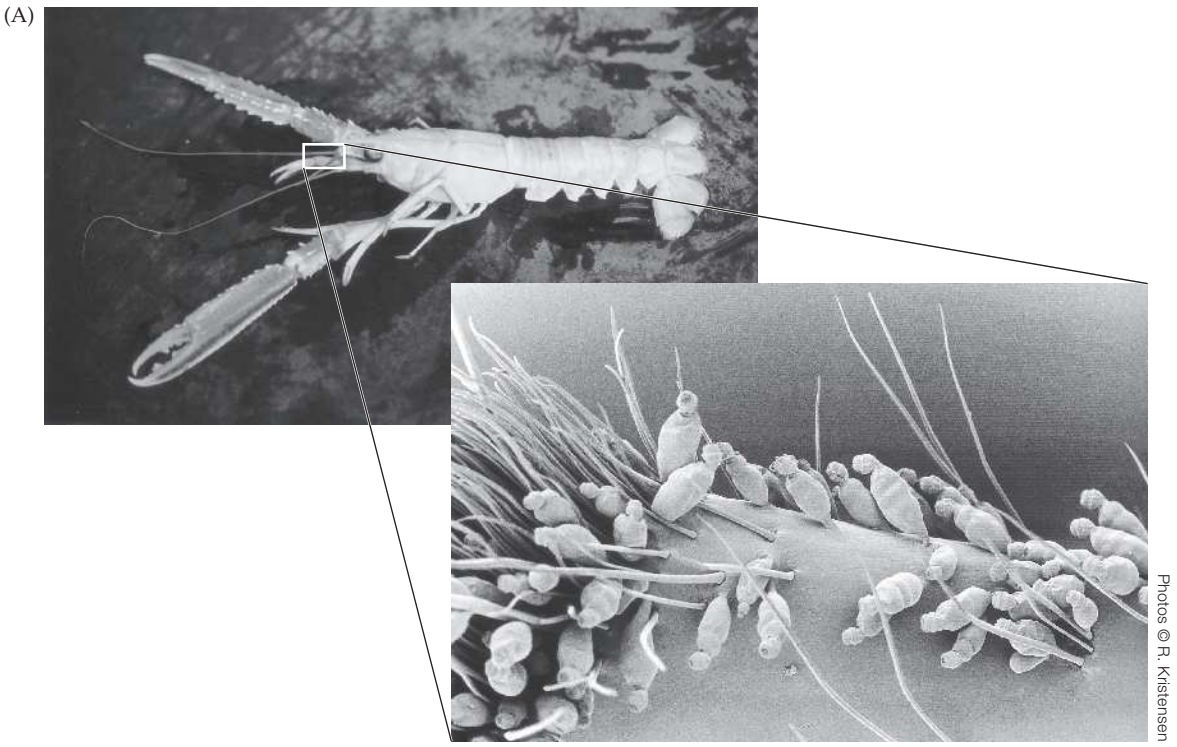
Phylum Cycliophora: The Cycliophorans

Symbion pandora is a microscopic marine animal first discovered in the 1960s living commensally on the mouthparts of the Norway lobster, *Nephrops norvegicus* (Figure 12.4; Box 12B). Not described until 1995, this apparently acoelomate animal was recognized as a separate phylum, Cycliophora. Since then, a second species, *Symbion americanus*, has been described from the American lobster, *Homarus americanus*, and investigations of the mouthparts of the European lobster (*Homarus gammarus*) suggest that a third species might also exist. The existence of one or more additional cryptic species on the American lobster has also been suggested by molecular studies. Cycliophorans appear to be highly host specific, though recent observations provided evidence for a possible symbiotic relationship between them and harpacticoid copepods. Although the role of copepods in the cycliophoran life cycle is unknown, two specimens of copepods carrying cycliophorans were collected from the mouthparts of a European lobster. The odd ecology of these minute metazoans is surpassed only by their bizarre anatomy and life history.

The life cycle of a cycliophoran is complex and involves various sexual and asexual phases alternating through a succession of stages. In striking contrast to sexual stages, asexual stages undergo a process of intense transcriptional and posttranscriptional regulation. Yet, whether this differential gene expression profile is connected with the shift to sexual reproduction remains inconclusive. The most conspicuous stage in the life cycle is an approximately 350 μm sessile individual

BOX 12B Characteristics of the Phylum Cycliophora

1. Triploblastic, bilateral, unsegmented, functionally acoelomate
2. Sessile, solitary symbionts of lobsters (feeding stage) or short-lived free-living phases; two described and two to three undescribed species known, all from Atlantic and Mediterranean lobsters
3. With layered cuticle, adhesive disc for attachment to host, and U-shaped gut
4. Suspension feeding, utilizing dense cilia situated on ring of multiciliate epidermal cells encircling opening of buccal funnel
5. Without circulatory system or respiratory organs
6. With one pair of protonephridia in the chordoid larva; excretory organs absent in all other stages
7. With a complex life cycle involving sexual and asexual stages that alternate through a succession of events
8. Cleavage apparently holoblastic, though pattern is unique among Spiralia
9. Maturation of the male involving a marked reduction of internal body volume, mainly by massive nuclei loss
10. With unique Pandora, Prometheus, and chordoid larvae



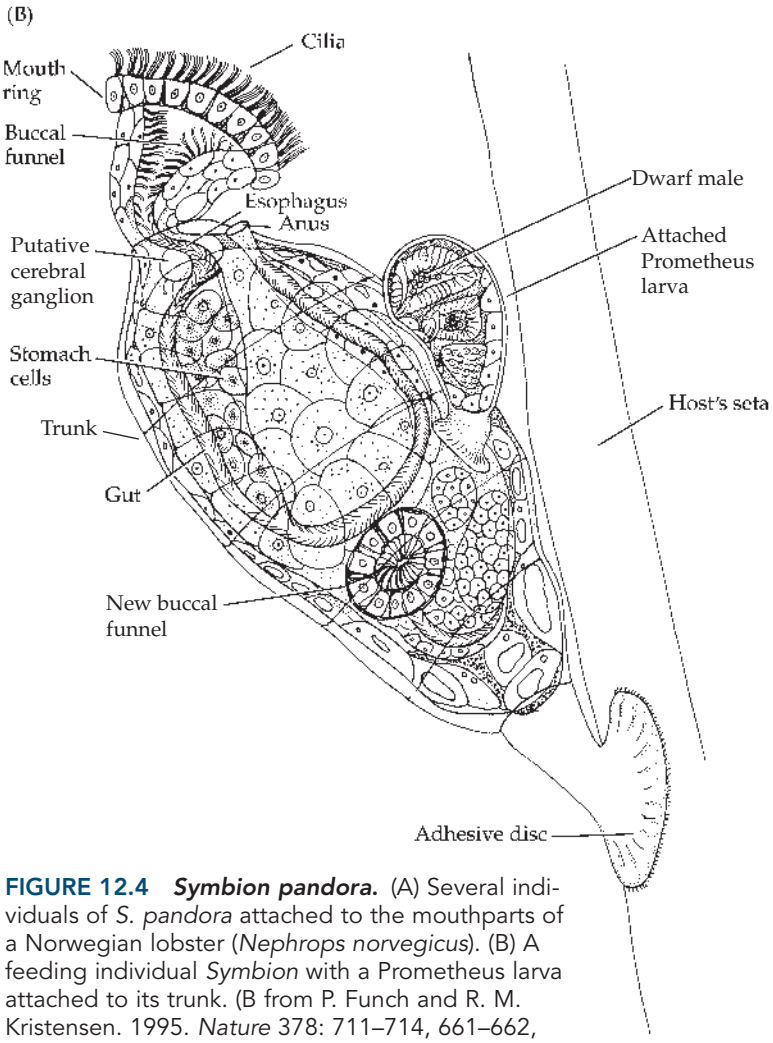


FIGURE 12.4 ***Symbion pandora.*** (A) Several individuals of *S. pandora* attached to the mouthparts of a Norwegian lobster (*Nephrops norvegicus*). (B) A feeding individual *Symbion* with a Prometheus larva attached to its trunk. (B from P. Funch and R. M. Kristensen. 1995. *Nature* 378: 711–714, 661–662, https://www.nature.com/articles/378711a0)

with a body divided into an anterior buccal funnel, an oval trunk, and a posterior adhesive disc by which the animal attaches to its host's setae (Figure 12.4). A layered cuticle covers the trunk and adhesive disc, the latter apparently composed entirely of cuticular material. Equipped with a U-shaped gut, this is the only cycliophoran stage able to feed—and the most likely stage to be found by a cycliophoran enthusiast. The region between the gut and body wall is packed with large mesenchymal cells, and no evidence of a body cavity has been observed. Suspension feeding is enhanced by creating water currents with dense cilia that are situated on a ring of epidermal cells encircling the open end of the buccal funnel. These multiciliate epidermal cells alternate with contractile myoepithelial cells, which form a pair of sphincters involved in the closure of the mouth opening. The U-shaped gut is ciliated along its entire length. The buccal funnel leads to a curved esophagus and then to a stomach consisting of large stomach cells that protrude into a narrow lumen. An intestine extends anteriorly to a short rectum and anus, located dorsally near the base of the buccal funnel. A complex sphincter is located proximally to the anus. The area between the gut and other organs is packed with a cellular mesenchyme. A pair of muscles span longitudinally along

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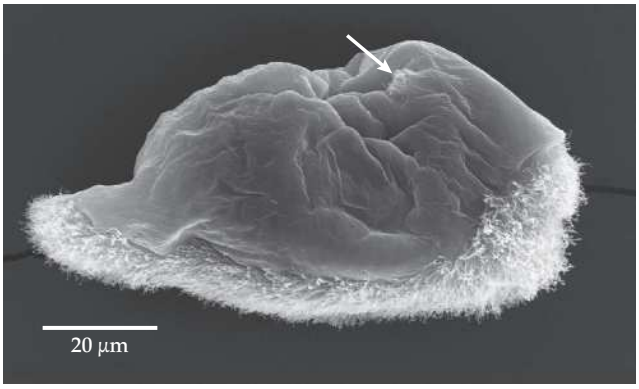
the buccal funnel, while several longitudinal muscle fibers (six in *S. americanus* and two to eight in *S. pandora*) begin at the most distal region of the trunk and span about two-thirds of its length.

Circulation and gas exchange are presumably accomplished by simple diffusion in these tiny animals. The nervous system is poorly understood, and two ganglia were originally described in the feeding individual: one ganglion located at the base of the buccal funnel, and the other partially surrounding the esophagus. However, further observations based on ultrastructural and immunohistochemical investigations have not confirmed the existence of these ganglia. Excretory organs have not been identified in the feeding individual, although a pair of protonephridia is present in one of the larval stages, the chordoid larva.

Feeding-stage individuals are able to reproduce asexually by a budding process that occurs inside the trunk and generates free-swimming stages, one at a time—these are the **Pandora larva**, the **Prometheus larva**, and the female. In order to rapidly increase the population density on a single host, the feeding individual generates Pandora larvae (170 μm long), which possess a buccal funnel inside their bodies. Once released, the Pandora larva settles close to the maternal individual on the lobster host and develops into a new feeding stage.

In the sexual part of the life cycle, a free-swimming Prometheus larva (120 μm long) settles on the trunk of a feeding individual and develops one to three dwarf males (40 μm long) inside its own body. Females (which like the males have also escaped from the maternal individual) carry a single oocyte and are impregnated by dwarf males in a process that is not yet well understood. A number of morphological structures might be involved in impregnation. For instance, a small (~3 μm in diameter), circular structure surrounded by cilia is located medially on the ventral side of the female body. This structure has been described as a putative gonopore, though a canal for the conductance of sperm is not evident. In addition, the external morphology of the male is characterized by a "penis" located ventroposteriorly, although its actual function as a true copulatory organ or as a mere anchoring and piercing device is uncertain. A recent investigation at the ultrastructural level revealed the presence of a sperm cell inside the penis of the dwarf male, which provides support for the former view. The female migrates from the body of the maternal cycliophoran individual to the lobster host, where it settles onto a sheltered area of the mouthparts and encysts, and the embryo develops into the so-called **chordoid larva**.

The chordoid larva (Figure 12.5) hatches from the cyst, swims away from it, and settles on a new host, where it eventually develops into a new feeding stage. This is probably the avenue by which dispersal to new host individuals is achieved. The anatomy of the chordoid larva was first described by Funch (1996), who suggested that it is a modified trochophore larva, homologous with those of many spiralians (e.g., annelids and molluscs). However, the overall neuroanatomy of this larval stage much more closely resembles the condition of adult rather than larval stages of spiralian taxa. The chordoid larva is also characterized by a ventral chordoid organ that spans the entire length of the body. The function of the chordoid organ is not known, although it might be supportive and locomotory; it is mainly muscular.



Courtesy of Ricardo Neves

FIGURE 12.5 ***Symbion pandora*, chordoid larva.** Note the dense ciliated field covering the ventral region of the body, from posterior (left) to anterior (right). The arrow points at the dorsal ciliated organ, which appears to have a sensory role.

Knowledge of cycliophoran development is quite limited. Details on early embryogenesis derive from observations on settled females bearing an internal embryo. The eight-cell-stage embryo is composed of a group of four macromeres and four micromeres. Cleavage appears to be holoblastic, though the arrangement of the blastomeres does not reveal any clear pattern similar to that seen in other spiralian taxa. As for asexual development, a recent study using serial block-face scanning electron microscopy provided new insights on the development of the dwarf male inside the attached Prometheus larva. During the maturation of a young male into a mature dwarf male, the body undergoes a reduction of about one-third in the internal body volume, mainly by extensive loss of nuclei in the majority of its somatic cells (but especially in cells of the muscles and epidermis). Organs seen in mature dwarf males—muscles, brain, testis, glands, etc.—are already formed in the young male. The young male stage possesses about 200 nucleated cells, whereas the mature male stage comprises only around 50 nucleated cells; muscle and epidermal cells of the mature male lack nuclei. Thus, contrary to typical development of metazoans, the cycliophoran dwarf male does not grow after organogenesis is concluded.

The external morphology of the Prometheus larva, the Pandora larva, and the female is similar in many respects. For example, an anteroventral ciliated field

and a posterior ciliated tuft, as well as four bundles of long cilia—which compose a sensory organ, or sensilla—are present in all these life cycle stages. In addition, all of these free-swimming stages possess a well-differentiated cuticle characterized by a polygonal sculptured surface. The external morphology of the chordoid larva differs from these stages in possessing anterior, ventral, and posterior ciliated fields, as well as a paired dorsal organ that appears to have a sensory role (Figure 12.5). The dwarf male is characterized by dense ventral and frontal ciliated fields, and sensilla situated laterally and frontally. The myoanatomy and nervous system of all cycliophoran free-swimming stages have been investigated by transmission electron and confocal laser scanning microscopy. In general, the musculature of the free stages is very complex and includes longitudinal muscles that span the body dorsally and ventrally, as well as dorsoventral muscles. All free-swimming stages possess a dorsal brain composed of a pair of lateral clusters of perikarya interconnected by a commissural neuropil. Moreover, the chordoid larva has four distinct ventral longitudinal neurites, while all the other free-swimming stages have only two. The typical spiralian apical organ is absent in all cycliophoran larval stages, thus rejecting a homology of any of these stages with a trochophore larva.

Chapter Summary

This chapter introduced you to the phyla Cycliophora and Entoprocta, two small taxa of minute size and uncertain affinity embedded in the large and highly diverse protostome clade called Platytrochozoa. Cycliophora and Entoprocta are fundamentally marine animals (two freshwater species of entoprocts are known), and both groups are so rare that common names don't exist for them. Entoprocts are small, probably acoelomate, solitary or colonial, polyplike creatures that have been known since the nineteenth century. Cycliophorans are microscopic, solitary, acoelomate symbionts on the mouthparts of lobsters, where they form large aggregations. They weren't discovered until the 1960s and are still quite poorly known, with their complex life cycle just beginning to be understood. Entoprocts show typical spiral development. Both phyla have planktonic larvae, those of Entoprocta probably being trochophores. Major research areas that are important to our understanding of these two phyla include their precise phylogenetic placement in the protostome tree of life, the nature of the cycliophoran symbiotic relationship with lobsters (and possibly also copepods), and the embryogeny and life cycle of cycliophorans.

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CHAPTER 13

Introduction to the Lophotrochozoa, and the Phylum Mollusca

In Chapters 8 and 10 we introduced you to the Protostomia and Deuterostomia, and to the two protostome clades Spiralia and Ecdysozoa. While these higher-level clades are well supported by molecular data, the relationships within Spiralia still remain to be sorted out. As you can see in the Classification of the Animal Kingdom, we recognize two large clades of Spiralia, Gnathifera and Platytrochozoa (plus the enigmatic Dicyemida). Within the Platytrochozoa, a group of six phyla almost always cluster in molecular phylogenies. These are the Mollusca, Nemertea, Annelida, and the three lophophorate phyla (Phoronida, Bryozoa, Brachiopoda). These six phyla comprise the clade **Lophotrochozoa**, and their Cambrian remains, in the form of the so-called "small shelly fossils," seem to be shells, spicules, and setae of extant groups such as molluscs, brachiopods, annelids, and some of their stem group members (e.g., halkieriids, wiwaxiids, hyoliths, and tommotiids). The presence of such structures with a seemingly similar developmental origin, originating as epidermal formations whose secretory cells develop into a cup or a follicle with microvilli at its base, may be the morphological character that unites the members of Lophotrochozoa. In fact, it has been proposed that there has been co-option of Hox genes for making shells, spicules, and chaetae (see Schiemann et al. 2017), pushing the case for homology. Interestingly, this clade of animals primarily with spicules and/or sclerites also includes animals without such hard parts, as for example nemerteans and phoronids.

As a disclaimer, the name Lophotrochozoa has been given different meaning by different authors. While some use it as a synonym for the whole clade Spiralia, we prefer to use the

The section on Mollusca was revised by David R. Lindberg and Winston F. Ponder.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

more restricted sense given here. The compound name of Lophotrochozoa refers to the clade Lophophorata (i.e., Brachiopoda, Bryozoa, and Phoronida), and the clade formerly known as Trochozoa (i.e., Annelida, Mollusca), plus other groups with a "cryptic trochophore" larva (Nemertea), and perhaps Entoprocta and Cycliophora. However, the position of the latter two phyla, probably closely related, is unstable in phylogenomic analyses. In this chapter we focus on one of the main lophotrochozoan phyla, the Mollusca.

Phylum Mollusca

Molluscs comprise the second largest phylum of animals (after arthropods) and include some of the best-known invertebrates; almost everyone is familiar with snails, clams, slugs, squid, and octopuses. Molluscan shells have been popular since ancient times, and some cultures still use them as tools, containers, musical devices, money, fetishes, religious symbols, ornaments, decorations, and art objects. Evidence of historical use and knowledge of molluscs is seen in ancient texts and hieroglyphics, on coins, in tribal customs, and in archaeological sites and aboriginal kitchen middens or shell mounds. Royal or Tyrian purple of ancient Greece and Rome, and even Biblical blue (Num. 15:38), were molluscan pigments extracted from certain marine snails.[1] Many aboriginal groups have for millennia relied on molluscs for a substantial portion of their diet and for use as tools. Today, coastal nations annually harvest millions of tons of molluscs commercially for food.

There are approximately 73,000 (±3,000) described, living mollusc species and about the same number of described fossil species. However, many species still await names and description, especially those from poorly studied regions and time periods. In addition to three familiar molluscan classes comprising the clams (Bivalvia), snails and slugs (Gastropoda), and squid and octopuses (Cephalopoda), there are five other extant classes: chitons (Polyplacophora), tusk shells (Scaphopoda), *Neopilina* and its kin (Monoplacophora), and the vermiform sclerite-bearing aplacophoran classes—Caudofoveata (or Chaetodermomorpha) and Solenogastres (or Neomeniomorpha). Although members of these eight classes differ enormously in superficial appearance, there is a suite of characters that diagnose their fundamental body plan (Box 13A).

BOX 13A Characteristics of the Phylum Mollusca

1. Bilaterally symmetrical (or secondarily asymmetrical), unsegmented, coelomate protostomes
2. Coelom limited to small spaces in nephridia, heart, and gonads
3. Principal body cavity a hemocoel (open circulatory system)
4. Viscera concentrated dorsally as a "visceral mass"
5. Body with a cuticle-covered epidermal sheet of skin, the mantle
6. Mantle with shell glands that secrete calcareous epidermal sclerites, shell plates, or shells
7. Mantle overhanging and forming a cavity (the mantle cavity) in which are housed the ctenidia, osphradia, nephridiopores, gonopores, and anus
8. Heart situated in a pericardial chamber and composed of a single ventricle and one or more separate atria
9. Typically with large, well-defined muscular foot, often with a flattened creeping sole
10. Buccal region provided with a radula and muscular odontophore
11. Complete (through) gut, with marked regional specialization, including large digestive glands
12. With large, complex metanephridial "kidneys"
13. Cleavage typically spiral and embryogeny protostomous, with cephalopods an exception
14. Typically with a trochophore larva, and a veliger larva in gastropods and bivalves; some groups with a test cell larva

Taxonomic History and Classification

Molluscs carry the burden of a very long and convoluted taxonomic history, in which hundreds of names for various taxa have come and gone. Aristotle recognized molluscs, dividing them into Malachia (the cephalopods) and Ostrachodermata (the shelled forms), the latter being divided into univalves and bivalves. Joannes Jonston (or Jonstonus) created the name Mollusca[2] in 1650 for the cephalopods and barnacles, but this name was not accepted until it was resurrected and redefined by Linnaeus nearly 100 years later. Linnaeus's Mollusca included cephalopods, slugs, and pteropods, as well as tunicates, anemones, medusae, echinoderms, and polychaetes—but he placed chitons, bivalves (including the unrelated brachiopods), univalves, nautilids, barnacles, and the serpulid

[1] Archaeological sites in Israel reveal the probable use of two muricid snails (*Bolinus brandaris* and *Hexaplex trunculus*) as sources of the royal purple dye.

[2] The vernacular for "Mollusca" is often spelled *mollusks* in the United States, whereas in many other parts of the world it is typically spelled *molluscs*. In biology, a vernacular or diminutive name is generally derived from the proper Latin name; thus the custom of altering the spelling of "Mollusca" by changing the *c* to *k* seems to be an aberration (although it may have its historic roots in the German language, which does not have the freestanding *c*; e.g., *Molluskenkunde*). We prefer the more widely used spelling *molluscs*, which seems to be the proper vernacularization and is in line with other accepted terms, such as "molluscan," "molluscoid," "molluscivore," etc.

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polychaetes (which secrete calcareous tubes) in another group, Testacea. In 1795 Georges Cuvier published a revised classification of the Mollusca that was the first to approximate modern views. Henri de Blainville (1825) altered the name Mollusca to Malacozoa, which won little favor but survives in the terms "malacology," "malacologist," etc.

Much of the nineteenth century passed before the phylum was purged of all extraneous groups. In the 1830s, J. Thompson and C. Brumeister identified the larval stages of barnacles and revealed them to be crustaceans, and in 1866 Alexander Kowalevsky removed the tunicates from Mollusca. Separation of the brachiopods from the molluscs was long and controversial and not resolved until near the end of the nineteenth century.

The first sclerite-covered, wormlike aplacophorans, members of what today we recognize as the class Caudofoveata, were discovered in 1841 by the Swedish naturalist Sven Lovén. He classified them with holothuroid echinoderms because of their vermiform bodies and the presence of calcareous sclerites in the body walls of both groups. In 1886, another Swede, Tycho Tullberg, described the first representative of the other aplacophoran group—the Solenogastres. Ludwig von Graff (1875) recognized both groups as molluscs, and in 1876 they were united in the Aplacophora by Hermann von Ihering. The Aculifera hypothesis of Amélie Scheltema unites molluscs that possess calcareous sclerites by placing Polyplacophora as the sister taxon of the aplacophorans (Caudofoveata + Solengastres). Aculifera was sometimes also called Amphineura, although this latter term has also been used by some workers to refer only to chitons. **Sclerites** are spicules, scales, and so on that cover or are embedded in the epidermis of molluscs and are often calcified.

The history of classification of species in the class Gastropoda has been volatile, undergoing constant change since Cuvier's time. Most modern malacologists have been influenced by the schemes of Henri Milne-Edwards (1848) and J. W. Spengel (1881). The former, basing his classification on the respiratory organs, recognized the groups Pulmonata, Opisthobranchia, and Prosobranchia. Spengel based his scheme on the nervous system and divided the gastropods into the Streptoneura and Euthyneura. In subsequent classifications, Streptoneura was equivalent to Prosobranchia; Euthyneura included Opisthobranchia and Pulmonata. The bivalves have been called Bivalvia, Pelecypoda, and Lamellibranchiata. More recently, anatomical, ultrastructural, and molecular studies have brought about considerable changes to molluscan classification. Also, many taxa have multiple names, and the more commonly encountered ones are noted below.

Molluscan classification at the genus and species levels can also be troublesome. Many species of gastropods and bivalves are also burdened with numerous names (synonyms) that have been proposed for the same species. This tangle is partly the result of a long history of amateur shell collecting, beginning with the natural history cabinets of seventeenth-century Europe, which required documentation and promoted multiple taxonomies and names based only on shell characters. Today, species are recognized based on a combination of shell, anatomical, and, most recently, molecular characters. However, because of the tremendous diversity of gastropods and bivalves many species still remain known only from their shells.

Only taxa with extant members are included in the following classification, and some examples of families are listed in Synopses of Major Molluscan Groups. The classification is mostly ranked, but in a few cases unranked group names are used. Examples of the major molluscan taxa appear in Figure 13.1.[3]

ABBREVIATED CLASSIFICATION OF LIVING MEMBERS OF THE PHYLUM MOLLUSCA[4]

CLASS CAUDOFOVEATA (= CHAETODERMOMORPHA)
Caudofoveatan aplacophorans (spicule worms)

CLASS SOLENOGASTRES (= NEOMENIOMORPHA)
Solenogaster aplacophorans (spicule worms)

CLASS MONOPLACOPHORA Monoplacophorans; deep sea, limpet-like

CLASS POLYPLACOPHORA Chitons, with eight shell valves

CLASS GASTROPODA Snails, slugs, and limpets

SUBCLASS EOGASTROPODA

INFRACLASS PATELLOGASTROPODA True limpets

[3]Multitudes of extinct molluscs have been described. Perhaps the most well known are some of the groups of cephalopods that had hard external shells, similar to those of living *Nautilus*. One of these groups was the ammonites. They differed from nautilids in having shell septa that were highly fluted on the periphery, forming complex mazelike septal sutures. Ammonites also had the siphuncle lying against the outer wall of the shell, as opposed to the condition seen in many nautilids where the siphuncle runs through the center of the shell.

[4]Note that the gastropod classification endorsed by Ponder and Lindberg (2020) dividing gastropods into Eogastropoda and Orthogastropoda and adopted in this chapter has been refuted by most molecular analyses (e.g., Aktipis et al. 2008), including phylogenomic analyses of gastropod relationships (Zapata et al. 2014; Cunha and Giribet 2019), which instead favor a sister group relationship of Patellogastropoda and Vetigastropoda, a clade named Psilogastropoda (Cunha and Giribet 2019). The remaining gastropods (Neritimorpha, Caenogastropoda, and Heterobranchia) are known as Adenogonogastropoda (Simone 2011) or Angiogastropoda (Cunha and Giribet 2019). Only some recent mitochondrial genome analyses support the Eogastropoda/Orthogastropoda division (Uribe et al. 2019).

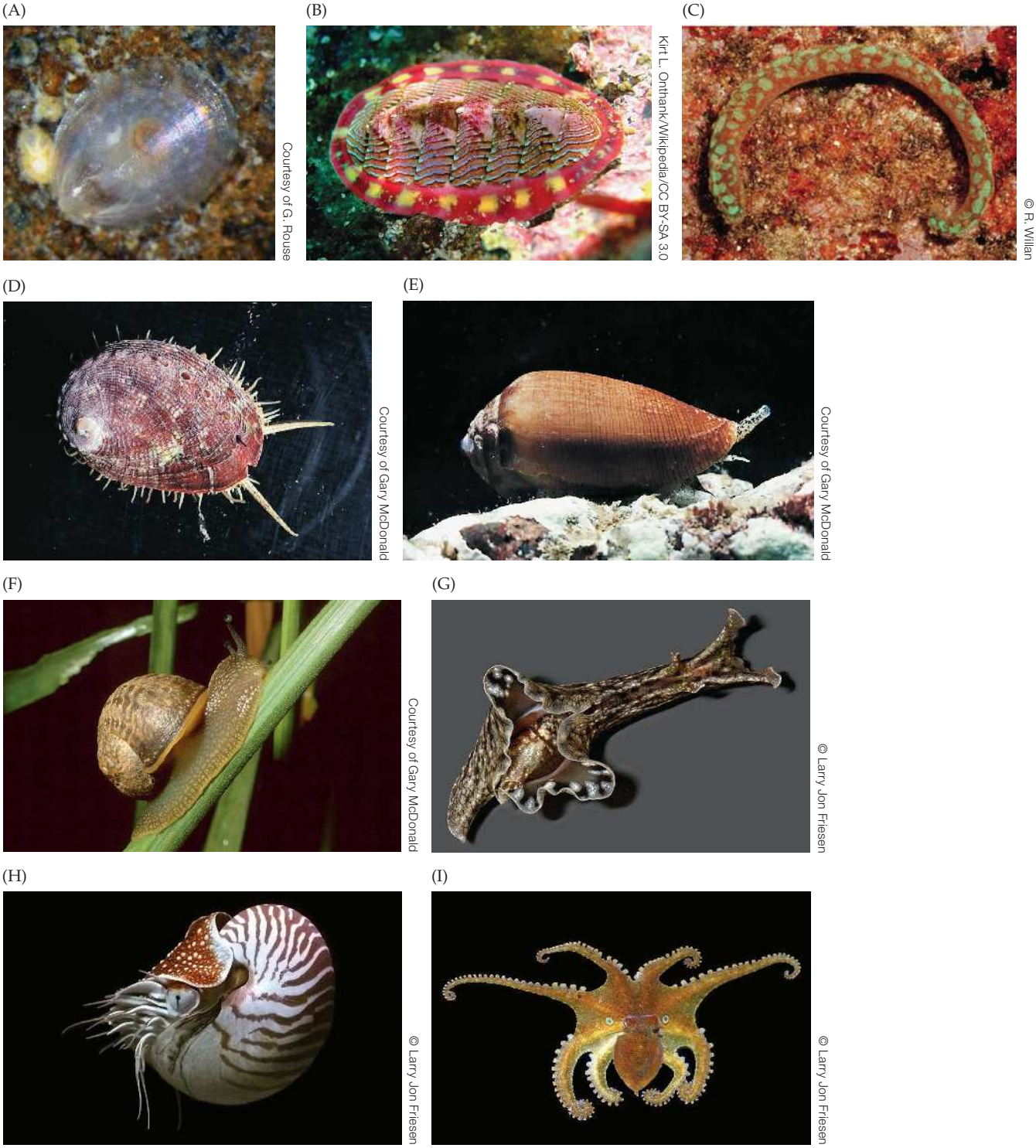

FIGURE 13.1 Morphological diversity among the molluscs. (A) *Laevipilina hyalina* (Monoplacophora). (B) *Tonicella lineata*, a lined chiton (Polyplacophora). (C) *Epimenia australis* (Solenogastres). (D) *Haliotis rufescens*, the red abalone (Gastropoda, Vetigastropoda); note the exhalant holes in the shell. (E) *Conus*, a predatory neogastropod; note anterior siphon extending beyond shell (Gastropoda, Hypsogastropoda). (F) A common garden snail, *Cornu aspersum* (Gastropoda, Panpulmonata). (G) *Aplysia*, the sea hare (Gastropoda, Euopisthobranchia). (H) The chambered *Nautilus* (Cephalopoda, Nautilida). (I) *Octopus bimaculoides* (Cephalopoda, Coleoida). (J) *Sepioteuthis lessoniana*, the bigfin reef squid (Cephalopoda, Coleoida). (K) *Histioteuthis*, a pelagic squid (Cephalopoda, Coleoida). (L) *Fustiaria*, a tusk shell (Scaphopoda). (M) Scallops (Bivalvia, Pteriomorphia), with a hermit crab in the foreground. (N) The giant clam *Tridacna maxima* (note zooxanthellate mantle), from the Marshall Islands, Northwest Pacific (Bivalvia, Heterodonta, Cardiida). (O) The European cockle *Acanthocardia tuberculata* (Bivalvia, Heterodonta, Cardiida). Note the partly extended foot. (P) *Lima*, a tropical clam that swims by clapping the valves together (Bivalvia, Pteriomorphia). (Q) The highly modified bivalve *Brechites* (Heterodonta, Anomalodesmata) known as watering-pot shells. It begins its life as a typical small bivalve but then secretes a large calcareous tube around itself through which water is pumped for suspension feeding.

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SUBCLASS ORTHOGASTROPODA

INFRACLASS VETIGASTROPODA "Primitive" marine top-shell snails, abalones and keyhole and slit "limpets"

INFRACLASS NERITIMORPHA Marine, land and freshwater nerite snails and "limpets"

INFRACLASS CAENOGASTROPODA Marine, freshwater and land snails (creepers, periwinkles, conchs, whelks, cowries etc.) and some "limpets"

"ARCHITAENIOGLOSSA" Nonmarine basal caenogastropods (paraphyletic)

COHORT SORBEOCONCHA All remaining caenogastropods

MEGAORDER CERITHIIMORPHA Creepers, turret shells, etc.

MEGAORDER HYPSOGASTROPODA Higher caenogastropods: periwinkles, cowries, triton shells, neogastropods (whelks, volutes, rock shells, etc.)

INFRACLASS HETEROBRANCHIA Marine, freshwater, and land snails, most sea slugs, all land slugs, and some "false limpets"

"LOWER HETEROBRANCHIA" A few primitive heterobranch groups, including sundial shells, valvatids, etc.

COHORT EUTHYNEURA Formerly included the "opisthobranchs" and "pulmonates"

SUPERORDER NUDIPLEURA Side-gilled sea slugs and nudibranchs

SUPERORDER EUOPISTHOBRANCHIA Bubble shells, sea hares, pteropods, etc.

SUPERORDER PANPULMONATA "Pulmonates," pyramidellids, sacoglossan sea slugs, most land snails, all land slugs

CLASS BIVALVIA Clams and their kin (bivalves)

SUBCLASS PROTOBRANCHIA "Primitive" deposit-feeding bivalves

SUBCLASS AUTOBRANCHIA "Lamellibranch" suspension-feeding bivalves

INFRACLASS PTERIOMORPHIA Mussels, oysters, scallops, and their kin

INFRACLASS HETEROCONCHIA Marine and freshwater clams

COHORT PALAEOHETERODONTA Freshwater clams (mussels), brooch shells

COHORT HETERODONTA Most marine clams

SUBCOHORT ARCHIHETERODONTA A few families of primitive marine clams

SUBCOHORT EUHETERODONTA The majority of marine and some freshwater clams

ANOMALODESMATA

IMPARIDENTIA

CLASS SCAPHOPODA Tusk shells

CLASS CEPHALOPODA Chambered nautilus, squid, octopuses

SUBCLASS PALCEPHALOPODA

COHORT NAUTILIA Chambered nautilus

SUBCLASS NEOCEPHALOPODA

COHORT COLEOIDA Octopuses, squid, cuttlefish

SUPERORDER OCTOBRACHIA Octopuses, vampire squid

SUPERORDER DECABRACHIA Cuttlefish, squid

SYNOPSES OF MAJOR MOLLUSCAN GROUPS

CLASS CAUDOFOVEATA (= CHAETODERMOMORPHA) (Figure 13.2A–C). Caudofoveatans, or spicule worms. Marine, benthic, burrowing; body vermiform, cylindrical, lacking any trace of a shell; body wall with a chitinous cuticle and imbricating scalelike aragonitic calcareous sclerites; mouth shield anterior to or surrounding the mouth; small posterior mantle cavity with a pair of bipectinate ctenidia; radula present; gonochoristic. Without foot, eyes, tentacles, statocysts, crystalline style, osphradia, or nephridia. About 130 species; burrow in muddy sediments and consume microorganisms such as foraminiferans. (e.g., *Chaetoderma, Chevroderma, Falcidens, Limifossor, Prochaetoderma, Psilodens*)

CLASS SOLENOGASTRES (= NEOMENIOMORPHA) (Figure 13.2D–K). Solenogasters, or spicule worms. Marine, benthic; body vermiform and nearly cylindrical; vestibulum (= atrium) with sensory papillae anterior to the mouth; small posterior mantle cavity lacking ctenidia but often with respiratory folds; body wall with a chitinous cuticle and imbued with calcareous sclerites (as spines or scales); with or without radula; hermaphroditic; pedal glands opening into a pre-pedal ciliary pit; foot weakly muscular, narrow, and retractable into a ventral furrow or "pedal groove." Without eyes, tentacles, statocysts, crystalline style, osphradia, or nephridia. About 260 described species, but many undescribed species are thought to exist; epibenthic carnivores, often found on (and consuming) cnidarians and a few other types of invertebrates. Solenogastres and Caudofoveata are sister groups in most phylogenetic schemes and are sometimes regarded as subclasses within the class Aplacophora. (e.g., *Alexandromenia*, *Dondersia*, *Epimenia*, *Kruppomenia*, *Neomenia*, *Proneomenia*, *Pruvotina*, *Rhopalomenia*, *Spengelomenia*, *Wirenia*)

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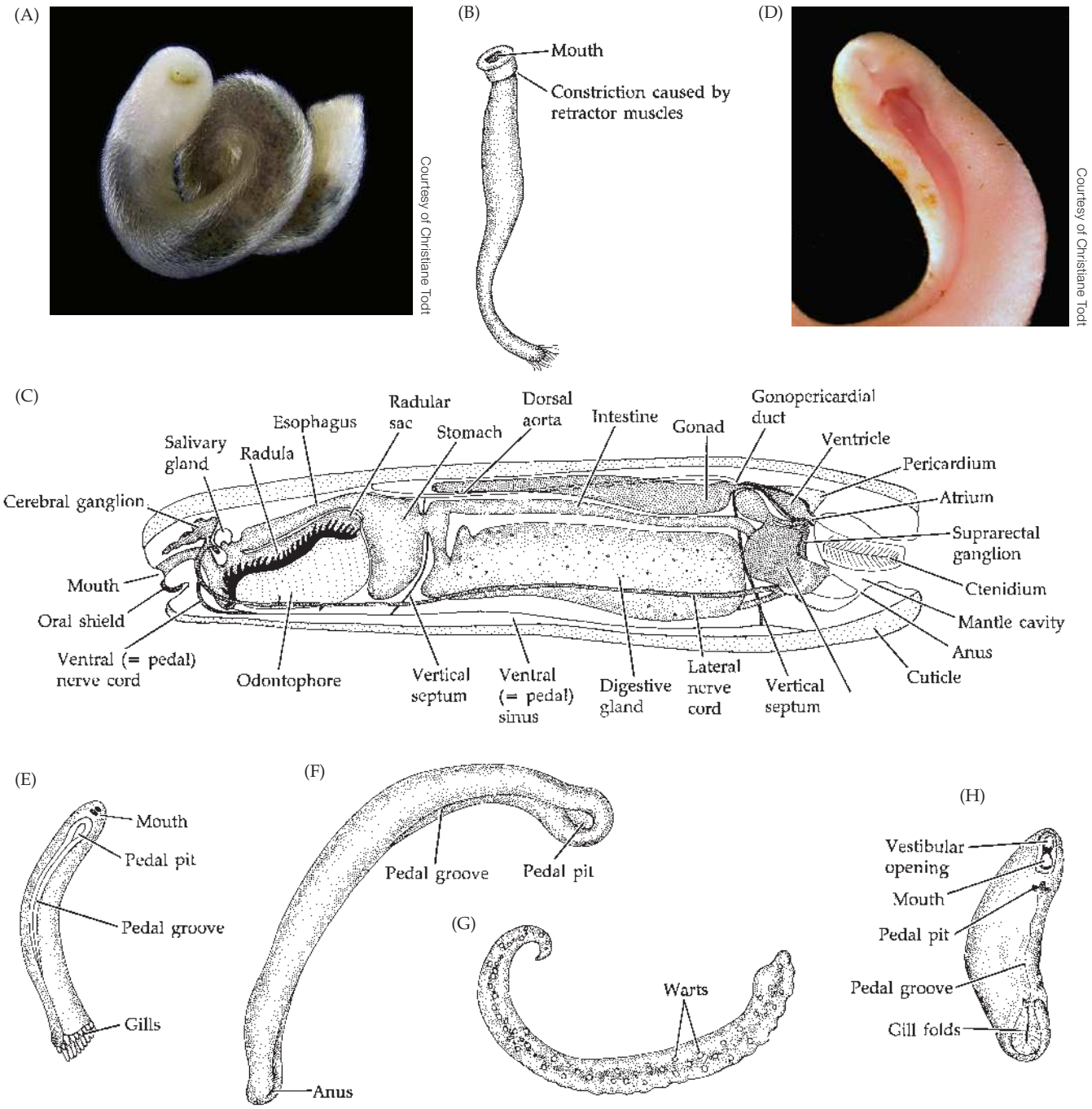

FIGURE 13.2 General anatomy of aplacophorans. (A–C) Caudofoveata. (A) *Chaetoderma productum*. (B) *Chaetoderma loveni*. (C) Internal anatomy of *Limifossor* (highly stylized sagittal section drawing). (D–L) Solenogastres. (D) *Kruppomenia minima*. (E) *Pruvotina impexa*, ventral view. (F) *Proneomenia antarctica*. (G) *Epimenia verrucosa*. The body is covered with warts. (H) *Neomenia carinata*, ventral view.

(*Continued on next page*)

CLASS MONOPLACOPHORA Monoplacophorans. With a single, caplike shell; foot forms weakly muscular ventral disc, with 8 pairs of retractor muscles; shallow mantle cavity around foot encloses 3–6 pairs of ctenidia; 2 pairs of gonads; 3–7 pairs of nephridia; 2 pairs of heart atria; a pair of statocysts; with radula and distinct but small head region; without eyes; short oral tentacles present around mouth; with posterior anus; without a crystalline style; gonochoristic or, rarely, hermaphroditic (Figures 13.1A and 13.3). Until the first living species (*Neopilina galatheae*) was discovered by the Danish Galathea Expedition in 1952, monoplacophorans were known only from Paleozoic (Cambrian to Devonian) fossils. Since then their unusual anatomy has been a source of much evolutionary speculation. Monoplacophorans are limpet-like in appearance, living species are less than

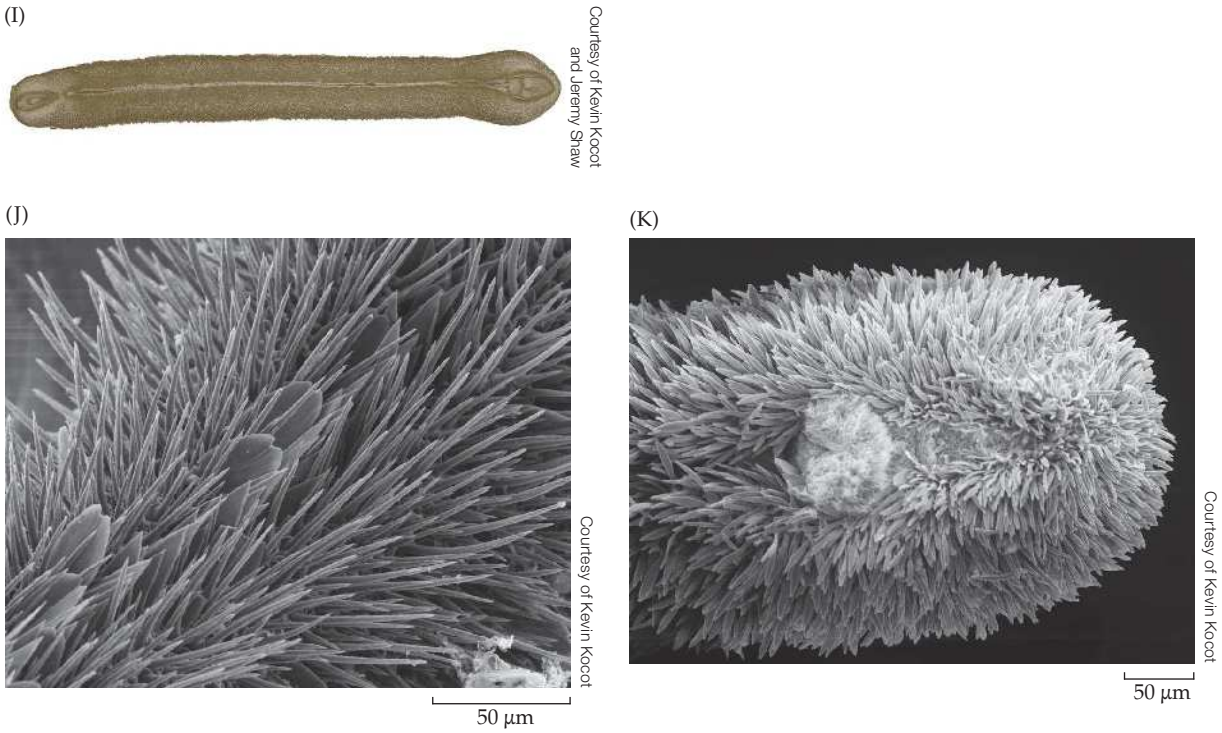

FIGURE 13.2 (*continued*) General anatomy of aplacophorans. (I) *Entonomenia tricarinata*, ventral view (X-ray micro-CT). (J) *Macellomenia morseae*. SEM of ventral surface showing two types of scalelike sclerites surrounding the foot and spiny sclerites covering the rest of the surface of the body. (K) *Macellomenia schanderi*. SEM of ventral surface of anterior end showing densely ciliated pedal pit and mouth. (L) Anterior region of *Spengelomenia bathybia* (highly stylized sagittal section drawing).

3 cm in length, and most live at considerable depths in the ocean. About 35 described species, in 8 genera (*Adenopilina*, *Laevipilina*, *Monoplacophorus*, *Neopilina*, *Rokopella*, *Veleropilina*, *Vema*, *Micropilina*).

CLASS POLYPLACOPHORA Chitons (Figures 13.1B and 13.4). Flattened, elongated molluscs with a broad ventral foot and 8 dorsal shell plates (composed of aragonite); mantle forms thick girdle that borders and may partly or entirely cover shell plates; epidermis of girdle usually with calcareous spines, scales, or bristles; mantle cavity encircles foot and bears from 6 to more than 80 pairs of bipectinate ctenidia; 1 pair of nephridia; head without eyes or tentacles; crystalline style, statocysts and osphradia absent; nervous system lacking discrete ganglia, except in buccal region; well-developed radula present. Shell canals (aesthetes) sometimes have eyes (which are image-forming in some species) (Figure 13.43C,D). Marine, intertidal to deep

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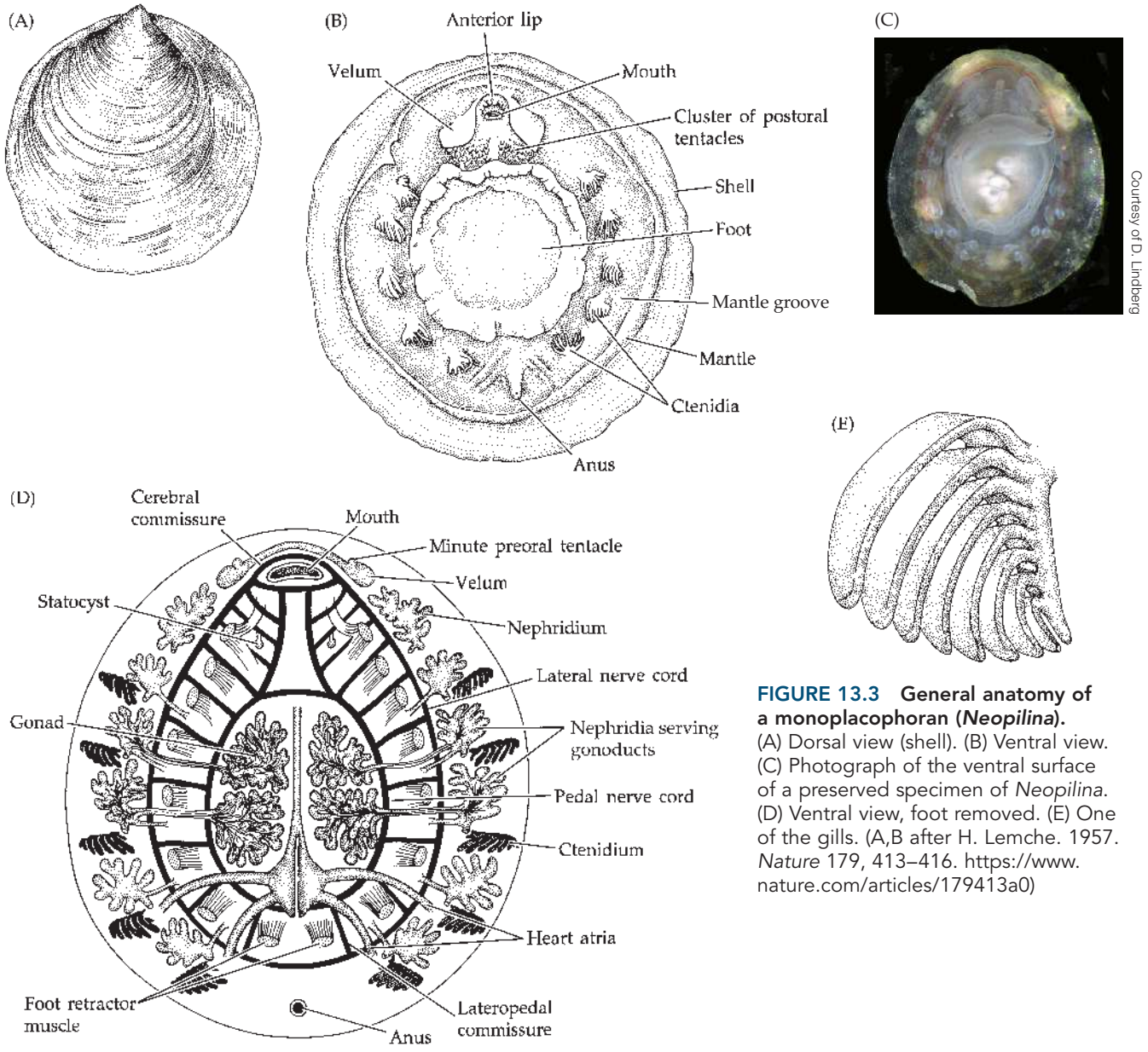


FIGURE 13.3 General anatomy of a monoplacophoran (*Neopilina*). (A) Dorsal view (shell). (B) Ventral view. (C) Photograph of the ventral surface of a preserved specimen of *Neopilina*. (D) Ventral view, foot removed. (E) One of the gills. (A,B after H. Lemche. 1957. *Nature* 179, 413–416. https://www.nature.com/articles/179413a0)

sea. Chitons are unique in their possession of 8 separate shell plates, called valves, and a thick marginal girdle; about 930 described species in one living order.[5]

SUBCLASS NEOLORICATA Shells with unique articulamentum layer, which forms insertion plates that interlock the valves.

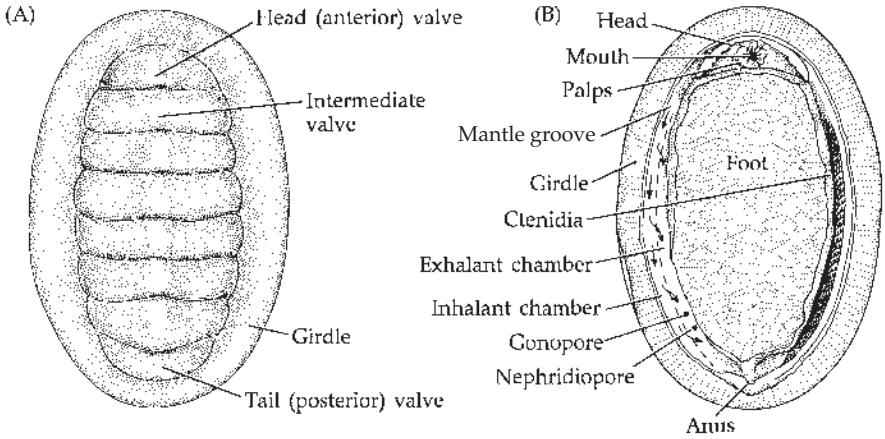
ORDER LEPIDOPLEURIDA Chitons with outer edge of shell plates lacking attachment teeth; girdle not extending over plates; ctenidia limited to a few posterior pairs; with smooth eggs. (e.g., *Choriplax*, *Lepidochiton*, *Lepidopleurus*, *Oldroydia*)

ORDER CALLOCHITONIDA Chitons with outer edges of shell plates with attachment teeth; girdle not extending over plates; ctenida lateral; with smooth eggs. (e.g., *Callochiton*)

ORDER CHITONIDA Outer edges of shell plates with attachment teeth; girdle not extending over plates, or extending partly or completely over plates; extension of the ctenidia variable; with elaborate egg hull. (e.g., *Acanthochitona*, *Callistochiton*, *Chaetopleura*, *Cryptochiton*, *Cryptoplax*, *Ischnochiton*, *Katharina*, *Lepidozona*, *Mopalia*, *Nuttallina*, *Placiphorella*, *Schizoplax*, *Tonicella*)

[5]Uncommon, aberrant individuals have been found with only 7 valves.

FIGURE 13.4 Generalized anatomy of chitons (Polyplacophora). (A,B) A typical chiton (dorsal and ventral views). (C) The Pacific lined chiton, *Tonicella lineata*. (D) Dorsal view of a chiton, shell plates (valves) removed. (E) Dorsal view of a chiton, dorsal musculature removed to reveal internal organs. (F) Dorsal view of a chiton, showing extensive nephridia. (G) The arrangement of internal organs in a chiton (lateral view).



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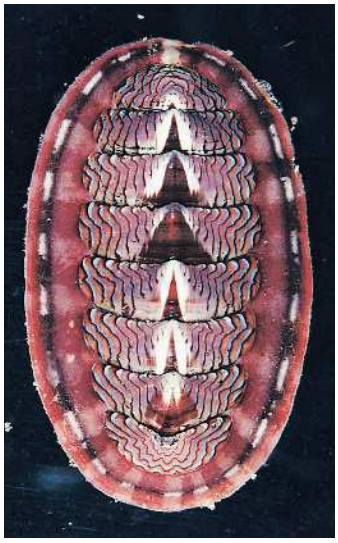

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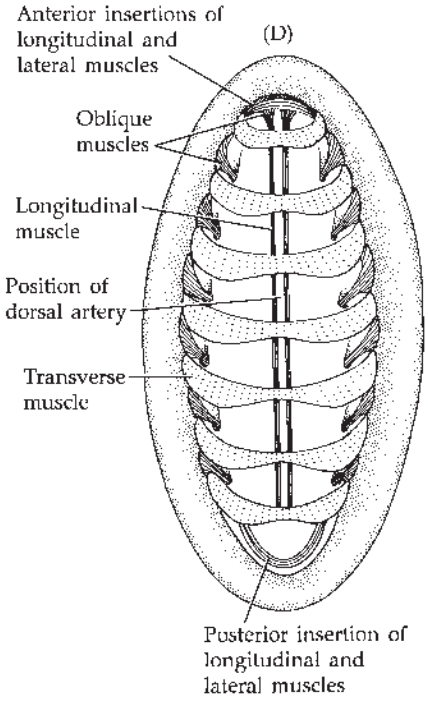

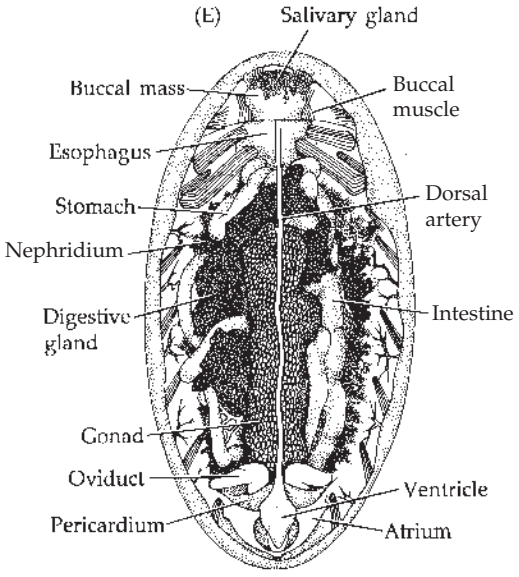

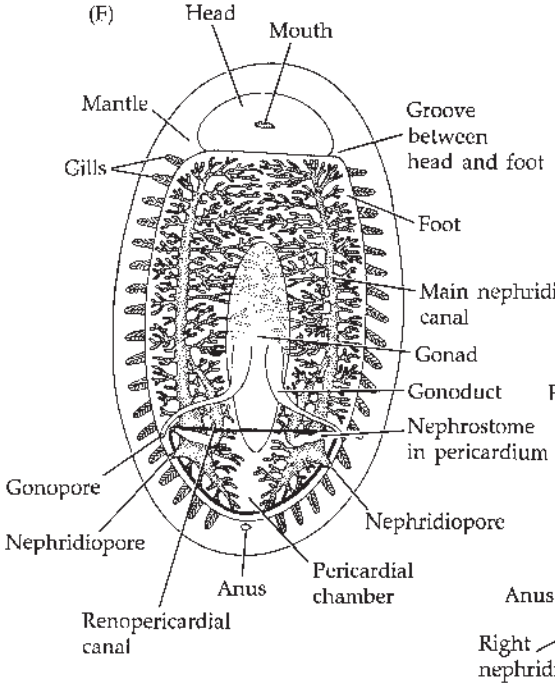

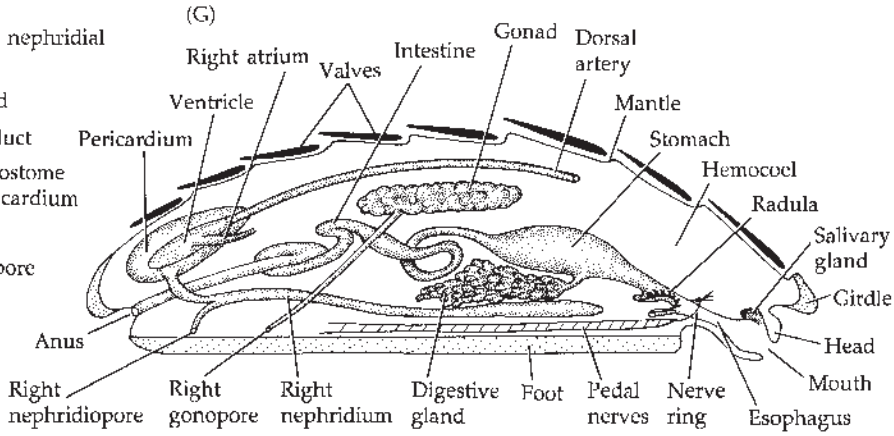

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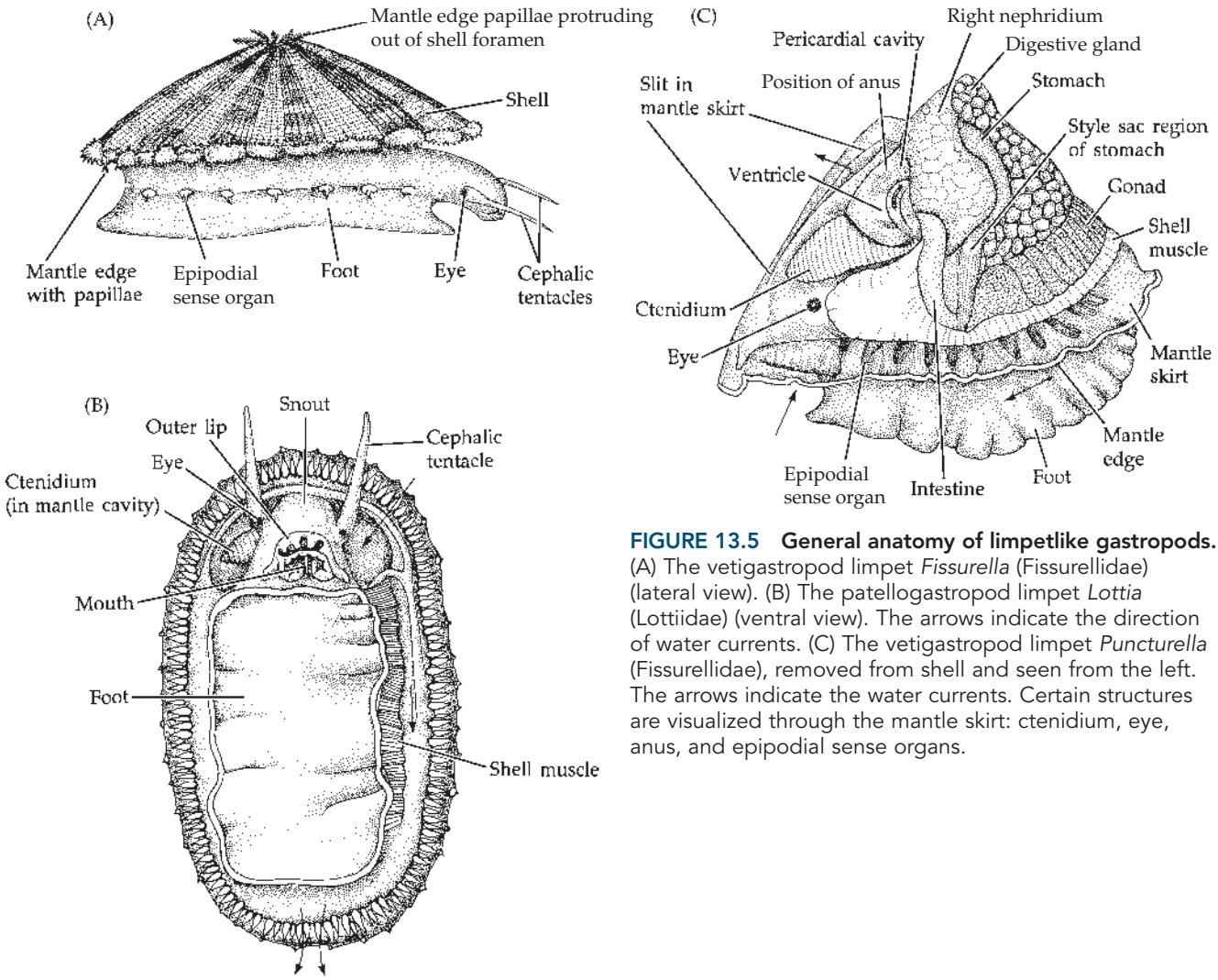

FIGURE 13.5 General anatomy of limpetlike gastropods. (A) The vetigastropod limpet *Fissurella* (Fissurellidae) (lateral view). (B) The patellogastropod limpet *Lottia* (Lottiidae) (ventral view). The arrows indicate the direction of water currents. (C) The vetigastropod limpet *Puncturella* (Fissurellidae), removed from shell and seen from the left. The arrows indicate the water currents. Certain structures are visualized through the mantle skirt: ctenidium, eye, anus, and epipodial sense organs.

CLASS GASTROPODA Snails, slugs and limpets (Figures 13.1D–G, 13.5, 13.6, and 13.7). Asymmetrical molluscs with single, usually spirally coiled shell into which body can be withdrawn; shell lost or reduced in many groups; during development, visceral mass and mantle rotate 90°–180° on foot (a process known as torsion), so mantle cavity lies anteriorly or on right side (rather than posteriorly as in other molluscs), and gut and nervous system are twisted; some taxa have partly or totally reversed the rotation (detorsion); with muscular creeping foot (modified in swimming and burrowing taxa); foot with operculum in larva and often in adult; head with eyes (often reduced or lost), and 1–2 pairs of tentacles, and a snout; most with radula and some with crystalline style, the latter being absent in most primitive and in many advanced groups; 1–2 nephridia; mantle (= pallium) usually forms anterior cavity housing ctenidia, osphradia, and hypobranchial glands; ctenidia sometimes lost and replaced with secondary gas exchange structures.

Gastropods comprise an estimated 32,000 described living species of marine, terrestrial, and freshwater snails and slugs. The class was traditionally divided into three groups treated as subclasses: prosobranchs (largely shelled marine snails), opisthobranchs (marine slugs), and pulmonates (terrestrial snails and slugs). However, recent anatomical and molecular studies have shown that classification to be incorrect.

SUBCLASS EOGASTROPODA Shell with foliated structure, lacking nacre; protoconch tubular; if limpet morphology, anterior dilation is exhibited. Foot lacks propodium; pedal muscle fibers not crossing. Radula docoglossate and stereoglossate, teeth with basal plates; jaw single, dorsal; odontophore with dorsolateral cartilages; style sac very long, intestine long, coiled. Hypobranchial glands absent. Blood lacks hemocyanin; ventricle attached to pericardium. Statocysts lateral to pedal ganglia; separate labial ganglia present; subradular organ well developed; osphradium with simple nerve endings; eyes lack lens. This grouping consists of mostly extinct Paleozoic taxa, with patellogastropods the only living clade.

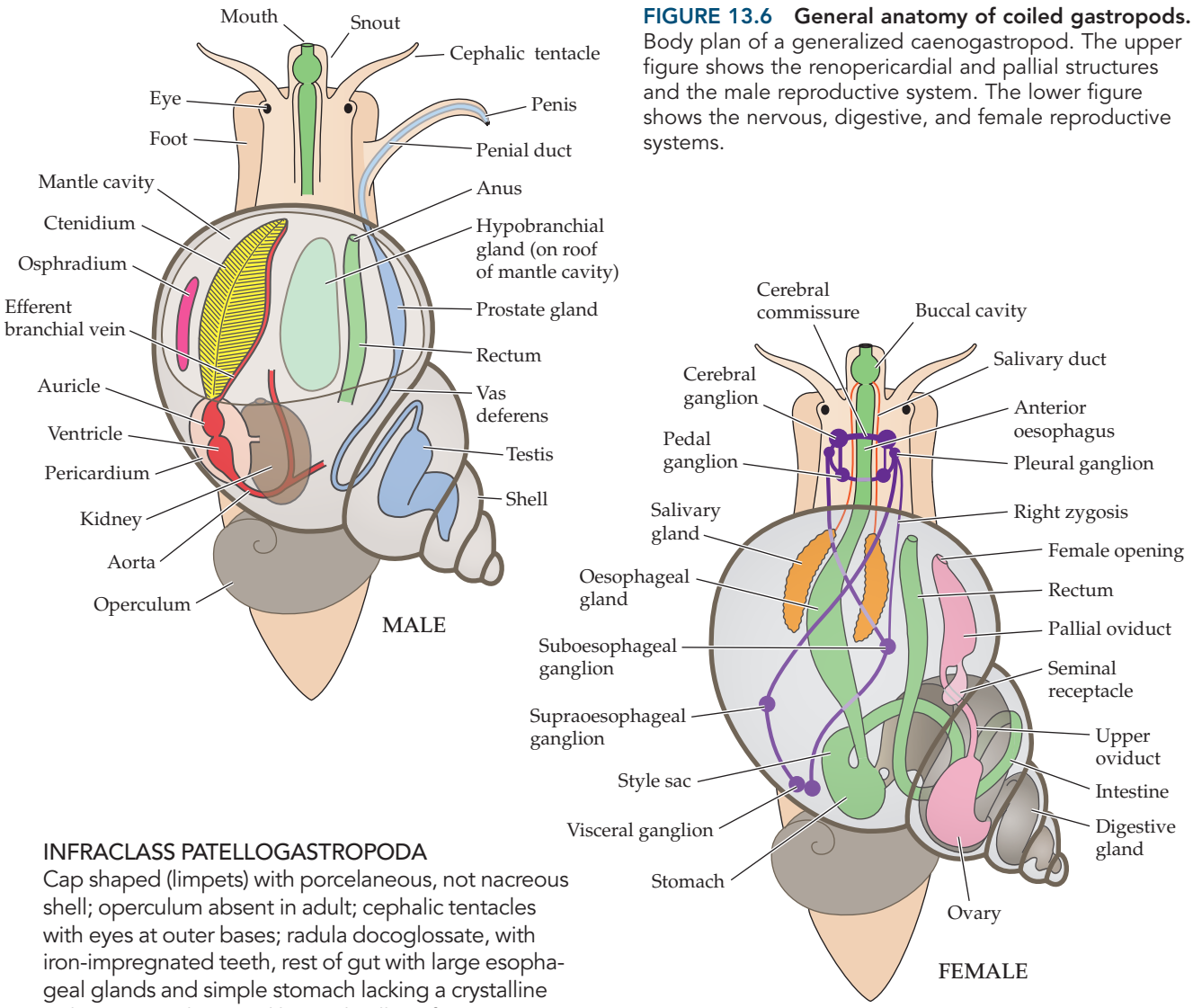

FIGURE 13.6 General anatomy of coiled gastropods. Body plan of a generalized caenogastropod. The upper figure shows the renopericardial and pallial structures and the male reproductive system. The lower figure shows the nervous, digestive, and female reproductive systems.

INFRACLASS PATELLOGASTROPODA
Cap shaped (limpets) with porcelaneous, not nacreous shell; operculum absent in adult; cephalic tentacles with eyes at outer bases; radula docoglossate, with iron-impregnated teeth, rest of gut with large esophageal glands and simple stomach lacking a crystalline style; intestine long and looped; gill configuration variable, single bipectinate ctenidium sometimes present (Figure 13.5B), and/or with mantle groove secondary gills, or gills lacking; shell muscle divided into discrete bundles; mantle cavity without siphon or hypobranchial glands; 2 rudimentary osphradia; single atria; 2 nephridia; usually gonochoristic; nervous system weakly concentrated, pleural ganglia near pedal ganglia, pedal and lateral cords present. Primarily marine with a few estuarine species; herbivorous. The patellogastropods include 6 families: Patellidae (e.g., *Patella*, *Scutellastra*), Nacellidae (e.g., *Cellana*), Lottiidae (e.g., *Lottia*), Acmaeidae (e.g., *Acmaea*), Lepetidae (e.g., *Lepeta*), and Neolepetopsidae (e.g., *Neolepetopsis*). These are often regarded as the "true" limpets.

SUBCLASS ORTHOGASTROPODA Shell without foliated structure, nacre present in some vetigastropods; protoconch coiled; if limpet morphology, posterior dilation exhibited; foot with propodium; pedal muscle fibers crossing. Radula flexoglossate, teeth lacking basal plates; odontophore lacking dorsolateral cartilages; jaw paired, lateral; style sac short to absent; intestine short with few coils or none. Hypobranchial glands present. Blood has hemocyanin; ventricle free from pericardium. Statocysts dorsal to pedal ganglia; labial ganglia fused with cerebral ganglia; subradular organ reduced or absent; osphradium with sensory cells; eyes with lens.

FIGURE 13.7 More gastropod anatomy: some caenogastropods and heterobranchs. (A–C) Caenogastropods. (A) The pelagic shelled heteropod *Carinaria* (Caenogastropoda). (B) Anatomy of *Carinaria*. (C) The shell-less heteropod *Pterotrachea* (Caenogastropoda). (D–J) Heterobranchs. (D) The pelagic shelled pteropod *Clio* (Heterobranchia, Euopisthobranchia). The arrows indicate the direction of water flow; water enters all around the narrow neck and is forcibly expelled by contraction of the sheath together with fecal, urinary, and genital products. (E) A swimming pteropod, *Corolla* (Heterobranchia, Euopisthobranchia). (F–I) Various nudibranchs (Heterobranchia, Nudipleura). (F) A doridid nudibranch, *Diaulula*. (G) An aeolid nudibranch, *Phidiana*.

(*Continued*)

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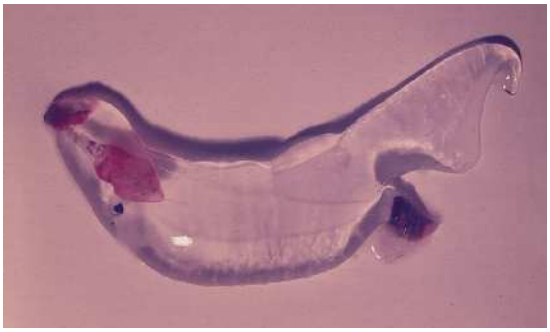

Courtesy of R. Brusca

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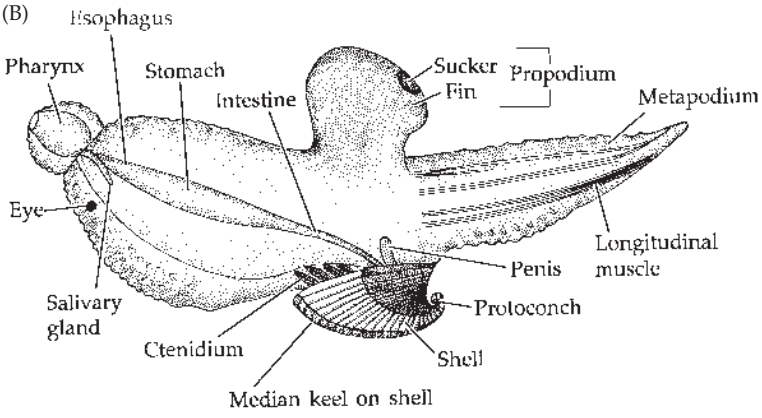

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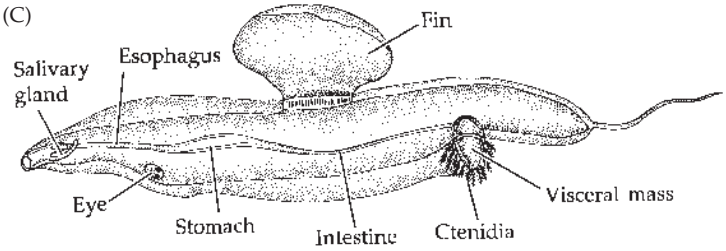

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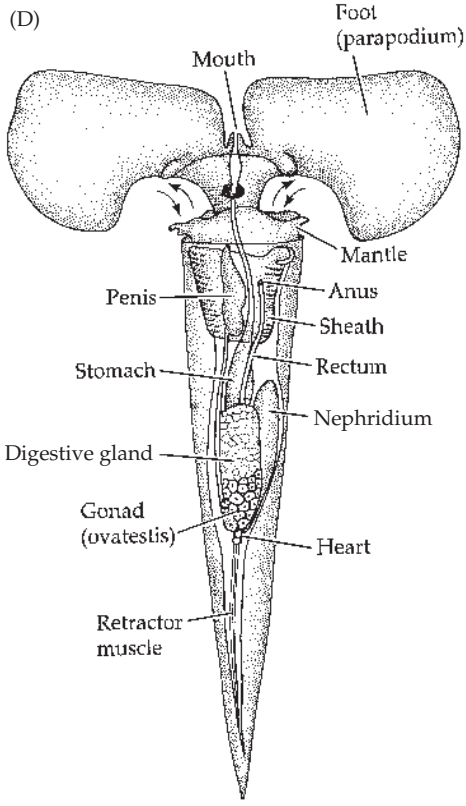

(E)

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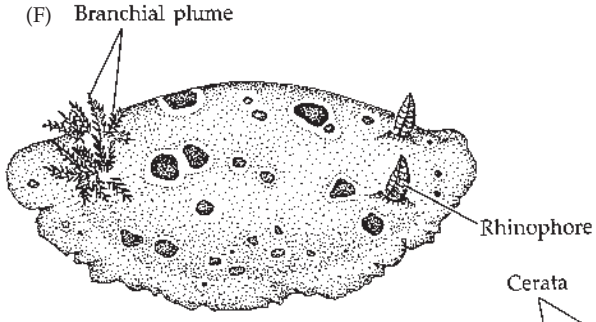

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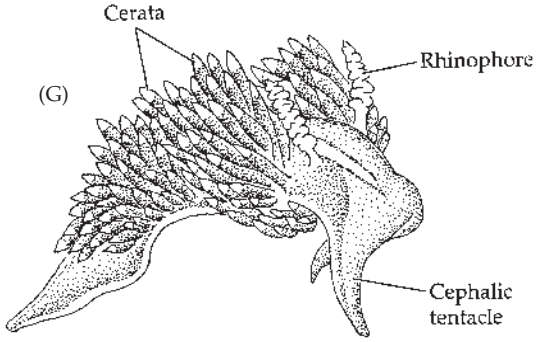

(H)

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(I)

Courtesy of R. Brusca

(J)

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FIGURE 13.7 (*continued*) More gastropod anatomy: some caenogastropods and heterobranchs. (H) A doridid nudibranch, *Goniobranchus geminus* (from the Red Sea). (I) The eastern Pacific "Spanish shawl" aeolid nudibranch, *Flabellina*. (J) The lettuce sea slug, *Elysia crispata* (Heterobranchia, Panpulmonata), from the Caribbean.

This group contains all the living gastropods except the patellogastropods.

INFRACLASS VETIGASTROPODA Shells both porcelaneous and nacreous; cephalic tentacles usually with eyes on short processes on outer bases; operculum usually circular, with a central nucleus and often many spirals, horny or calcareous; radula usually rhipidoglossate (with numerous transverse rows of teeth), rest of gut with esophagus having large glands, complex stomach with style sac but no crystalline style, looped intestine; 1–2 bipectinate ctenidia; shell muscles paired or single; mantle cavity with 1–2 hypobranchial glands, 1–2 atria, and 1–2 nephridia; usually gonochoristic; male generally without penis; nervous system weakly concentrated, ganglia poorly formed, pedal cords present; 1–2 osphradia, small, inconspicuous. All marine and benthic. Many species are microdetritivores or feed on films of bacteria or other organisms, or are microherbivores; some are macroherbivores, some grazing carnivores, and a few suspension feeders. Most gastropods found at hydrothermal vents, at cold seeps, and on deep-sea hard substrates are vetigastropods. Vetigastropods comprise about 42 living families, and their internal classification remains unsettled.

Vetigastropods include the slit-shelled snails Pleurotomariidae (e.g., *Entemnotrochus*, *Perotrochus*), Scissurellidae (e.g., *Scissurella*), and Anatomidae (e.g., *Anatoma*); the abalones Haliotidae (e.g., *Haliotis*); the keyhole and slit limpets Fissurellidae (e.g., *Diodora*, *Fissurella*, *Lucapinella*, *Puncturella*); deep-sea limpets comprising the Lepetellidae and related families (e.g., *Lepetella*, *Pseudococculina*); trochids Trochidae (e.g., *Trochus, Monodonta*); and related families such as Calliostomatidae (e.g., *Calliostoma*), Margaritidae (e.g., *Margarites*), Tegulidae (e.g., *Tegula*), and turbans Turbinidae (e.g., *Astraea*, *Turbo*); many of the hot-vent snails and limpets Neomphalidae (e.g., *Neomphalus*), Peltospiridae (e.g., *Hirtopelta*, *Peltaspira*), and Lepetodrilidae (e.g., *Lepetodrilus*); and the small, deep-sea wood and bone limpets Cocculinidae and Bathysciadiidae (e.g., *Cocculina*).

INFRACLASS NERITIMORPHA Shell coiled, limpet-like, or lost (Titiscaniidae). Shell porcelaneous, with interior whorls reabsorbed in many coiled groups; operculum typically present, of few spirals and with noncentral nucleus, horny or calcified, usually with internal peg; shell muscle divided into discrete bundles; only left ctenidium present; hypobranchial glands often lost on left side; stomach highly modified; right nephridium incorporated into complex reproductive system with multiple openings into mantle cavity; radula rhipidoglossate; most species gonochoristic, with copulatory structures; nervous system with ganglia concentrated, pleural ganglia near pedal ganglia, pedal cords present. Globally distributed in marine, estuarine, freshwater, and terrestrial habitats. There are 9 families of neritimorphans, of which Helicinidae (e.g., *Alcadia, Helicina*), Hydrocenidae (*Georissa*, *Hydrocena*), Proserpinellidae (e.g., *Proserpinella*), and Proserpinidae (*Proserpina*) are exclusively terrestrial. The five other families are Neritopsidae (*Neritopsis*), Titiscaniidae (*Titiscania*), Neritidae (e.g., *Nerita*, *Theodoxus*), Neritiliidae (cave nerites, e.g., *Neritilia, Pisulina*), and Phenacolepadidae (*Phenacolepas*).

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INFRACLASS CAENOGASTROPODA Shell mainly porcelaneous; operculum usually present and corneous, rarely calcified, with few spirals and usually with a noncentral nucleus, mostly not nacreous, rarely with internal peg(s); head with pair of cephalic tentacles, with eyes at outer bases; mantle cavity asymmetrical, with incurrent opening on anterior left, sometimes elaborated into an inhalant siphon; right ctenidium lost; left ctenidium monopectinate; right hypobranchial gland lost; right nephridium lost except for remnant incorporated into reproductive system; heart with only left atrium. Radula taenioglossate (7 rows of teeth), ptenoglossate (many rows of similar teeth), rachiglossate (1–3 rows of teeth), or toxoglossate (teeth modified as harpoons) or occasionally lost. Higher forms with concentrated ganglia, pleural ganglia usually near cerebral ganglia, pedal cords usually absent; osphradium conspicuous, often large, sometimes surface subdivided into lamellae. Most caenogastropods are gonochoristic and marine, but there are several freshwater groups and a few are terrestrial. The caenogastropods comprise the former "mesogastropods" and neogastropods, and they are often divided into two groups, as follows:

"ARCHITAENIOGLOSSA" Although this is not a monophyletic group, we retain it informally. Architaenioglossans differ from other caenogastropods in details of their nervous system and in the ultrastructure of their sperm and osphradia. They are divided among 13 extant families, including the freshwater Ampullariidae (apple snails, e.g., *Ampullaria, Pila*, *Pomacea*) and Viviparidae (river snails, e.g., *Viviparus*) and the terrestrial Cyclophoridae (e.g., *Cyclophorus*) and several related families such as Diplommatinidae (e.g., *Diplommatina*, *Opisthostoma*). Also included here are the marine families Campanilidae, Plesiotrochidae, and Ampullinidae.

COHORT SORBEOCONCHA This grouping contains the rest of the caenogastropods. These are divided into two main groups, Cerithiimorpha and Hypsogastropoda.

MEGAORDER CERITHIIMORPHA Usually without a penis; eggs usually laid in jelly, often in strings, or are brooded. The anterior aperture may or may not have a notch, housing a short siphon. Marine, brackish, and freshwater species are included. About 20 extant families are recognized, including the marine Cerithiidae (horn shells, e.g., *Cerithidea, Cerithium*, *Liocerithium*), Siliquariidae (slit worm shells, e.g., *Siliquaria*), and Turritellidae (tower or turret shells, e.g., *Turritella*) and the freshwater Melanopsidae (e.g., *Melanopsis*), Thiaridae (e.g., *Thiara*), and Pleuroceridae (e.g., *Pleurocera*).

MEGAORDER HYPSOGASTROPODA Comprises the remaining caenogastropods. The anterior mantle may be simple or can be enrolled, forming an anterior siphon that emerges from an anterior notch in the aperture or, in some, is contained within an extension of the shell, the siphonal canal. Male with cephalic penis; eggs usually laid in capsules or sometimes brooded. Nervous system concentrated; operculum, if present, chitinous, rarely calcareous. The classification of this group is unsettled. It includes the marine grazing snails Littorinidae (periwinkles, e.g., *Littorina*); several marine and freshwater families of small-sized taxa, including the Rissoidae (e.g., *Rissoa*, *Alvania*); and larger marine snails such as the Strombidae (conchs or strombids, e.g., *Aliger*, *Lambis, Strombus*) and the carrier shells, Xenophoridae (e.g., *Xenophora*). Also includes the uncoiled suspension-feeding worm snails (Vermetidae, e.g., *Dendropoma*, *Serpulorbis*) and the limpetlike Hipponicidae (e.g., *Hipponix*) which are deposit feeders, while Capulidae (e.g., *Capulus*) attach to other molluscs and mostly feed on their feces. The slipper shells Calyptraeidae (e.g., *Calyptraea*, *Crepidula*, *Crucibulum*) are suspension feeders. The Carinariidae (one of several families of pelagic molluscs collectively called heteropods, e.g., *Carinaria*) also have a cap-shaped shell.[6] Cypraeidae (cowries, e.g., *Cypraea*) are herbivores or grazing carnivores, while several other snail-like families are strictly carnivorous, including Naticidae (moon snails, e.g., *Natica*, *Polinices*) that feed mostly on bivalves, the ascidian-feeding Eratoidae (coffee bean shells, e.g., *Erato*, *Trivia*), and the soft-coral-feeding Ovulidae (egg shells, e.g., *Jenneria*, *Ovula*, *Simnia*). Tonnidae (tun shells, e.g., *Malea*) and related families such as Cassididae (helmet shells, e.g., *Cassis*) mainly feed on echinoderms, whereas Ficidae (fig shells, e.g., *Ficus*) are primarily polychaete feeders. Epitoniidae (wentletraps, e.g., *Epitonium*) feed on cnidarians and include the floating violet snails (e.g., *Janthina,* formerly in the family Janthinidae), which feed on siphonophores that drift on the surface of the ocean. Eulimidae are ectoparasites on echinoderms, and the sponge-feeding Triphoridae (e.g., *Triphora*) and Cerithiopsidae (e.g., *Cerithiopsis*) are highly diverse. There are some speciose families of small-sized freshwater snails such as the Hydrobiidae (e.g., *Hydrobia*) and several related families including the Pomatiopsidae (e.g., *Pomatiopsis*, *Tricula*), and there are also a few terrestrial taxa in families such as Pomatiasidae (e.g., *Pomatias*) and the otherwise mainly supralittoral Assimineidae and Truncatellidae.

[6]The term "heteropod" is an old taxonomic name now used informally for a group of planktonic, predatory caenogastropods that have a reduced shell or no shell at all.

The most derived hypsogastropod clade is the Neogastropoda. Its members have a rachiglossate or toxoglossate radula, with 1–5 teeth in each row; an anterior siphon is present; and the operculum, if present, is chitinous; the osphradium is large and pectinate and lies near the base of the anterior siphon. This highly diverse group comprises mostly carnivorous taxa. The neogastropods comprise about 45 living families of almost entirely marine snails, including whelks such as Buccinidae (e.g., *Buccinum*, *Cantharus*, *Macron*, *Neptunea*); Fasciolariidae (tulip shells and spindle shells, e.g., *Fasciolaria*, *Fusinus*, *Leucozonia*, *Troschelia*); Melongenidae (e.g., *Melongena*); Nassariidae (dog whelks and basket shells, e.g., *Nassarius* and the Asian freshwater genus *Clea*); dove shells, Columbellidae (e.g., *Anachis*, *Columbella*, *Mitrella*, *Pyrene*, *Strombina*); harp shells, Harpidae (e.g., *Harpa*); margin shells, Marginellidae (e.g., *Granula*, *Marginella*); miter shells, Mitridae (e.g., *Mitra*, *Subcancilla*) and Costellariidae (e.g., *Pusia*, *Vexillum*); rock shells and thaids, Muricidae (e.g., *Acanthina*, *Hexaplex*, *Morula*, *Murex*, *Neorapana*, *Nucella*, *Phyllonotus*, *Pterynotus*, *Purpura*, *Thais, Urosalpinx*), including the coral-associated subfamily Coralliophilinae (e.g., *Coralliophila*, *Latiaxis*); Olividae (olive shells, e.g., *Agaronia*, *Oliva*); Olivellidae (e.g., *Olivella*); the volutes, Volutidae (e.g., *Cymbium*, *Lyria*, *Voluta*) and nutmeg shells, Cancellariidae (e.g., *Admete*, *Cancellaria*); cone shells, Conidae (e.g., *Conus*) and the related Turridae (e.g., *Turris*); and several other allied families, including the auger shells, Terebridae (e.g., *Terebra*).

INFRACLASS HETEROBRANCHIA The heterobranchs were previously organized as two subclasses—Opisthobranchia (sea slugs and their kin) and Pulmonata (air-breathing snails). Although this division was long accepted, recent morphological and molecular studies now divide the heterobranchs into two main groups—an informal paraphyletic group often referred to as the "Lower Heterobranchia" (= Allogastropoda, Heterostropha) and the Euthyneura, which includes both pulmonates and the opisthobranchs.

The heterobranchs are characterized by lacking a true ctenidium and, usually, by a small to absent osphradium, a simple gut with the esophagus lacking glands, the stomach lacking a crystalline style in all but one group, and the intestine usually being short. The radula is highly variable, ranging from rhipidoglossate to consisting of a single row of teeth or being lost altogether. The shell may be well developed, reduced, or absent; the operculum, if present, is horny; the larval shell is heterostrophic (i.e., coils in a different plane than the adult shell). The head bears one or two pairs of tentacles, with the eyes variously placed; all are hermaphroditic. The nervous system is streptoneurous or euthyneurous with various degrees of concentration of the ganglia; pleural ganglia near pedal or cerebral ganglia, pedal cords absent. Mostly benthic; with marine, freshwater, and terrestrial species.

"LOWER HETEROBRANCHS" This informal group includes some snails long thought to be "Mesogastropoda," such as staircase or sundial shells Architectonicidae (e.g., *Architectonica, Philippia*) and some groups of small-sized marine snails, including Rissoellidae (e.g., *Rissoella*), Omalogyridae (e.g., *Omalogyra*), and the freshwater Valvatidae (e.g., *Valvata*). There are also several marine families such as Cornirostridae, Hyalogyrinidae, and Orbitestellidae. These snails are superficially similar to caenogastropods but often possess secondary gills and long cephalic tentacles with cephalic eyes set in the middle of their bases or on their inner sides. Another group included here are tiny interstitial slugs of the family Rhodopidae.

COHORT EUTHYNEURA Include most of the former opisthobranchs and pulmonates. The euthyneuran body has the shell either external or internal, or lost altogether; a heterostrophic larval shell; and a horny operculum, often absent in adult. Body variously detorted; head usually with one or two pairs of tentacles, eyes on inner sides or on separate stalks; ctenidia and mantle cavity usually reduced or lost; hermaphroditic; euthyneurous with various degrees of nervous system concentration. Mostly benthic; with marine, freshwater, and terrestrial species. Among other things, marine slugs are notable for their use of chemical defense; in most cases the compounds have dietary origin, and several lineages have the ability to biosynthesize metabolites de novo. The Euthyneura is divided into three major groups, which we treat here as superorders.

SUPERORDER NUDIPLEURA Includes both the internal-shelled Pleurobranchidae (e.g., *Berthella*, *Pleurobranchus*) and the Nudibranchia (shell-less or "true" nudibranchs), which includes many families. The doridoid nudibranchs include the Onchidoridiidae (e.g., *Acanthodoris, Corambe*), Polyceridae (e.g., *Gymnodoris, Polycera, Tambja*), Aegiretidae (e.g., *Aegires*), Chromodorididae (e.g., *Chromodoris*), Phyllidiidae (e.g., *Phyllidia*), Dendrodorididae (e.g., *Dendrodoris*), Discodorididae (e.g., *Discodoris*, *Diaulula, Rostanga*), Doridiidae (e.g., *Doris*), Platydoridiidae (e.g., *Platydoris*), Hexibranchidae (e.g., *Hexabranchus*), and Goniodorididae (e.g., *Okenia*). The cladobranch nudibranchs include the Arminidae (*Armina*), Proctonotidae (e.g.,

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Janolus), Embletoniidae (e.g., *Embletonia*), Scyllaeidae (e.g., *Scyllaea*), Tritoniidae (e.g., *Tritonia*), and Dendronotidae (e.g., *Dendronotus*). Also included are the cladobranch group collectively known as aeolididoids—including the Aeolidiidae (e.g., *Aeolidia*), Flabellinidae (e.g., *Coryphella*), Fionidae (e.g., *Fiona*), Facelinidae (e.g., *Hermissenda, Phidiana*), Tergipedidae (e.g., *Trinchesia*), Tethydidae (e.g., *Melibe*), and Glaucidae (e.g., *Glaucus*).

SUPERORDER EUOPISTHOBRANCHIA
Includes six main groups: (1) the basal acteonoideans, including Acteonidae (barrel or bubble snails, e.g., *Acteon, Pupa, Rictaxis*); (2) several families grouped as Cephalaspidea, for example, the slugs Aglajidae (e.g., *Aglaja, Chelidonura, Navanax*), Bullidae (bubble shells, e.g., *Bulla*), Haminoeidae (e.g., *Haminoea*), Retusidae (e.g., *Retusa*), and Scaphandridae (e.g., *Scaphander*); (3) the Runcinoidea, containing two families of tiny slugs, Ilbiidae (e.g., *Ilbia*) and Runcinidae (e.g., *Runcina*); (4) the Aplysiida or sea hares, including Aplysiidae (e.g., *Aplysia*, *Dolabella*, *Stylocheilus*); (5) the pelagic pteropods, comprising (a) the Thecosomata or shelled pteropods, which include the families Cavoliniidae (e.g., *Clio*, *Cavolinia*) and Limacinidae (e.g., *Limacina*), and (b) the distant group Gymnosomata or naked pteropods, which include Clionidae (e.g., *Clione*); and (6) the Umbraculida, composed of the umbrella slugs, Umbraculidae (e.g., *Umbraculum*) and Tylodinidae (e.g., *Tylodina*).

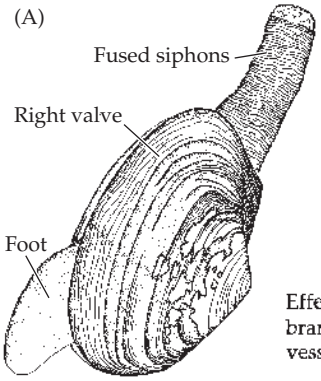
SUPERORDER PANPULMONATA This highly diverse group is characterized by reduction or loss of shell or variable shell shape of minute or moderate size; generally spirally coiled, planispiral, or limpet shaped; usually without an operculum as adults; eyes at bases of sensory stalks; secondary gills present in some members (e.g., *Pyramidella, Siphonaria*); body detorted; nervous system highly concentrated (euthyneurous); mantle-cavity-derived lung in the derived groups, with a contractile aperture in the Eupulmonata; marine (intertidal), brackish, freshwater, and amphibious.

Other panpulmonate groups include the sap-sucking sea slugs Sacoglossa (e.g., *Berthelinia*, *Elysia*, *Oxynoe*, *Tridachia,* and the "bivalved gastropods" Juliidae), which are shelled or shell-less; the small shell-less and sometimes spiculate acochlidian slugs that are often interstitial and usually marine (although there are some freshwater species); and the ectoparasitic Pyramidelloidea (e.g., *Odostomia, Pyramidella*, *Turbonilla*, *Amathina*), all of which were previously included in the Opisthobranchia. The remaining panpulmonates include all the members of the group previously known as Pulmonata, namely the mainly intertidal Siphonariidae (false limpets, e.g., *Siphonaria*, *Williamia*); two operculate families, the freshwater Glacidorbidae (e.g., *Glacidorbis*) and the estuarine Amphibolidae (*Amphibola, Salinator*); and the Hygrophila, including the mainly freshwater South American Chilinidae (e.g., *Chilina*) and freshwater Physidae (e.g., *Physa*), Planorbidae (e.g., *Ancylus*, *Bulinus*, *Planorbis*), and Lymnaeidae (e.g., *Lanx*, *Lymnaea*). These latter families are mostly snails, but some, such as *Lanx* and *Ancylus*, are limpets. The remaining "pulmonates" are contained within Eupulmonata. The best-known and largest group of eupulmonates is the Stylommatophora, comprising the land snails and slugs. In some of the shelled forms, the shell is partly or completely enveloped by the dorsal mantle. Their eyes are on the tips of long sensory stalks, and there is an anterior pair of tentacles. Eupulmonates are all terrestrial and are an enormous group with over 26,000 described species in 104 families. Some of those included are the land snail families Helicidae (e.g., *Cornu* [= *Helix*], *Cepaea*), Achatinidae (e.g., *Achatina*), Bulimulidae (e.g., *Bulimulus*), Haplotrematidae (e.g., *Haplotrema*), Orthalicidae (e.g., *Liguus*), Cerionidae (e.g., *Cerion*), Oreohelicidae (e.g., *Oreohelix*), Pupillidae (e.g., *Pupilla*), Testacellidae (*Testacella*), Cerastidae (e.g., *Rhachis*), Succineidae (e.g., *Succinea*), and Vertiginidae (e.g., *Vertigo*), as well as terrestrial slug families such as Arionidae (e.g., *Arion*) and Limacidae (e.g., *Limax*).

The remaining Eupulmonata include the orders Systellommatophora and Ellobiida. The former are sluglike, without internal or external shell; dorsal mantle integument forms a keeled or rounded notum; head usually with 2 pairs of tentacles, upper ones forming contractile stalks bearing eyes. Included are the mainly marine family Onchidiidae (e.g., *Onchidella*, *Onchidium*) and the terrestrial Veronicellidae (e.g., *Veronicella*). The Ellobiida include two superfamilies: the mainly supralittoral hollow-shelled ear snails, Ellobioidea (e.g., *Carychium, Ellobium, Melampus, Ovatella*), and the limpets and small intertidal snails or slugs of the Trimusculoidea (e.g., *Otina*, *Trimusculus*).

CLASS BIVALVIA (= PELECYPODA, LAMELLIBRANCHIATA)
Clams, oysters, mussels, scallops, etc. (Figures 13.1M–Q and 13.8). Laterally compressed; shell typically of two valves hinged together dorsally by elastic ligament and usually by a toothed hinge; shells closed by adductor muscles derived from mantle muscles; head rudimentary, without eyes, tentacles, or radula, but eyes may occur elsewhere on body, and tentacles may arise from the mantle edges; pair of large labial palps present

FIGURE 13.8 General anatomy of bivalves. (A) *Tresus*, a deep-burrowing eulamellibranch (Mactridae), with a digging foot and long, fused siphons. (B) A typical eulamellibranch (cross section). (C) The eulamellibranch *Mercenaria* (Veneridae), with the left shell valve and mantle removed. (D) Internal anatomy of *Mercenaria*. The visceral mass is opened up, the foot is dissected, and most of the gills are cut away. (E) The common mussel, *Mytilus* (Mytilidae), seen from the right side after removal of the right shell valve and mantle. (F) *Mytilus*, with the visceral mass opened up, the foot dissected, and most of the gills cut away.



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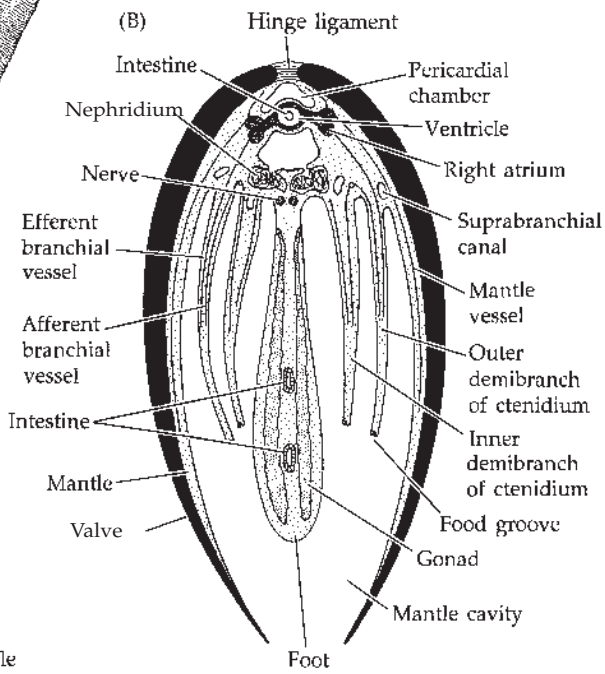

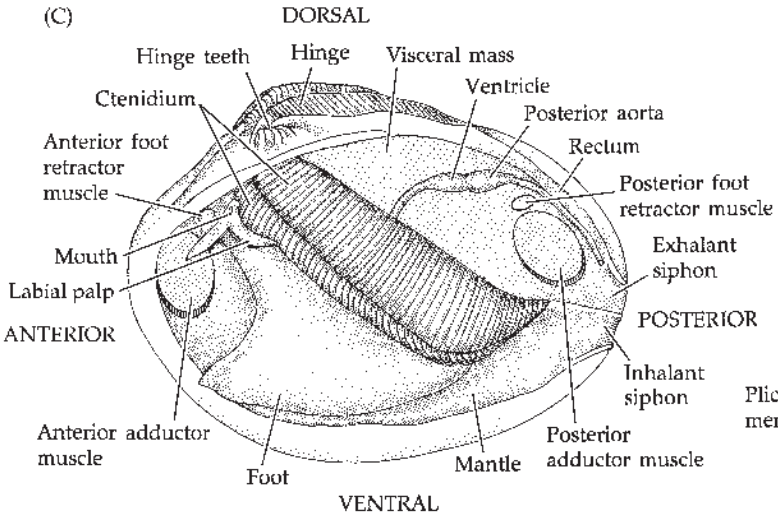

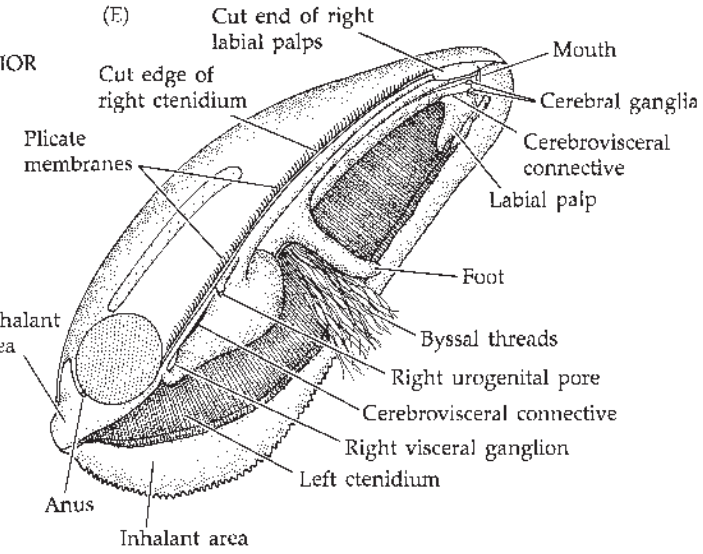

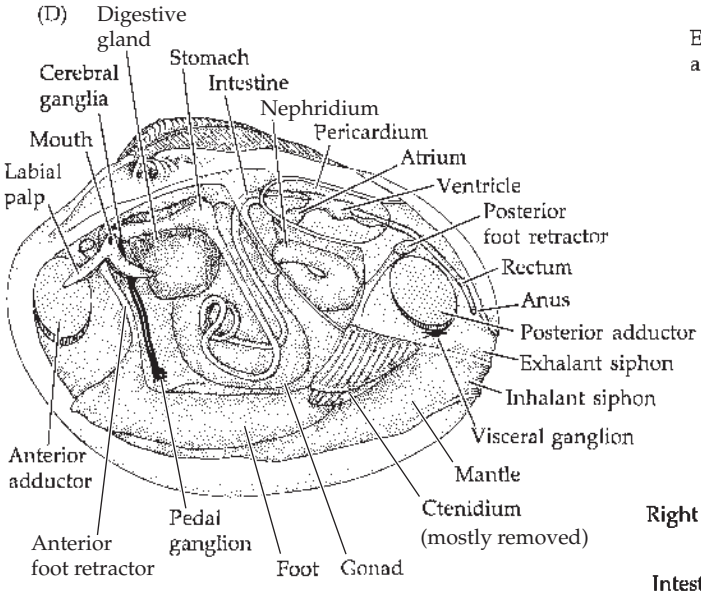

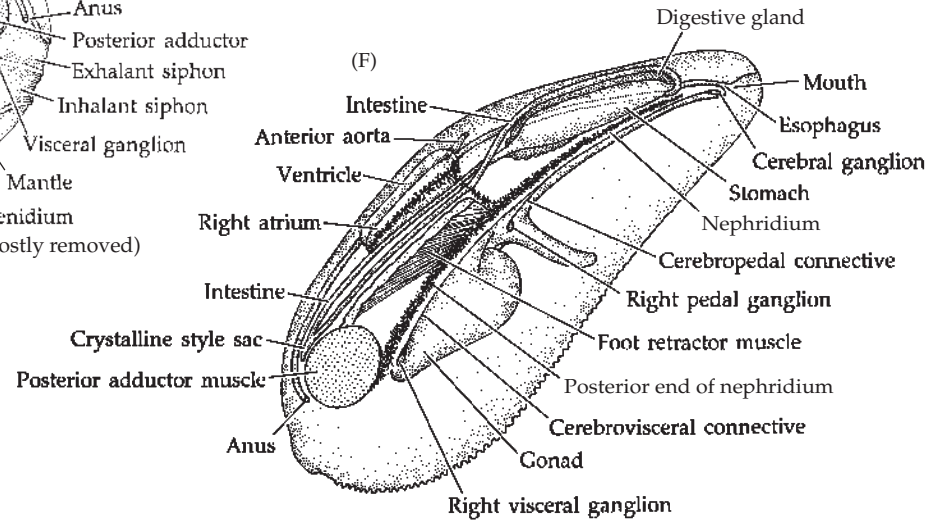

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composed of inner and outer parts that lie against one another; pair of statocysts present, associated with pedal ganglia, foot typically laterally compressed, often without a sole; 1 pair of large bipectinate ctenidia; large mantle cavity surrounds animal; mantle may be variously fused, sometimes forming extensions (siphons); 1 pair of nephridia; nervous system simple, typically composed of cerebropleural, pedal, and visceral ganglia.

Bivalves are marine or freshwater molluscs, primarily microphagous or suspension feeders. The class includes nearly 10,000 living species represented at all depths and in all marine environments. Bivalve classification had been unsettled until quite recently. Higher taxa have been delimited on the basis of shell characters (e.g., hinge anatomy, position of muscle scars), or, in other classifications, internal organ anatomy (e.g., ctenidia, stomach) has been used. However, beginning with the work of Giribet and Wheeler (2002), bivalve taxonomy has become more stable as both molecules and morphology have been combined with the fossil record to understand the relationships of the class.

SUBCLASS PROTOBRANCHIA Includes the former Palaeotaxodonta in part. Ctenidia are 2 pairs of simple, unfolded, bipectinate, platelike leaflets suspended in the mantle cavity. The ctenidia are mainly respiratory structures, while the labial palps are the primary food-collecting organs. The foot is longitudinally grooved and with a plantar sole, without byssal gland, and the nervous system is primitive, often with incomplete union of cerebral and pleural ganglia. These are the most primitive living bivalves, comprising three orders. The first two orders share the following characters: mantle open, with inhalant water entering anteriorly; shells with nacre; and gill filaments along ctenidial axis arranged opposite one another.

ORDER NUCULIDA Shell aragonitic, interior nacreous or porcelaneous; periostracum smooth; shell valves equal and taxodont (i.e., the valves have a row of similar interlocking short teeth along the hinge margins); adductor muscles equal in size; with large labial palps extended as proboscides used for food collection; ctenidia small, for respiration; marine (particularly in the deep sea), mainly infaunal detritivores. (e.g., Nuculidae, *Nucula*)

ORDER SOLEMYIDA (= CRYPTODONTA) Shell valves thin, elongate, and equal in size; uncalcified along outer edges, without hinge teeth; anterior adductor muscle larger than posterior one; ctenidia large, used mainly for housing symbiotic bacteria. Gut reduced or absent. (e.g., Solemyidae, *Solemya*). A fourth order, Manzanellida, can also be recognized, containing only a few living species (e.g., *Nucinella*). This monomyarian group shares the opposite gill filaments seen in the Nuculida and Solemyida, but it is often classified with Solemyida.

ORDER NUCULANIDA Mantle fused posteriorly, with siphons, inhalant water entering posteriorly; shells without nacre and gill filaments alternate along ctenidial axis. Several mainly deep-sea families, including Nuculanidae (e.g., *Nuculana*), Malletiidae (e.g., *Malletia*), and Sareptidae (e.g., *Yoldia*).

SUBCLASS AUTOBRANCHIA (= AUTOLAMELLIBRANCHIATA) Paired ctenidia, with very long filaments folded back on themselves so that each row of filaments forms two lamellae; adjacent filaments usually attached to one another by ciliary tufts (filibranch condition) or by tissue bridges (eulamellibranch condition). The greatly enlarged ctenidia are used in combination with the two pairs of labial palps in ciliary feeding; ctenidial surfaces capture waterborne particles and transfer them to the labial palps where the captured debris is sorted and potential food particles routed to the mouth. Gill filaments alternate on opposite sides of the gill axis. Shells with or without nacre.

INFRACLASS PTERIOMORPHIA (= FILIBRANCHIA) Ctenidia with outer fold not connected dorsally to visceral mass, with free filaments or with adjacent filaments attached by ciliary tufts (filibranch condition); shell aragonitic or calcitic, sometimes nacreous; mantle margin unfused, with weakly differentiated inhalant and exhalant apertures or siphons; mantle margins often form tentacles; foot well developed or extremely reduced; usually attached by byssal threads or cemented to substratum (or secondarily free). These primitive bivalves include several divergent ancient lineages separated as orders.

ORDER MYTILIDA The true (mostly marine) mussels, Mytilidae (e.g., *Adula, Brachidontes, Lithophaga, Modiolus, Mytilus*).

ORDER ARCIDA The ark shells, Arcidae (e.g., *Anadara, Arca, Barbatia*) and dog cockles, Glycymerididae (e.g., *Glycymeris*).

ORDER OSTREIDA The true oysters, Ostreidae (e.g., *Crassostrea, Ostrea*).

ORDER PTERIIDA Pearl oysters and their relatives, Pteriidae (e.g., *Pinctada, Pteria*); hammer oysters, Malleidae (e.g., *Malleus*); and pen shells, Pinnidae (e.g., *Atrina, Pinna*).

ORDER LIMIDA File shells, Limidae (e.g., *Lima*).

ORDER PECTINIDA Scallops, Pectinidae (e.g., *Chlamys, Lyropecten, Pecten*); thorny oysters, Spondylidae (e.g., *Spondylus*); jingle shells, Anomiidae (e.g., *Anomia, Pododesmus*).

INFRACLASS HETEROCONCHIA This clade encompasses the Palaeoheterodonta and Heterodonta, previously treated as separate higher groups but shown to be sister groups in recent molecular phylogenies.

COHORT PALAEOHETERODONTA Shell aragonitic, pearly internally; periostracum usually well developed; valves usually equal, with few hinge teeth; elongate lateral teeth (when present) are not separated from the large cardinal teeth; usually dimyarian; mantle opens broadly ventrally, mostly unfused posteriorly but with exhalant and inhalant apertures. About 1,200 species of marine and freshwater clams. With two very distinct groups, classified as orders.

ORDER TRIGONIIDA The relictual marine brooch shells (Trigoniidae), with only a few living species of *Neotrigonia* in Australia.

ORDER UNIONIDA Entirely freshwater, including the freshwater clams (or mussels), e.g., Unionidae (e.g., *Anodonta, Unio*), Margaritiferidae (e.g., *Margaritifera*), and Hyriidae (e.g., *Hyridella*). Many species threatened by human disturbance of streams and rivers.

COHORT HETERODONTA Two main groups, ranked as subcohorts, are recognized—the Archiheterodonta (with a single living order) and the Euheterodonta (with 4 living orders).

SUBCOHORT ARCHIHETERODONTA

ORDER CARDITIDA This group of primitive heterodonts is represented by the families Crassatellidae (e.g., *Crassatella*), Carditidae (e.g., *Cardita*), and Astartidae (e.g., *Astarte*).

SUBCOHORT EUHETERODONTA

ANOMALODESMATA Shells equivalved or inaequivalved, aragonitic, of 2–3 layers, innermost consisting of sheet nacre; periostracum often incorporates granulations; with 0–1 hinge teeth; generally isomyarian, rarely amyarian; posterior siphons usually well developed; mantle usually fused ventrally, with anteroventral pedal gape, and posteriorly with ventral inhalant and dorsal exhalant apertures or siphons; ctenidia eulamellibranchiate or septibranchiate (modified as a muscular pumping horizontal septum). This ancient and very diverse group of marine bivalves includes about 20 living families, including the rare deep-water Pholadomyidae (e.g., *Pholadomya*) and the aberrant watering-pot shells Clavagellidae (e.g., *Brechites*), as well as Pandoridae, Poromyidae, Cuspidariidae, Laternulidae, Thraciidae, Cleidothaeridae, Myochamidae, and Periplomatidae.

IMPARIDENTIA

ORDER LUCINIDA Includes the families Luncinidae (e.g., *Codakia*, *Lucina*), a group with symbiotic bacteria in their gills and an anterior water current, and Thysiridae.

ORDER VENERIDA Usually thick-valved, equivalve, and isomyarian, with posterior siphons. Includes surf clams, Mactridae (e.g., *Mactra*); solens, Solenidae (e.g., *Ensis*, *Solen*); tellins, Tellinidae (e.g., *Florimetis*, *Macoma*, *Tellina*); semelids, Semelidae (e.g., *Leptomya*, *Semele*); wedge shells, Donacidae (e.g., *Donax*); and Venus clams, Veneridae (e.g., *Chione*, *Dosinia*, *Pitar*, *Protothaca*, *Tivela*).

ORDER CARDIIDA Includes cockles and their kin, Cardiidae (e.g., *Cardium*, *Clinocardium*, *Laevicardium*, *Trachycardium,* and the giant clams, e.g., *Tridacna*).

ORDER SPHAERIIDA Contains the freshwater pea clams, Sphaeriidae (e.g., *Sphaerium, Pisidium*); the estuarine-to-freshwater Cyrenidae (e.g., *Corbicula, Batissa*); and the brackish-to-freshwater zebra mussels, Dreissenidae (e.g., *Dreissena*). The latter two families contain important invasive species.

ORDER MYIDA Burrowing forms with well-developed siphons. Includes soft-shell clams, Myidae (e.g., *Mya*); rock borers or piddocks, Pholadidae (e.g., *Barnea*, *Martesia*, *Pholas*); shipworms, Teredinidae (e.g., *Bankia*, *Teredo*); and basket clams, Corbulidae (e.g., *Corbula*). The monophyly of this order is uncertain.

CLASS SCAPHOPODA Tusk shells (Figures 13.1L and 13.9). Shell of one piece, tubular, usually tapering, open at both ends; head rudimentary, projecting from larger aperture; mantle cavity long, extending along entire posterior surface; without ctenidia or eyes; with radula; long, snoutlike "proboscis" and paired clusters of long, thin contractile tentacles with clubbed ends (captacula) that serve to capture and manipulate minute prey; heart absent; foot somewhat cylindrical, with epipodium-like fringe. Over 500 species, all marine, benthic, in 14 families and 2 orders.

ORDER DENTALIIDA Shell regularly tapering. Paired digestive gland with a muscular foot terminating in epipodial lobes and a cone-shaped process. Several families, including Dentaliidae (e.g., *Dentalium*, *Fustiaria*) and Laevidentaliidae (e.g., *Laevidentalium*).

ORDER GADILIDA Shell regularly tapering or bulbous with maximum shell diameter approximately nearer center of shell. Single digestive gland and foot with a terminal disk surrounded by epipodial papilla. Families include Pulsellidae (e.g., *Pulsellum*, *Annulipulsellum*) and Gadilidae (e.g., *Cadulus*, *Gadila*).

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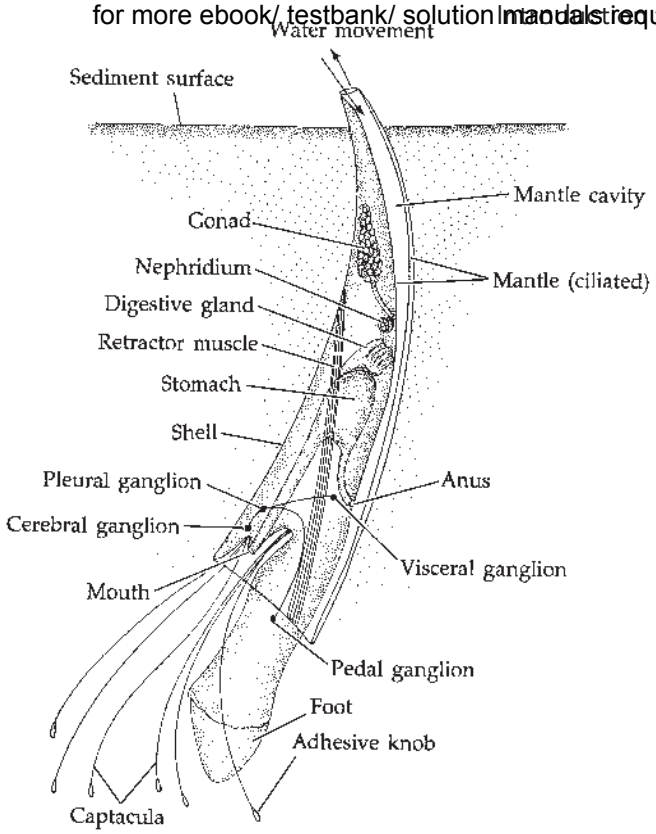

FIGURE 13.9 **General anatomy of a scaphopod.**

CLASS CEPHALOPODA Chambered nautilus, squid, cuttlefish, and octopuses (Figures 13.1H–K, 13.10, 13.11, 13.12, 13.17, and 13.22). With linearly chambered shell, usually reduced or lost in living taxa; if external shell present (*Nautilus*), animal inhabits last (youngest) chamber, with a filament of living tissue (the siphuncle) extending through older chambers; circulatory system largely closed; head with large, complex eyes and circle of prehensile arms or tentacles around mouth; with radula and beak; 1–2 pairs ctenidia, and 1–2 pairs complex nephridia; mantle forms large ventral mantle cavity containing 1–2 pairs of ctenidia; with muscular funnel (the siphon) through which water is forced, providing jet propulsion; some tentacles of male modified for copulation; benthic or pelagic, marine; about 750 living species.

SUBCLASS PALCEPHALOPODA Includes many fossil taxa, all with external shells, as well as the living chambered (pearly) nautilus.

ORDER NAUTILIDA (= TETRABRANCHIATA) The chambered (pearly) nautilus. Shell external, many-chambered, coiled in one plane, exterior porcelaneous, interior nacreous (pearly); head with many (80–90) suckerless tentacles (4 modified as spadix in male for copulation and protected by a fleshy hood); 13 tooth rows in radula; beak of chitin and calcium carbonate; funnel of 2 separate folds; 2 pairs of ctenidia ("tetrabranchiate"); 2 pairs of nephridia; eyes like a pinhole camera, without cornea or lens; nervous system with anterior elements concentrated into a brain, optic lobes large; statocyst simple; without chromatophores or ink sac. Fossil record rich but represented today by a single order (Nautilida) and two genera, *Allonautilus* and *Nautilus*, with 5 or 6 Indo-Pacific species.

SUBCLASS NEOCEPHALOPODA Includes one large fossil group (the ammonites) in addition to the coleoids. The shell is reduced and internal in most (and in all living taxa).

COHORT COLEOIDA (= DIBRANCHIATA) Octopuses, squid, and their kin. Shell reduced and internal or absent; head and foot united into a common anterior structure bearing 8 or 10 prehensile appendages (arms and tentacles) bearing suckers and, often, cirri, one arm usually modified in male for copulation; 7 tooth rows in radula; with chitinous beak; funnel a single closed tube; 1 pair of ctenidia ("dibranchiate"); 1 pair of nephridia; eyes complex, with lens and often with cornea; nervous system well developed and concentrated into a brain; with a complex statocyst; with chromatophores and ink sac.

SUPERORDER OCTOBRACHIA Members of this group, which includes the octopuses and vampire squid, do not have the head distinctly separated from the rest of the body; have 8 arms, with 2 additional retractile filaments in the vampire squid; lateral fins on the body are present or absent.

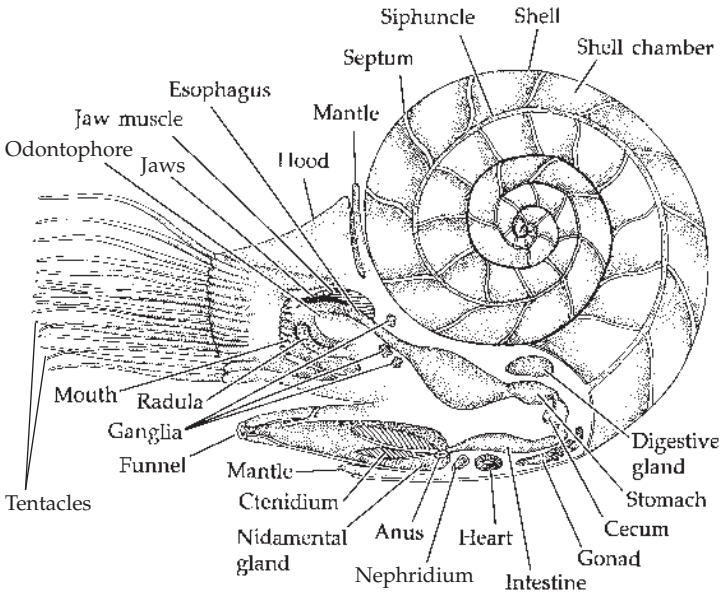

FIGURE 13.10 **The anatomy of *Nautilus* (diagrammatic sagittal section).**

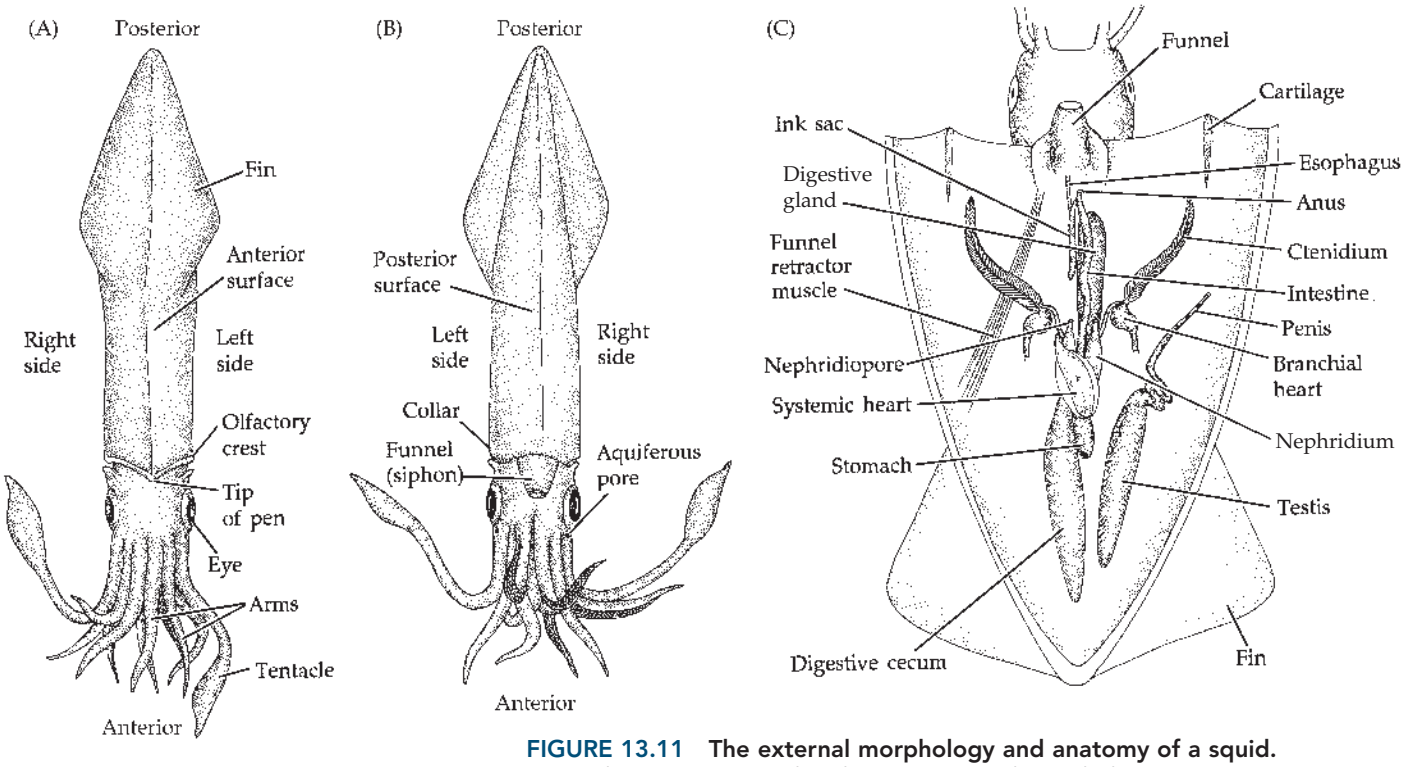

FIGURE 13.11 The external morphology and anatomy of a squid. (A–C) The common squid, *Loligo*. (A) External morphology (anterior view). (B) External morphology (posterior view). (C) Internal anatomy of a male. The mantle is dissected open and pulled aside. (D) The giant squid (*Architeuthis dux*) netted off the coast of New Zealand in 1997.

(D)

Stringer/Reuters

ORDER OCTOPODA Octopuses. Body short, round, usually without fins; internal shell vestigial or absent; 8 similar arms joined by web of skin (interbrachial web); suckers with narrow stalks; most are benthic. About 200 species, in two groups: the Incirrata, including the benthic octopuses and some pelagic taxa that lack fins and cirri, examples being Octopodidae (e.g., *Octopus*) and Argonautidae (*Argonauta*), the paper nautilus; and Cirrata, which are mainly pelagic deep-sea cephalopods with fins and cirri, such as Cirroteuthidae (e.g., *Cirroteuthis*), Opisthoteuthidae (e.g., *Opisthoteuthis*), and Stauroteuthidae (e.g., *Stauroteuthis*).

ORDER VAMPYROMORPHA The vampire squid. Body plump, with 1 pair of fins; shell reduced to thin, leaf-shaped, uncalcified, transparent vestige; 4 pairs of equal-sized arms, each with 1 row of unstalked distal suckers and 2 rows of cirri; arms joined by extensive web of skin (interbrachial membrane); fifth pair of arms represented by 2 tendril-like, retractable filaments; hectocotylus lacking; radula well developed; ink sac degenerate; mostly in deep water. One living species, *Vampyroteuthis infernalis*, that lives in the oxygen minimum zone of the deep sea.

SUPERORDER DECABRACHIA (= DECAPODA) Members of this group, which includes the squid and cuttlefish, have the head distinctly separated from the rest of the body; with 8 arms and 2 retractile (into pits) tentacles with suckers only on expanded tips; suckers with wide bases, sometimes with spines or hooks; lateral fins on body. The internal shell is large (as in the cuttlefish or in *Spirula*), reduced to an uncalcified gladius, or lost.

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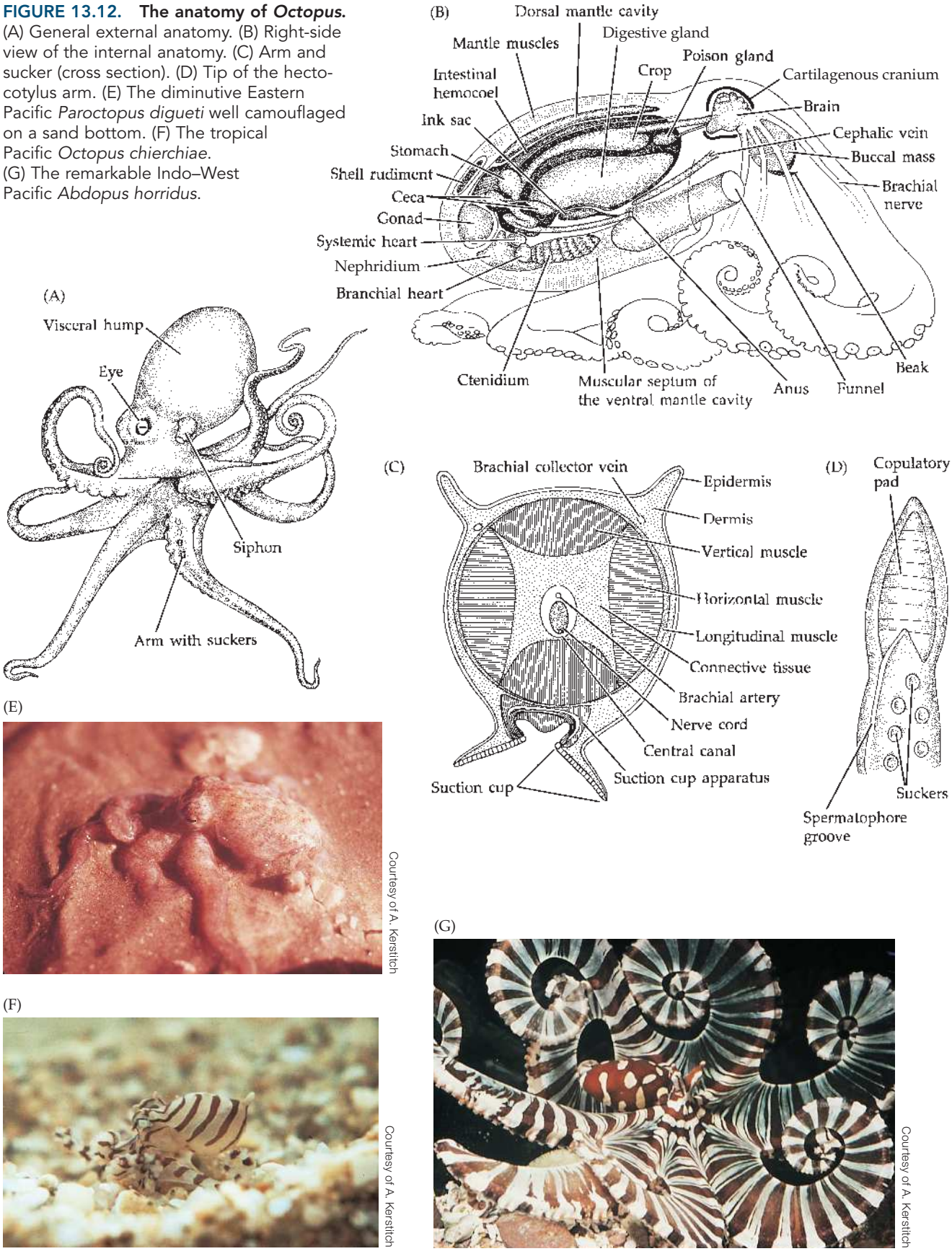
FIGURE 13.12. The anatomy of *Octopus*. (A) General external anatomy. (B) Right-side view of the internal anatomy. (C) Arm and sucker (cross section). (D) Tip of the hectocotylus arm. (E) The diminutive Eastern Pacific *Paroctopus digueti* well camouflaged on a sand bottom. (F) The tropical Pacific *Octopus chierchiae*. (G) The remarkable Indo–West Pacific *Abdopus horridus*.



Courtesy of A. Kerstitch

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ORDER SPIRULIDA The only living species is the ram's horn, *Spirula spirula* (Spirulidae), a small deep-sea squid with a coiled, internal, chambered shell.

ORDER SEPIIDA Cuttlefish. Body short, dorsoventrally flattened, with lateral fins; shell internal, calcareous, straight or slightly curved, chambered, or shell horny or absent; 8 short arms and 2 long tentacles; suckers lack hooks. Includes the shell-less Sepiolidae (e.g., *Rossia*, *Sepiola*); the Sepiidae (e.g., *Sepia*) with an internal calcareous shell, the cuttlebone; and Idiosepiidae (e.g., *Idiosepis*), being tiny squid that live in seagrass to which they attach with a special sucker. Their shell is reduced to a horny gladius.

ORDER MYOPSIDA Squid with the eye covered with a cornea and having a well-developed gladius. Body elongate, tubular, with lateral fins. Two families, Loliginidae (e.g., *Loligo*, *Doryteuthis*) and Australiteuthidae (*Australiteuthis*).

ORDER OEGOPSIDA Includes the majority of squid (and the former Teuthoida in part); the eye lacks a cornea and the shell is a gladius. Body elongate, tubular, with lateral fins; suckers often with hooks. Some of the many families in this group include Architeuthidae (*Architeuthis*), Bathyteuthidae (e.g., *Bathyteuthis*, sometimes treated as a separate order), Chiroteuthidae (e.g., *Chiroteuthis*), Ommastrephidae (e.g., *Ommastrephes*, *Dosidiscus*, *Illex*), Gonatidae (e.g., *Gonatus*), Histioteuthidae (e.g., *Histioteuthis*), Lycoteuthidae (e.g., *Lycoteuthis*), and Octopoteuthidae (e.g., *Octopoteuthis*).

The Molluscan Body Plan

Mollusca is probably the most morphologically diverse phylum in the animal kingdom. Molluscs range in size from microscopic solenogasters, bivalves, snails, and slugs, to whelks attaining 70 cm in length, giant clams (Cardiidae) over 1 m in length, and giant squid (*Architeuthis*) reaching at least 13 m in overall length (body plus tentacles). The giant Pacific octopus (*Octopus dofleini*) commonly attains an arm span of 3–5 m and a weight of over 40 kg. It is the largest living octopus, and one particularly large specimen was estimated to have an arm span of nearly 10 m and a weight of over 250 kg! Despite their differences, giant squid, cowries, garden slugs, eight-plated chitons, and wormlike aplacophorans are all related and share a common body plan (Box 13A). In fact, the myriad ways in which evolution has shaped the basic molluscan body plan provide some of the best lessons in homology and adaptive radiation in the animal kingdom.

Molluscs are bilaterally symmetrical, coelomate protostomes, but the coelom generally exists only as small vestiges around the heart (the **pericardial chamber**), the gonads, and parts of the nephridia (kidneys). The principal body cavity is a hemocoel composed of several large sinuses of the open circulatory system, except in some cephalopods that have a largely closed system. In general, the body comprises three distinguishable regions: a head, foot, and centrally concentrated visceral mass, but the configuration differs in different classes (Figure 13.13). The head may bear various sensory structures, most notably eyes and tentacles; statocysts may be located in the foot region, and chemosensory structures can also be present.

The visceral mass is covered by a thick epidermis called the **mantle** (also known as the pallium), which is sometimes covered in cuticle and plays a critical role in the organization of the body. It secretes the hard calcareous skeleton, either as minute sclerites, or plates, that are embedded in the body wall or as an internal or external shell. Ventrally the body usually bears a large, muscular **foot**, which typically has a creeping **sole**.

Surrounding or posterior to the visceral mass is a cavity—a space between the visceral mass and folds of the mantle itself. This **mantle cavity** (also known as the pallial cavity) often houses the gills (the original molluscan gills are known as **ctenidia**), along with the openings of the gut, excretory, and reproductive systems, and, in addition, special patches of chemosensory epithelium in many groups, notably the osphradia. In aquatic forms, water is circulated through this cavity, passing over the ctenidia, excretory pores, anus, and other structures.

Molluscs have a complete, or through gut that is regionally specialized. The buccal region of the foregut typically bears a uniquely molluscan structure, the **radula**, which is a toothed, rasping, tonguelike strap used in feeding. It is located on a muscular **odontophore** that moves the radula through its feeding motions. The circulatory system usually includes a heart in a pericardial cavity and a few large vessels that empty into or drain hemocoelic spaces. The excretory system consists of one or more pairs of metanephridial kidneys (here simply referred to as nephridia), with openings (nephrostomes) to the pericardium via renopericardial canals and to the mantle cavity via a nephridiopore. The nervous system typically includes a pair of dorsal cerebral ganglia, a circumenteric nerve ring (encircling the buccal area or esophagus), and two pairs of longitudinal nerve cords that arise from paired pleural ganglia and connect with the visceral ganglia posteriorly in the body. Other anterior paired ganglia (buccal and labial) may be present. Pedal ganglia lie in the foot and may give off pedal nerve cords.

Gametes are produced by the gonad in the visceral mass, and fertilization may be external or internal. Development is typically protostomous, with spiral cleavage and a trochophore larval stage. There is also a

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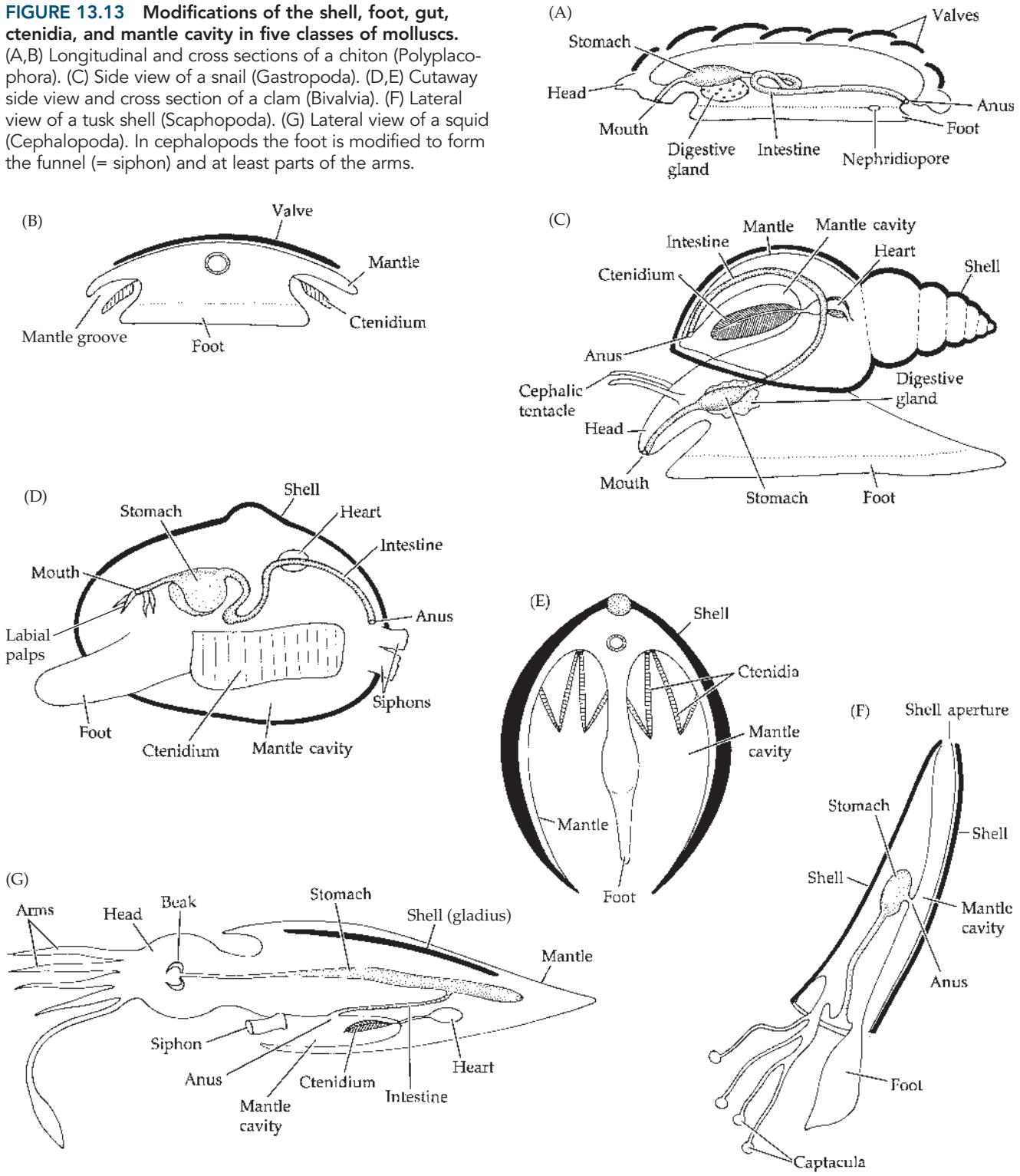

FIGURE 13.13 Modifications of the shell, foot, gut, ctenidia, and mantle cavity in five classes of molluscs. (A,B) Longitudinal and cross sections of a chiton (Polyplacophora). (C) Side view of a snail (Gastropoda). (D,E) Cutaway side view and cross section of a clam (Bivalvia). (F) Lateral view of a tusk shell (Scaphopoda). (G) Lateral view of a squid (Cephalopoda). In cephalopods the foot is modified to form the funnel (= siphon) and at least parts of the arms.

secondary larval form unique to gastropod and bivalve molluscs called the **veliger**.

Although this general summary describes the basic body plan of most molluscs, notable modifications occur and are discussed throughout this chapter. The eight classes have been characterized (see Abbreviated Classification of Living Members of the Phylum Mollusca) and are briefly summarized here.

Some of the most bizarre molluscs are the "aplacophorans"—Solenogastres and Caudofoveata (Figures 13.1C and 13.2). Members of these groups are wormlike and typically small and either burrow in sediment (Caudofoveata) or may spend their entire lives on the branches of various cnidarians such as gorgonians, or bryozoans, upon which they feed (Solenogastres). Caudofoveata lack a foot, but a reduced one

is present in the Solenogastres, and neither group has a solid shell. Aplacophorans also have no distinct head, eyes, or tentacles. They were traditionally considered primitive molluscs that evolved before the appearance of solid shells, but some data suggest they may be derived forms that have lost the shell and have acquired a paedomorphic body morphology.

Polyplacophorans, or chitons, are oval molluscs that bear eight (seven in some Paleoloricata) separate articulating shell plates on their dorsal surface (Figures 13.1B and 13.4). They range in length from about 7 mm to over 35 cm. These marine animals are inhabitants of deep-sea to intertidal regions around the world, at all latitudes.

Monoplacophorans are limpetlike molluscs with a single cap-shaped shell ranging from about 1 mm to about 4 cm in length (Figures 13.1A and 13.3). Most live in the deep sea, some at great depths (>6,000 m). Their most notable feature is the repetitive arrangement of gills, gonads, and nephridia, a condition that has led some biologists to speculate that they must represent a link to some ancient segmented ancestor of the Mollusca (an idea no longer deemed correct).

Gastropods are by far the largest group of molluscs and include some of the best-studied species (Figures 13.1D–G, 13.5, 13.6, and 13.7). This class includes the common snails and slugs in all marine and many freshwater habitats; they are the only molluscan class to have successfully invaded terrestrial environments, and they have done this multiple times. They are the only molluscs that undergo torsion during early development, a process involving a 90°–180° rotation of the visceral mass relative to the foot (for details see Torsion, or "How the Gastropod Got its Twist").

Bivalves include the clams, oysters, mussels, and their kin (Figures 13.1M–Q and 13.8). They possess two separate shells, called **valves**, hinged dorsally. The smallest bivalves are in the marine family Carditidae, some of which are about 1 mm in length; the largest are giant tropical clams (*Tridacna*), one species of which (*T. gigas*) may weigh over 400 kg! Bivalves inhabit all marine environments and many freshwater habitats.

Scaphopods, the tusk shells, live in marine surface sediments at various depths. Their distinctive single, tubular uncoiled shell opens at both ends and ranges from a few millimeters to about 15 cm in length (Figures 13.1L and 13.9).

The cephalopods are among the most highly modified molluscs and include the chambered (pearly) nautilus, squid, cuttlefish, octopuses, and a host of extinct forms, including the ammonites (Figures 13.1I–K, 13.10, 13.11, 13.12, 13.17, and 13.22). This group includes the largest of all living invertebrates, the giant squid, with body and tentacle lengths around 13 m. Among living cephalopods, only the species of nautilus have an external shell. The cephalopods differ markedly from other molluscs in several ways. For example, they have a spacious body cavity that includes the pericardium, gonadal cavity, nephriopericardial connections, and gonoducts, all of which form an interconnected system representing a highly modified but true coelom. In addition, unlike all other molluscs, many coleoid cephalopods have a functionally closed circulatory system. The nervous system of cephalopods is the most sophisticated of all invertebrates, with unparalleled learning and memory abilities. Most of these modifications are associated with the adoption of an active predatory lifestyle by these remarkable creatures.

The Body Wall

The body wall of molluscs typically comprises three main layers: the cuticle (when present), epidermis, and muscles (see Figure 13.15A). The cuticle is composed largely of various amino acids and sclerotized proteins (called conchin), but it apparently does not contain chitin (except in the aplacophorans). The epidermis is usually a single layer of cuboidal to columnar cells, which are ciliated on much of the body. Many of the epidermal cells participate in secretion of the cuticle. Other kinds of secretory gland cells can also be present, some of which secrete mucus, and these can be very abundant on external surfaces such as the sole of the foot. Other specialized epidermal cells occur on the dorsal body wall, or mantle. Many of these cells constitute the molluscan **shell glands**, which produce the calcareous sclerites or shells characteristic of this phylum. Still other epidermal cells are sensory receptors. The epidermis and outermost muscle layer are often separated by a basement membrane and occasionally a dermislike layer.

The body wall usually includes three distinct layers of smooth muscle fibers: an outer circular layer, a middle diagonal layer, and an inner longitudinal layer. The diagonal muscles are often in two groups with fibers running at right angles to each other. The degree of development of each of these muscle layers differs among the classes (e.g., in solenogasters the diagonal layers are frequently absent).

The Mantle and Mantle Cavity

The significance of the mantle cavity and its importance in the evolutionary success of molluscs has already been alluded to. Here we offer a brief summary of the nature of the mantle cavity and its disposition in each of the major groups of molluscs.

The mantle, as the name implies, is a sheetlike organ that forms the dorsal body wall, and in most molluscs it grows during development to envelop the molluscan body. At its edge there are one or two folds that contain muscle layers and hemocoelic channels (see Figure 13.15C). The outward growth creates a space lying between the mantle fold(s) and the body proper. This space, the mantle cavity, may be in the form of a groove surrounding the foot or a primitively posterior

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chamber through which water is passed by ciliary or, in more derived taxa, by muscular action. Generally, the mantle cavity houses the respiratory surface (usually the ctenidia or other gill-like structures) and receives the fecal material discharged from the anus and excretory waste from the nephridia. Gametes are also primitively discharged into the mantle cavity. Incoming water provides a source of oxygen for respiration and a means of flushing waste and, in some instances, also carries food for suspension feeding.

The mantle cavity of chitons is a groove surrounding the foot (Figures 13.4A and 13.13A,B). Water enters the groove from the front and sides, passing medially over the ctenidia and then posteriorly between the ctenidia and the foot. After passing over the gonopores and nephridiopores, water exits the back end of the groove and carries away fecal material from the posteriorly located anus.

The aplacophorans have a small mantle cavity, with either a pair of ctenidia (Caudofoveata) or lamella-like folds or papillae on the mantle cavity wall (Solenogastres). The paired coelomoducts and the anus also open into the mantle cavity.

The mantle cavity of gastropods originates during development as a ventrally located chamber. As development proceeds, however, most gastropods undergo a rotation of the visceral mass and shell to bring the mantle cavity over the head (Figures 13.5, 13.6, and 13.13C) (see the Torsion, or "How the Gastropod Got its Twist" section). The different orientation does not affect the water flow, which still passes through this chamber via the ctenidia and then past the anus, gonopores, and nephridiopores. A great many secondary modifications on this plan have evolved in the Gastropoda, including rerouting of current patterns; loss or modification of associated structures such as the gills, hypobranchial glands, and sensory organs; and even "detorsion," as discussed in later sections of this chapter.

Bivalves possess a greatly enlarged mantle cavity that surrounds both sides of the foot and visceral mass (Figures 13.8 and 13.13D,E). The mantle lines the laterally placed shells, and the folds making up the mantle edges are often fused in various ways posteriorly to form inhalant and exhalant siphons, through which water enters and leaves the mantle cavity. The water passes over and through the ctenidia that, in autobranch bivalves, extract suspended food material as well as accomplishing gas exchange. The water flow then sweeps across the gonopores and nephridiopores and finally past the anus as it exits through the exhalant siphon.

Scaphopods have a tapered, tubular shell opening at both ends (Figures 13.9 and 13.13F). Water enters and leaves the elongate mantle cavity through the small opening in the top of the shell and flushes over the mantle surface, which, in the absence of ctenidia, is the site of gas exchange. The anus, nephridiopores, and gonopores also empty into the mantle cavity.

While no detailed studies of the functioning of the monoplacophoran mantle cavity have been made, observations of the first living specimens in 1977 revealed that the gills vibrated, apparently circulating water through the mantle groove. It was also noted that shell movement was accompanied by an acceleration of gill beating. Vibrating gills are also found in some protobranch bivalves. In other molluscs ciliary action, sometimes assisted by muscular contractions, moves water through the mantle cavity. The anus, nephridiopores, and gonopores also open into the mantle cavity.

With the exception of monoplacophorans and some protobranch bivalves, in all of the above cases water is moved through the mantle cavity by the action of long lateral cilia on the ctenidia. In cephalopods the ctenidial gills are not ciliated; in *Nautilus* a ventilatory current is passed through the mantle cavity by the undulatory movements of two muscular flaps associated with the funnel lobes. In the coleoid cephalopods, however, well-developed, highly innervated mantle muscles perform this function through the regular pulsation of the mantle wall. The exposed, fleshy body surface of squid and octopuses is, in fact, the mantle itself (Figures 13.11, 13.12, and 13.13G). Unconstrained by an external shell, the mantle of these molluscs expands and contracts to draw water into the mantle cavity and then forces it out through the narrow muscular **funnel** (= **siphon**). The forceful expelling of this jet of exhalant water can also provide a means of rapid locomotion for most cephalopods. In the mantle cavity the water passes through the ctenidia and then past the anus, reproductive pores, and excretory openings.

The remarkable adaptive qualities of the molluscan body plan are manifested in these variations in the position and function of the mantle cavity and its associated structures. In fact, the nature of many other structures is also influenced by mantle cavity arrangement, as shown schematically in Figure 13.14. That molluscs have been able to successfully exploit an extremely broad range of habitats and lifestyles can be explained in part by these variations, which are central to the story of molluscan evolution. We will have more to say about these matters throughout this chapter.

The Molluscan Shell

Except for the two aplacophoran classes, all mollusc classes have solid calcareous shells (composed of either aragonite or calcite) produced by shell glands in the mantle. In the Caudofoveata and Solenogastres, aragonite sclerites (spicules or scales) are formed extracellularly in the mantle epidermis and are embedded in the cuticle. In the other classes molluscan shells vary greatly in shape and size, but they all adhere to the basic construction plan of calcium carbonate produced extracellularly, laid down on a protein matrix

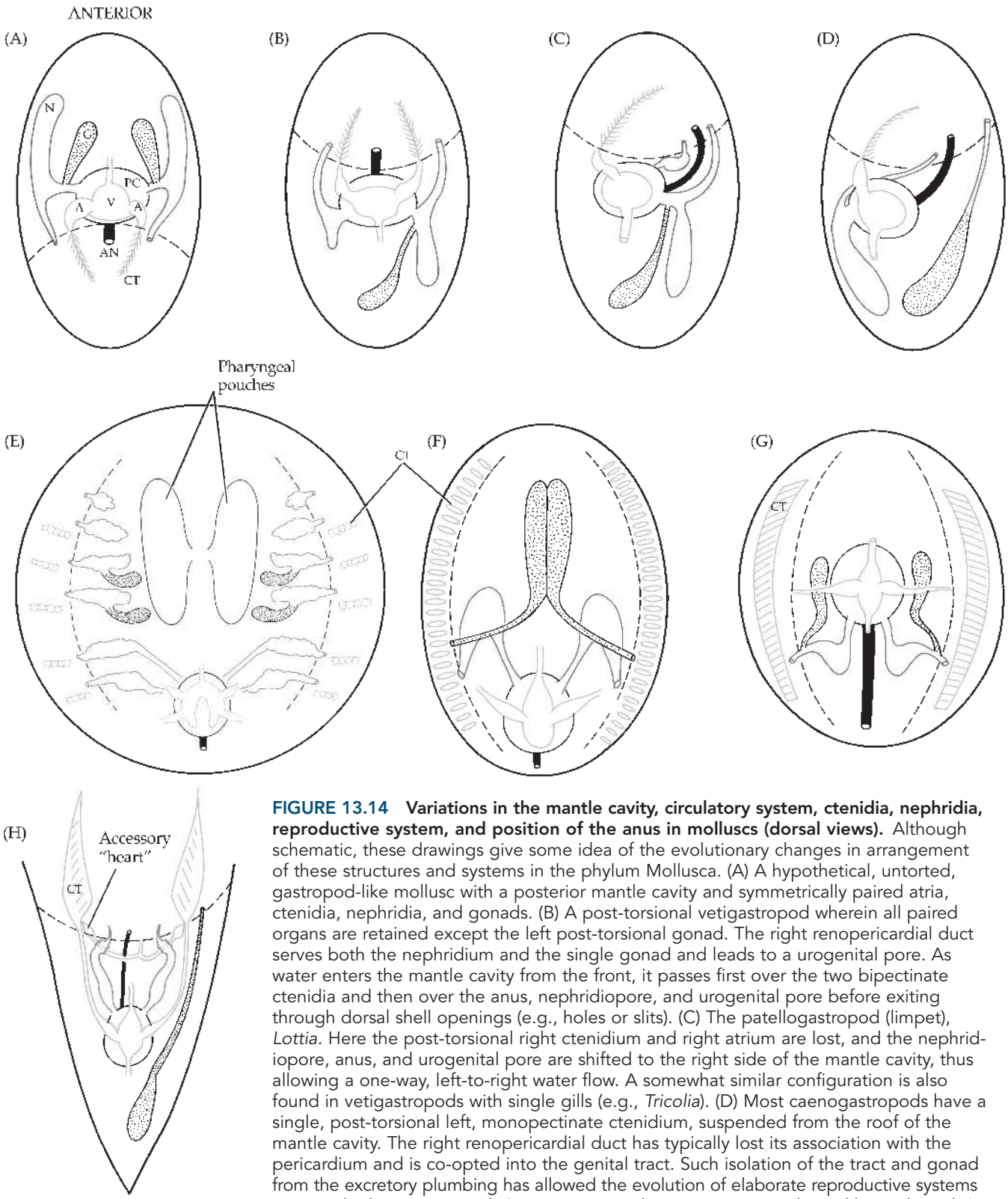

FIGURE 13.14 Variations in the mantle cavity, circulatory system, ctenidia, nephridia, reproductive system, and position of the anus in molluscs (dorsal views). Although schematic, these drawings give some idea of the evolutionary changes in arrangement of these structures and systems in the phylum Mollusca. (A) A hypothetical, untorted, gastropod-like mollusc with a posterior mantle cavity and symmetrically paired atria, ctenidia, nephridia, and gonads. (B) A post-torsional vetigastropod wherein all paired organs are retained except the left post-torsional gonad. The right renopericardial duct serves both the nephridium and the single gonad and leads to a urogenital pore. As water enters the mantle cavity from the front, it passes first over the two bipectinate ctenidia and then over the anus, nephridiopore, and urogenital pore before exiting through dorsal shell openings (e.g., holes or slits). (C) The patellogastropod (limpet), *Lottia*. Here the post-torsional right ctenidium and right atrium are lost, and the nephridiopore, anus, and urogenital pore are shifted to the right side of the mantle cavity, thus allowing a one-way, left-to-right water flow. A somewhat similar configuration is also found in vetigastropods with single gills (e.g., *Tricolia*). (D) Most caenogastropods have a single, post-torsional left, monopectinate ctenidium, suspended from the roof of the mantle cavity. The right renopericardial duct has typically lost its association with the pericardium and is co-opted into the genital tract. Such isolation of the tract and gonad from the excretory plumbing has allowed the evolution of elaborate reproductive systems among "higher" gastropods (e.g., neritomorphs, caenogastropods, and heterobranchs) and is probably important in the story of gastropod success. (E) The condition in monoplacophorans includes the serial repetition of several organs. (F) In polyplacophorans, the gonoducts and nephridioducts open separately into the exhalant regions of the lateral mantle grooves. (G) A generalized bivalve condition. The gonads and nephridia may share common pores, as shown here, or else open separately into the lateral mantle chambers. (H) The condition in a generalized cephalopod with a single, isolated reproductive system and an effectively closed circulatory system.

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in layers, and often covered by a thin organic surface coating called a **periostracum** (Figure 13.15). The periostracum is composed of a type of conchin (largely quinone-tanned proteins) similar to that found in the epidermal cuticle. The calcium layers have four crystal types: prismatic, spherulitic, laminar, and crossed structures. All incorporate conchin onto which the calcareous crystals precipitate. The majority of living molluscs have an outer prismatic layer and an inner porcelaneous, crossed layer. In monoplacophorans, cephalopods, and some gastropods and bivalves, an iridescent, nacre (laminar) layer replaces the layer of crossed crystals. Shells are often made up of multiple layers of different crystal types.

Molluscs are noted for their wonderfully intricate and often flamboyant shell color patterns and sculpturing (Figure 13.16), but very little is known about the evolutionary origins and functions of these features. Some molluscan pigments are metabolic by-products, and thus shell colors might largely represent strategically deposited food residues, while others appear to have no relationship to diet. Molluscan shell pigments include such compounds as pyrroles and porphyrins. Melanins are common in the integument (cuticle and epidermis), the eyes, and internal organs, but they are rare in shells.

Some shell sculpture patterns are correlated with specific behaviors or habitats. For example, shells with low spires are more stable in areas of heavy wave shock or on vertical rock surfaces. Similarly, the low, cap-shaped shells of limpets (Figures 13.5A and 13.16H,I) are presumably adapted for withstanding exposure to strong waves or currents and have evolved in multiple lineages of gastropods. Heavy ribbing, thick or inflated shells, and a narrow gape in bivalves are all possible adaptations to provide protection from predators. In some gastropods, fluted shell ribs help them land upright when they are dislodged from rocks. Several groups of soft-bottom benthic gastropods and bivalves have long spines on the shell that may help stabilize the animals in loose sediments as well as provide some protection from predators. Many molluscs, particularly clams, have shells covered with living epizootic organisms such as sponges, annelid tube worms, bryozoans, entoprocts, and hydroids. Some studies suggest that predators have difficulty recognizing such camouflaged molluscs as potential prey.

Molluscs may have one shell, two shells, eight shells, or no shell. In the last case, the outer body wall may contain calcareous sclerites of various sorts. In the aplacophorans, for example, the cuticular sclerites vary in shape and range in length from microscopic to about 4 mm. These sclerites are essentially crystals composed almost entirely of calcium carbonate as aragonite. Caudofoveates produce platelike cuticular sclerites that give their body surface a

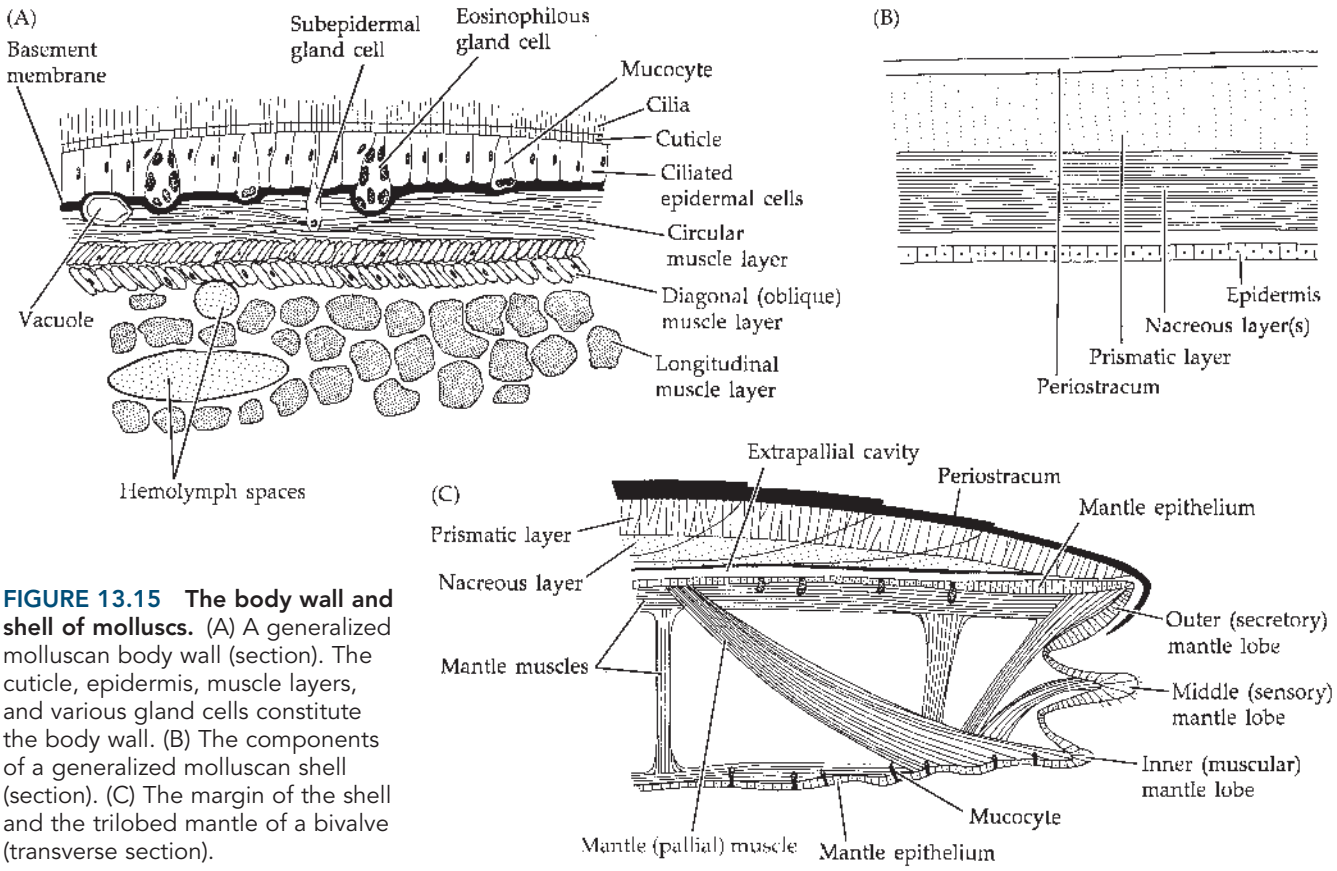

FIGURE 13.15 The body wall and shell of molluscs. (A) A generalized molluscan body wall (section). The cuticle, epidermis, muscle layers, and various gland cells constitute the body wall. (B) The components of a generalized molluscan shell (section). (C) The margin of the shell and the trilobed mantle of a bivalve (transverse section).

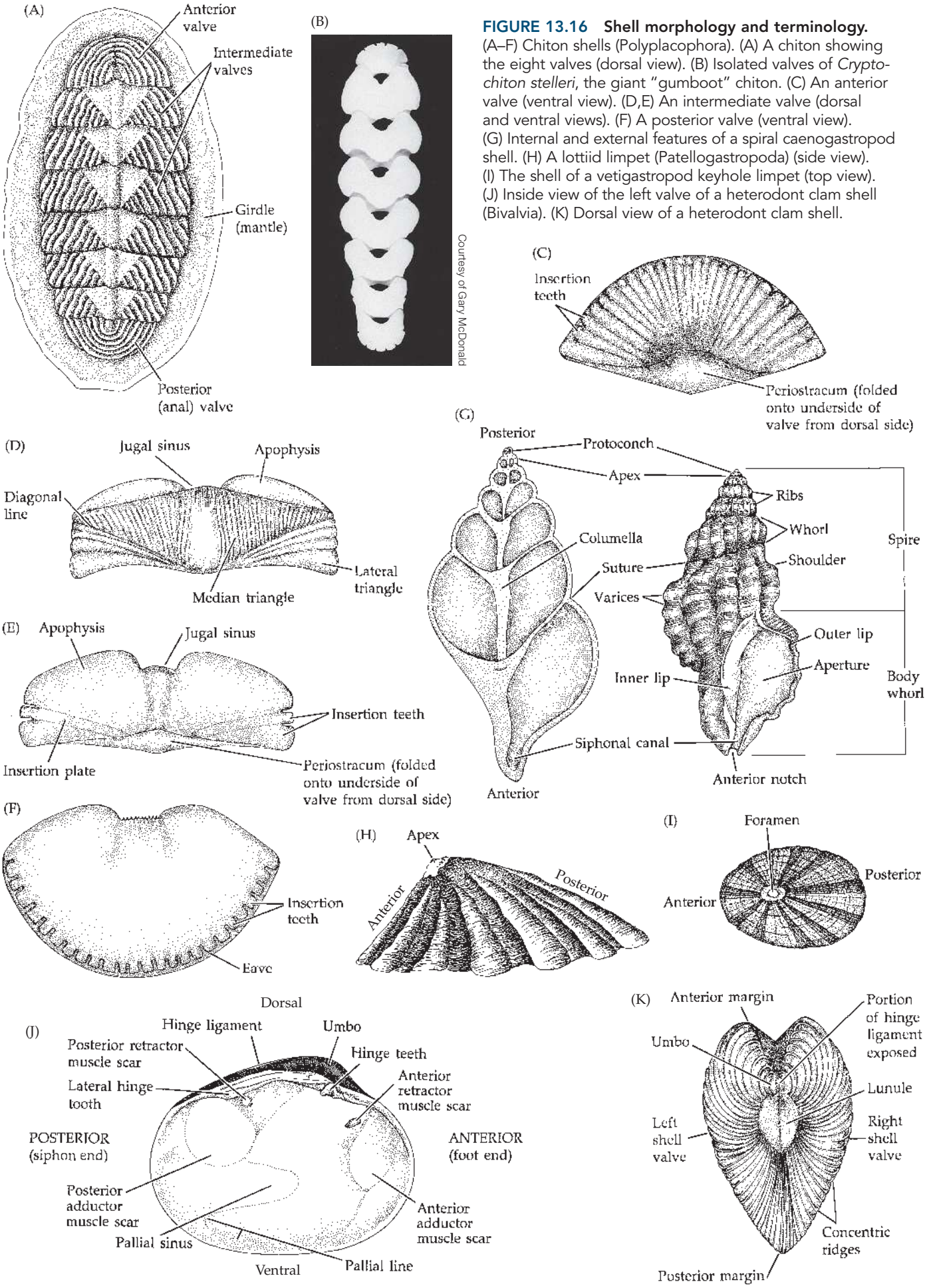

FIGURE 13.16 Shell morphology and terminology. (A–F) Chiton shells (Polyplacophora). (A) A chiton showing the eight valves (dorsal view). (B) Isolated valves of *Cryptochiton stelleri*, the giant "gumboot" chiton. (C) An anterior valve (ventral view). (D,E) An intermediate valve (dorsal and ventral views). (F) A posterior valve (ventral view). (G) Internal and external features of a spiral caenogastropod shell. (H) A lottiid limpet (Patellogastropoda) (side view). (I) The shell of a vetigastropod keyhole limpet (top view). (J) Inside view of the left valve of a heterodont clam shell (Bivalvia). (K) Dorsal view of a heterodont clam shell.

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scaly texture and appearance. The sclerites in both taxa appear to be secreted by a diffuse network of specialized groups of cells, and different shapes are found in different regions of the body.

The eight transverse plates, or valves (Figures 13.4 and 13.16A–F), of polyplacophorans are encircled by and embedded in a thickened region of the mantle called the **girdle**. The size of the girdle varies from narrow to broad and may cover much of the valves. In the giant Pacific "gumboot" chiton, *Cryptochiton stelleri*, the girdle completely covers the valves. The girdle is thick, heavily cuticularized, and usually covered with calcareous sclerites, spines, scales, or noncalcareous bristles secreted by specialized epidermal cells. These sclerites are probably homologous with those in the body wall of aplacophorans.

The anterior and posterior valves of chitons are referred to as the end valves, or cephalic (= anterior) and anal (= posterior) plates; the six other valves are called the intermediate valves. Some details of chiton valves are shown in Figure 13.16A–F. The shells of chitons have three layers, with an outer periostracum, a colored **tegmentum**, and an inner calcareous layer, or **articulamentum** (with an underlying hypostracum). The periostracum is a very thin, delicate organic membrane and is not easily seen. The tegmentum is composed of organic material (probably a form of conchin) and calcium carbonate suffused with various pigments. It is penetrated by vertical canals (**aesthetes**) that lead to minute pores in the surface of the valves. The pores are of two sizes: the larger ones (megalopores) house the **megaesthetes,** and the smaller ones (micropores) the **microaesthetes**. In some species, megaesthetes may be modified as **shell eyes** (see section on Sense Organs), with compound lenses made of large crystals of aragonite. The vertical aesthete canals arise from a layer of horizontal canals in the lower part of the tegmentum and the articulamentum (see Figure 13.43C), and some pass through the articulamentum to join with nerves in the mantle at the lower edge of the shell valve. The articulamentum is a thick, calcareous, porcelaneous layer that differs in certain ways from the shell layers of other molluscs.

Monoplacophorans have a single, limpetlike shell with the apex situated far forward (Figures 13.1A and 13.3). The shell has a distinctive outer prismatic layer and an inner layer formed of foliated aragonite in most species. As in chitons, the mantle encircles the body and foot as a circular fold, forming lateral mantle grooves.

The bivalves possess two shells, or **valves**, that are connected dorsally by an elastic, proteinaceous **ligament** and enclose the body and spacious mantle cavity (Figures 13.1M–P, 13.8, and 13.16J,K). Shells of bivalves typically have a thin periostracum, covering two to four calcareous layers that vary in composition and structure. The calcareous layers are often aragonite or an aragonite/calcite mixture, and they usually have a substantial organic framework. The periostracum and organic matrix may account for over 70% of the shell's dry weight in some thin-shelled taxa. Each valve has a dorsal protuberance called the umbo, which is the oldest part of the shell or larval shell (the **prodissoconch**). Concentric growth lines radiate outward from the umbo. When the valves are closed by contraction of the adductor muscles, the outer part of the ligament is stretched and the inner part is compressed. Thus, when the adductor muscles relax, the resilient ligament causes the valves to open. The hinge apparatus comprises various sockets and toothlike pegs or flanges (hinge teeth) that align the valves and prevent lateral movement. In most bivalves, the adductor muscles contain both striated and smooth fibers, facilitating both rapid and sustained closure of the valves. This division of labor is apparent in some bivalves, as for example in oysters, where the large single adductor muscle is clearly composed of two parts, a dark striated region that functions as a rapid-closure muscle, and a white smoother region (the catch muscle) that functions to hold the shell tightly closed for long periods of time.

The thin mantle lines the inner valve surfaces in bivalves and separates the visceral mass from the shell. The edge of a bivalve mantle bears three longitudinal ridges or folds—the inner, middle, and outer folds (Figure 13.15C). The innermost fold is the largest and contains radial and circular muscles, some of which attach the mantle to the shell. The line of mantle attachment appears on the inner surface of each valve as a scar called the **pallial line** (Figure 13.16J), and this scar is often a useful diagnostic character. The middle mantle fold is sensory in function, and the outer fold is responsible for secreting the shell. The cells of the outer lobe are specialized: the medial cells lay down the periostracum, and the lateral cells secrete the first calcareous layer. The entire mantle surface is then responsible for secreting the remaining innermost calcareous portion of the shell. A thin extrapallial space lies between the mantle and the shell, and it is into this space that materials for shell formation are secreted and mixed. Should a foreign object, such as a sand grain, lodge between the mantle and the shell, it may become the nucleus around which are deposited concentric layers of smooth nacreous or porcelaneous shell. The result is a pearl, either free in the extrapallial space or partly embedded in the growing shell.[7]

Scaphopod shells resemble miniature, hollow elephant tusks, hence the vernacular names "tusk shell" and "tooth shell" (Figures 13.1L and 13.9). The scaphopod shell is open at both ends, with the smaller opening at the dorsal end of the body. Most tusk shells are slightly curved, the concave side being equivalent to the anterior of other molluscs. The mantle is long, lining the entire posterior side of the shell. The dorsal aperture serves for both inhalant and exhalant water currents.

[7]Pearls are also found in some gastropods with nacreous inner shell layers, such as abalone.

Most extant cephalopods have a reduced shell or are shell-less. A completely developed external shell is found only in fossil forms and the living species of *Nautilus* and *Allonautilus*. In squid and cuttlefish the shell is reduced and internal, and in octopuses it is entirely lacking or present only as a small rudiment.

The shell of *Nautilus* is coiled in a planispiral fashion (whorls lie in a single plane) and has a thin periostracum (Figures 13.10, 13.17A, and 13.22B). *Nautilus* shells (and all cephalopod shells) are divided into internal chambers by transverse septa, and only the last chamber is occupied by the body of the living animal. As the animal grows, it periodically moves forward, and the posterior part of the mantle secretes a new septum behind it. Each septum is interconnected by a tube through which extends a cord of tissue called the **siphuncle**. The siphuncle helps to regulate buoyancy of the animal by varying the amounts of gas and fluid in the shell chambers. The shell is composed of an inner nacreous layer and an outer porcelaneous layer containing prisms of calcium carbonate and an organic matrix. The outer surface may be pigmented or pearly white. The junctions between septa and the shell wall are called **sutures** and are simple and straight, or slightly waved (as in *Nautilus*), or were highly convoluted (as in the extinct ammonites). In cuttlefish (order Sepiida), the shell is highly modified and internal, with chambers that are very narrow spaces separated by thin septa. Like *Nautilus*, a cuttlefish can regulate the relative amounts of fluid and gas in its shell chambers. The small, open-coiled, septate, gas-filled internal shells of the deep-water "squid" *Spirula* are often found washed up on beaches.

Fossil data suggest that the first cephalopod shells were probably small curved cones. From these ancestors both straight and coiled shells evolved, although secondary uncoiling occurred in several groups. Some straight-shelled cephalopods from the Ordovician Period exceeded 5 m in length, and some Cretaceous coiled species had shell diameters of 2 m or more.

Gastropod shells are extremely diverse in size and shape (Figure 13.1D,G). The smallest are microscopic (less than 1 mm), and the largest may reach 70 cm in length. The "typical" shape is the familiar conical spiral wound around a central axis or columella (Figure 13.16G). The turns of the spire form whorls, demarcated by lines called sutures. The largest whorl is the last (or body) whorl, which bears the aperture through which the foot and head protrude. The traditional view of a coiled gastropod shell with the spire uppermost is actually "upside down," since the lower edge of the aperture is anterior and the apex of the shell spire is posterior. The first few, very small, whorls at the apex are the larval shell, or **protoconch** (or its remnant), which usually differs in sculpturing and color from the rest of the shell. The last whorl and aperture may be notched and drawn out into an anterior **siphonal canal**, to house a siphon when present. A smaller posterior canal may also be present on the rear edge of the aperture that houses a siphonlike fold of the mantle where waste and water are expelled.

Every imaginable variation on the basic spiraled shell occurs among the gastropods (and some unimaginable): the shell may be long and slender (e.g., auger shells) or short and plump (e.g., trochids), or the shell may be flattened (e.g., sundials). In some the spire may be more or less incorporated into the last whorl and eventually disappear from view (as in cowries). In some with a much larger last whorl, the aperture may be reduced to an elongated slit (Figure 13.1E) (e.g., cowries, olives, and cones). In a few groups the shell may coil so loosely as to form a meandering wormlike tube (e.g., the so-called "tube snails," vermetids and siliquariids; see Figure 13.19E). In a number of gastropod groups, the shell may be reduced and overgrown by the mantle; it may disappear entirely, resulting in a slug, or, as in the

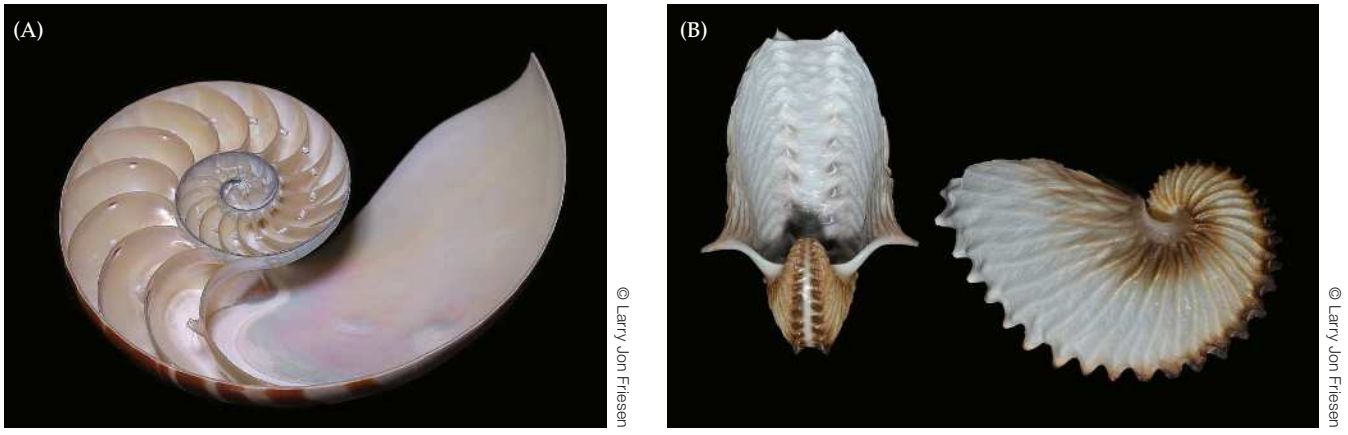

FIGURE 13.17 Two very different kinds of cephalopod shells. (A) The chambered shell of *Nautilus*, cut in longitudinal section. (B) The egg case "shell" of the paper nautilus, *Argonauta*, which is secreted by modified arms, not the mantle.

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sacoglossan family Juliidae, it may even be bivalved. Most gastropods spiral clockwise; that is, they show right-handed, or dextral, coiling. Some are sinistral (left-handed), and some normally dextral species may occasionally produce sinistral individuals. In limpets the shell is cap shaped, with a low conical shape with no or little visible coiling (Figure 13.16H,I). The limpet shell form has been derived from coiled ancestors on numerous occasions during gastropod evolution.

Gastropod shells consist of an outer thin organic periostracum and two or three calcareous layers: an outer prismatic (or palisade) layer, and middle and inner lamellar or crossed layers. In many vetigastropods the inner layer is nacreous. In some patellogastropods up to six calcareous layers are distinguishable, but in the great majority of living gastropods, the shell structure is primarily one layer composed of crossed crystals (crossed lamellar shell structure). Gastropods in which the shell is habitually covered by mantle lobes lack a periostracum (e.g., olives and cowries), but in some other groups the periostracum is very thick, and sometimes it is produced into lamellae or hairs. The prismatic and lamellate layers consist largely of calcium carbonate, either as calcite or aragonite. These two forms of calcium are chemically identical, but they crystallize differently and can be identified by microscopic examination of sections of the shell. Small amounts of other inorganic constituents are incorporated into the calcium carbonate framework, including chemicals such as phosphate, calcium sulfate, magnesium carbonate, and salts of aluminum, iron, copper, strontium, barium, silicon, manganese, iodine, and fluorine.

An intriguing aspect of gastropod evolution is shell loss and the achievement of the "slug" form. Despite the fact that evolution of the coiled shell led to great success for the gastropods—75% of all living molluscs are snails—secondary loss of the shell occurred many times in this class but mostly in various groups of euthyneurans such as the sea slugs and land slugs. In forms such as the land and sea slugs, the shell may persist as a small vestige covered by the dorsal mantle (e.g., in the euthyneuran sea slugs Aplysiidae and Pleurobranchidae and the caenogastropod family Velutinidae), or it may persist as a small external rudiment, as in the carnivorous land slug *Testacella* (Panpulmonata), or it may be lost altogether (e.g., in the nudibranchs, the systellommatophorans and some terrestrial stylommatophoran slugs, and in the neritimorph *Titiscania*). In the nudibranchs the larval shell is first covered, then resorbed, by the mantle during ontogeny. Shell loss occurred numerous times in gastropods, particularly among the sea slugs (the former "opisthobranchs") and stylommatophoran pulmonates. Shells are energetically expensive to produce and require a reliable source of calcium in the environment, so it might be advantageous to eliminate them if compensatory mechanisms exist. For example, most, if not all, sea slugs secrete chemicals that make them distasteful to predators. In addition, the bright coloration of many nudibranchs may serve a defensive function. In some species, the color matches the animal's background, such as in the small red nudibranch, *Rostanga pulchra*, which matches almost perfectly the red sponge on which it feeds. Many nudibranchs are, however, conspicuous in nature. In these cases, the color may serve to warn predators of the noxious taste of the slug, or as suggested by Rudman (1991), predators may simply ignore such bright "novelties" in their environment. Because of their secondary metabolites, many heterobranchs are thus a focus for studies in chemical ecology and drug development.

Torsion, or "How the Gastropod Got its Twist"

One of the most remarkable and dramatic steps taken during the course of molluscan evolution was the advent of torsion, a unique synapomorphy of gastropods, a process quite unlike anything else in the animal kingdom. Traditionally, it is described as the rotation of the visceral mass and shell by as much as 180° with respect to the head and foot. This twisting is always counterclockwise (viewing the animal from above), and this concept has been referred to as the **rotational hypothesis** (Figures 13.18 and 13.53). However, numerous recent studies have called this description into question, and a more complex and accurate picture of torsion is emerging. This alternative hypothesis is called the **asymmetry hypothesis** and was proposed by Louise Page in 2006.

Gastropod torsion is best characterized as a developmental phenomenon and is proceeded by **ano-pedal flexure**—the movement of the telotroch in the trochophore from its posterior position to a ventral position behind the forming foot and blastopore (mouth) (see Figure 13.51). This placement gives rise to the subsequent formation of a U-shaped gut, and this movement is produced by differential cell proliferation during the formation of the dorsal shell gland. The mantle cavity first becomes apparent as an invagination on the right side of the larva behind the foot and through differential growth moves dorsally to lie over the forming head of the snail. This process is not accompanied by shell rotation in the asymmetry hypothesis. Thus, it is this ventral to dorsal movement of the developing viscera and mantle cavity that produces the crossed nerves and rotated gut so characteristic of gastropods that have undergone torsion.

However, like any anatomical feature or developmental process, torsion has been subject to subsequent evolution over the course of gastropod history. The above summary is based primarily on two early groups—the Patellogastropoda and Vetigastropoda. In other taxa, specifics and the sequence of events may differ, including the occurrence of detorsion. For example,

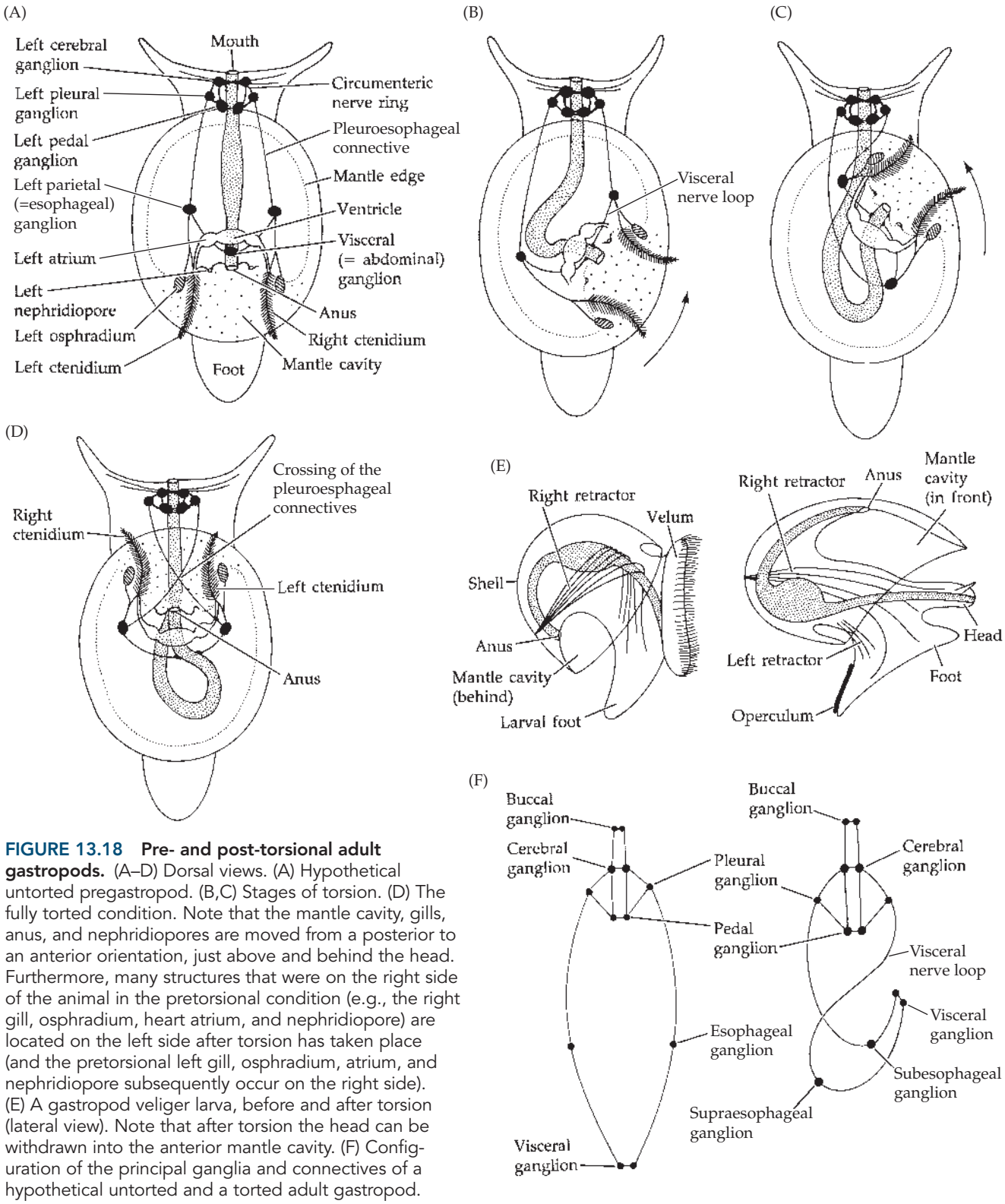

FIGURE 13.18 Pre- and post-torsional adult gastropods. (A–D) Dorsal views. (A) Hypothetical untorted pregastropod. (B,C) Stages of torsion. (D) The fully torted condition. Note that the mantle cavity, gills, anus, and nephridiopores are moved from a posterior to an anterior orientation, just above and behind the head. Furthermore, many structures that were on the right side of the animal in the pretorsional condition (e.g., the right gill, osphradium, heart atrium, and nephridiopore) are located on the left side after torsion has taken place (and the pretorsional left gill, osphradium, atrium, and nephridiopore subsequently occur on the right side). (E) A gastropod veliger larva, before and after torsion (lateral view). Note that after torsion the head can be withdrawn into the anterior mantle cavity. (F) Configuration of the principal ganglia and connectives of a hypothetical untorted and a torted adult gastropod.

the size and position of the early mantle cavity varies in different taxa, and its enlargement and the appearance of mantle cavity components (gills, sense organs, excretory openings) typically occur after the mantle is in its final position—not before, as in the rotational hypothesis. In other taxa, larval shell rotation and viscera rotation are not synchronous but disassociated. In the abalone *Haliotis kamtschatkana,* the shell obtains a full 180° rotation, while the mantle cavity rudiment has rotated only 90°. Additional differential growth expands the mantle cavity into a more central and dorsal position. Similar disassociation of shell and mantle cavity rotation has

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been observed in some Caenogastropoda and Heterobranchia. In the heterobranch *Ovatella* the mantle cavity does not even invaginate until torsion is completed.

Gastropods that retain torsion into adulthood are said to be **torted**; those that have secondarily reverted back to a partially or fully untorted state in adulthood are **detorted**. The torted, figure-eight configuration of the nervous system is referred to as **streptoneury**. The detorted condition, in which the visceral nerves are secondarily untwisted, is referred to as **euthyneury**. Detorted gastropods, such as many heterobranchs, undergo a postveliger series of changes through which the original torsion is reversed to various degrees. The process shifts the mantle cavity and at least some of the associated organs about 90° back to the right (as in many "pulmonates" and some sea slugs), or in some cases all the way back to the rear of the animal (the detorsion seen in some nudibranchs). Like torsion, detorsion is not a single developmental event, but rather an adult character suite achieved through a variety of different developmental pathways and, often, further dissociation of the components of the mantle cavity.

After torsion the anus lies in front; this means that the first gastropods could no longer grow in length easily. Subsequent increase in body size thus occurred by the development of loops or bulges in the middle portion of the gut region, thereby producing the characteristic coiled visceral hump. The first signs of torsion and coiling occur at about the same time during gastropod development. The earliest coiled gastropod shells in the fossil record include both planispiral and conispiral forms, and it is possible that coiling predated the appearance of torsion in gastropods. Once both features were established, they coevolved in various ways to produce what we see today in living gastropods.

The evolution of asymmetrically coiled shells had the effect of restricting the right side of the mantle cavity, a restriction that led to reduction or loss of the structures it contained on the adult right side (the original pre-torsional left ctenidium, atrium, and osphradium). At the same time, these structures on the adult left side (the original pre-torsional right ctenidium, atrium, and osphradium) tended to enlarge. Possibly correlated with torsion and coiling was the loss of the left post-torsional gonad. The single remaining gonad opens on the right side via the post-torsional right nephridial duct and nephridiopore. Patellogastropods and most vetigastropods retain two functional nephridia, the plesiomorphic condition in gastropods, although the post-torsional left one is often reduced. In other gastropods the post-torsional right nephridium is lost, but its duct and pore remain associated with the reproductive tract in neritimorphs and caenogastropods. Such profound changes in spatial relations between major body regions as those brought about by torsion and spiral coiling in gastropods are rare among other animals.

Several theories on the adaptive significance of torsion have been proposed and are still being argued. The great zoologist Walter Garstang suggested that torsion was an adaptation of the veliger larva that served to protect the soft head and larval ciliated velum from predators (see the Development section). When disturbed, the immediate reaction of a veliger is to withdraw the head and foot into the larval shell, whereupon the larva begins to sink rapidly. This theory may seem reasonable for evasion of very small planktonic predators, but it seems illogical as a means of escape from larger predators in the sea, which no doubt consume veligers whole—and any adaptive value to adults is not explained. Two zoologists finally tested Garstang's theory by offering torted and untorted abalone veligers to various planktonic predators; they found that, in general, torted veligers were not consumed any less frequently than untorted ones (Pennington and Chia 1985).

Other workers have hypothesized that torsion was an adult adaptation that might have created more space for retraction of the head into the shell (perhaps also for protection from predators) or for directing the mantle cavity with its gills and water-sensing osphradia anteriorly. Still another theory asserts that torsion evolved in concert with the evolution of a coiled shell—as a mechanism to align the tall spiraling shells from a position in which they stuck out to one side (and were presumably poorly balanced and growth limiting) to a position more in alignment with the longitudinal (head–foot) axis of the body. The latter position would theoretically allow for greater growth and elongation of the shell while reducing the tendency of the animal to topple over sideways.

No matter what the evolutionary forces were that led to torsion in the earliest gastropods, the results were to move the adult anus, nephridiopores, and gonopores to a more anterior position, corresponding to the new position of the mantle cavity. It should be noted, however, that the actual position and arrangement of the mantle cavity and its associated structures show great variation; in many gastropods these structures, while pointing forward, may actually be positioned farther toward the posterior region of the animal's body. Torsion is not a perfectly symmetrical process.

Most of the stories of gastropod evolution focus on changes in the mantle cavity and its associated structures, and many of these changes seem to have been driven by some negative impacts of torsion. Many anatomical modifications of gastropods appear to be adaptations to avoid fouling, for without a change in the original flow of water through the mantle cavity in a primitive gastropod with two ctenidia, waste from the centrally positioned anus (and perhaps the nephridia) would be dumped on top of the head and potentially pollute the mouth and ctenidia. Hence, it has long been hypothesized that the first

step, subsequent to the evolution of torsion, was the development of slits or holes in the shell, thus altering water flow so that a one-way current passed first over the ctenidia, then over the anus and nephridiopore, and finally out the slit or shell holes. This arrangement is seen in some vetigastropods, such as the slit shells (Pleurotomarioidea) and abalone and keyhole limpets (Figures 13.1D, 13.16I, and 13.36). As reasonable as it sounds, there has been surprisingly little empirical evidence in support of this hypothesis. In addition, the adaptive significance of shell holes was examined by Voltzow and Collin (1995), who found that blocking the holes in keyhole limpets did not result in damage to the organs of the mantle cavity. Thus, the adaptive significance of torsion in gastropod evolution remains an open question.

Once evolutionary reduction or loss of the gill and osphradium on the right side had taken place, water flow through the mantle cavity was from left to right, passing through the left gill and osphradium first, then across the nephridiopore and anus, and on out the right side. This strategy also had the effect of allowing structures on the left side to enlarge and eventually to develop more control over water flow into and out of the mantle cavity, including the evolution of long siphons. While most gastropods have retained full or partial torsion, many heterobranchs, all of which lost the original ctenidium, have undergone various degrees of detorsion, and a host of other modifications, perhaps in response to the absence of constraints originally brought on by torsion.

Locomotion

The foot in aplacophorans is either rudimentary or lost (Figure 13.2). Caudofoveata are mostly infaunal burrowers and move by peristaltic movements of the body wall, using the anterior mouth shield as a burrowing device and anchor. The foot of solenogasters is only weakly muscular, and locomotion is primarily by slow ciliary gliding movements through or upon the substratum, as they are largely symbiotic on various cnidarians. Most other molluscs possess a distinct and obvious foot, with the exception of the cephalopods, where it is very highly modified. In chitons, monoplacophorans, and most gastropods, the foot often forms a flat, ventral, creeping sole (Figures 13.3B, 13.4B, 13.5B, and 13.19). The sole is ciliated and imbued with numerous gland cells that produce a mucous trail over which the animal glides. In gastropods, enlarged pedal glands supply substantial amounts of mucus (slime), this being especially important in terrestrial species that must glide on relatively dry surfaces. In most gastropods, there are anterior mucous glands, which open in a slit on or just behind the anterior edge of the foot. This anterior lobe is called the **propodium**, the rest of the foot the **metapodium**. In some caenogastropods, an enlarged metapodial mucous gland opens into the middle of the sole. Small molluscs may move largely by ciliary propulsion, but most move primarily by waves of muscular contractions along the foot.

The gastropod foot possesses pedal retractor muscles, which attach to the shell. These and smaller muscles in the foot act in concert to raise and lower the sole or to shorten it in either a longitudinal or a transverse direction. Contraction waves may move from back to front (direct waves), or from front to back (retrograde waves) (Figure 13.19A,B). Direct waves depend on contraction of longitudinal and dorsoventral muscles beginning at the posterior end of the foot; successive sections of the foot are thus "pushed" forward. Retrograde waves involve contraction of transverse muscles interacting with hemocoelic pressure to extend the anterior part of the foot forward, followed by contraction of longitudinal muscles. The result is that successive areas of the foot are "pulled" forward (Figure 13.19A,B). In some gastropods the muscles of the foot are separated by a midventral line, so the two sides of the sole operate somewhat independently of each other. The right and left sides of the foot alternate in their forward motion, almost in a stepping fashion, resulting in a sort of "bipedal" locomotion.

Modifications of this general benthic locomotory scheme occur in many groups. Some gastropods, such as moon snails (Figure 13.19D), plow through the sediment, and some even burrow beneath the sediment surface. Such gastropods often possess an enlarged, shieldlike propodium that acts like a plough, and some naticids and cephalaspideans possess a dorsal flaplike fold of the foot that covers the head as a protective shield. Other burrowers, such as augers, dig by thrusting the foot into the substratum, anchoring it by engorgement with hemolymph, and then pulling the body forward by contraction of longitudinal muscles. In the conch *Stombus*, the operculum forms a large "claw" that digs into the substratum and is used as a pivot point as the animal thrusts itself forward using its muscular, highly modified foot. In some heterobranchs, notably the sea hares (Aplysiidae), lateral flaps of the foot expand dorsally as parapodia, and these are fused dorsally in some species.

Some molluscs that inhabit high-energy littoral habitats, such as chitons and limpets, have a very broad foot that can adhere tightly to hard substrata. Chitons also use their broad girdle for additional adhesion to the substratum by clamping down tightly and raising the inner margin to create a slight vacuum. Some snails, such as the Vermetidae and Siliquariidae, are entirely sessile, the former attached to hard substrata, the latter (Figure 13.19E) living in sponges. These gastropods have typical larval and juvenile shells; but after they settle and start to grow, the shell whorls become increasingly separated from

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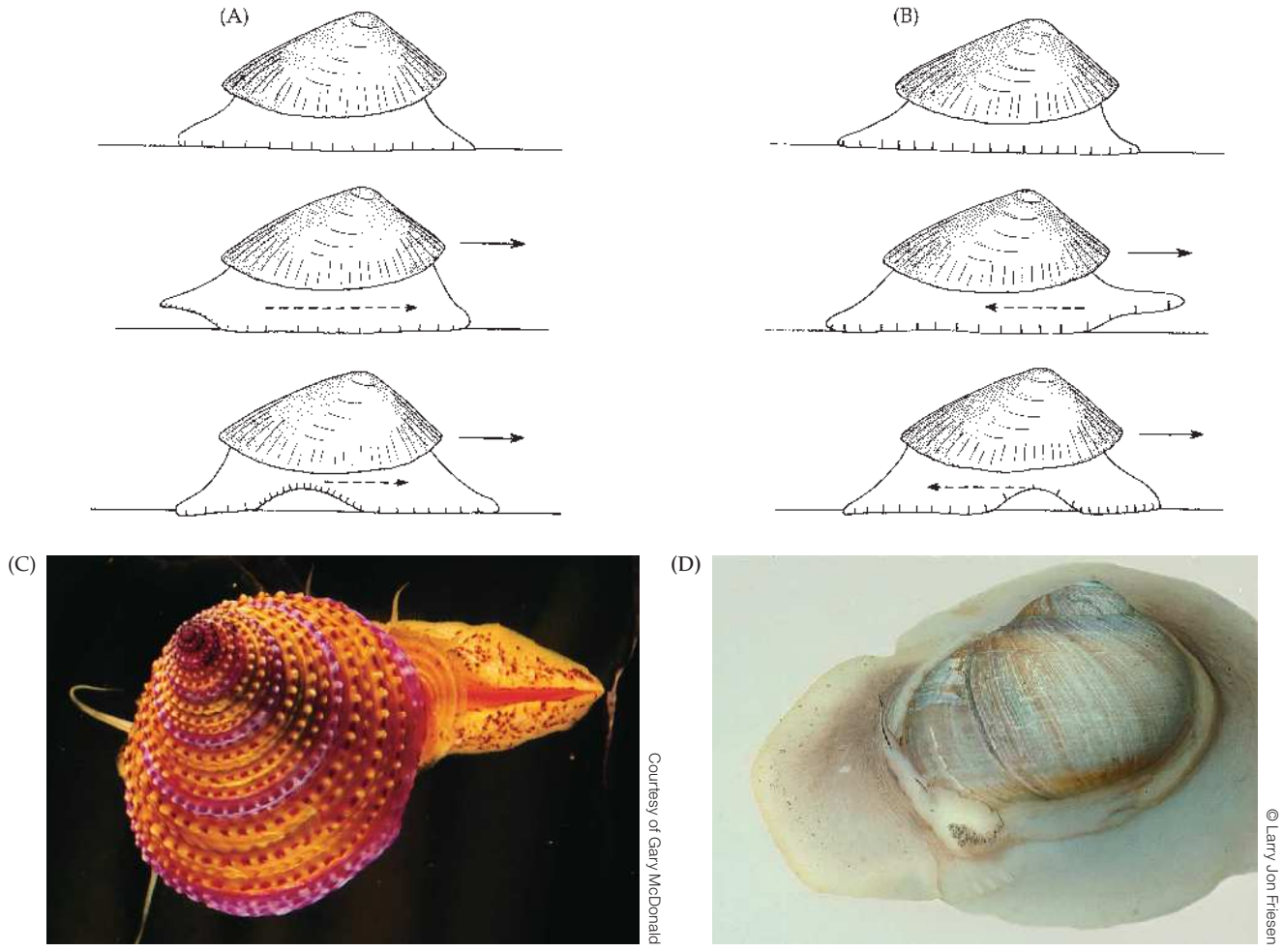

FIGURE 13.19 Locomotion in gastropods. (A,B) Locomotion in a benthic gastropod moving to the right by waves of contraction of the pedal and foot muscles (solid arrow indicates direction of animal movement; dashed arrow indicates direction of muscle wave). In (A) the waves of contraction are moving in the same direction as the animal, from back to front (direct waves). Muscles at the rear of the animal contract to lift the foot off the substratum; the foot shortens in the contracted region and then elongates as it is placed back down on the substratum after the wave passes. In this way, successive sections of the foot are "pushed" forward. In (B) the animal moves forward as the contraction waves pass in the opposite direction, from front to back (retrograde waves). In this case, the pedal muscles lift the anterior part of the foot off the substratum, and the foot elongates, is placed back on the substratum, then contracts to "pull" the animal forward, rather like "stepping." (C) *Calliostoma*, a vetigastropod (Calliostomatidae) adapted to crawling on hard substrata. Note the line separating the right and left sides of the trailing foot; the line denotes a separation of muscle masses that allows a somewhat "bipedal-like" motion as the animal moves (see text for further details). (D) The moon snail, *Polinices* (Naticidae), has a huge foot that can be inflated by incorporating water into a network of channels in its tissue, thus allowing the animal to plow through the surface layer of soft sediments. (E) *Tenagodus* (Siliquariidae), a sessile siliquariid worm snail.

one another, resulting in a corkscrew or twisted shape. Other gastropods, such as slipper shells, are sedentary. They tend to remain in one location and feed on organic particles in the surrounding water. The sole of the hipponicid limpets secretes a calcareous plate, and the adults are thus oysterlike and deposit feed by using their long snout.

Some limpets and a few chitons exhibit homing behaviors. These activities are usually associated with feeding excursions stimulated by changing tide levels or darkness, after which the animals return to their homesites, which are seen as a scar or even a depression on the rock surface. Homing behaviors are also seen in some land snails and slugs.

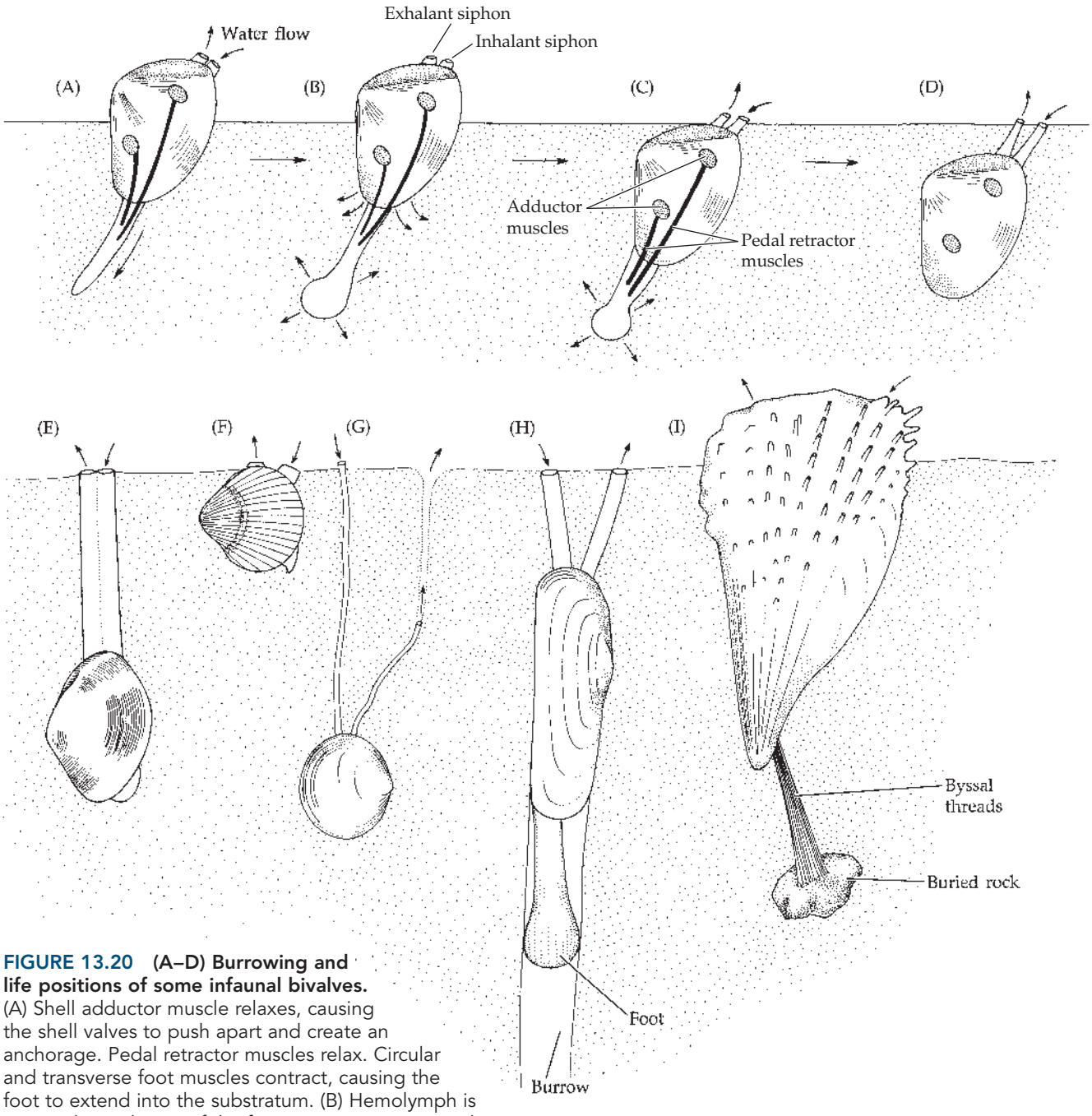

FIGURE 13.20 (A–D) Burrowing and life positions of some infaunal bivalves. (A) Shell adductor muscle relaxes, causing the shell valves to push apart and create an anchorage. Pedal retractor muscles relax. Circular and transverse foot muscles contract, causing the foot to extend into the substratum. (B) Hemolymph is pumped into the tip of the foot, causing it to expand and form an anchorage. Siphons close and withdraw as the shell adductor muscles contract, closing the shell and forcing water out between the valves and around the foot. (C) Anterior and posterior pedal retractor muscles contract, pulling the clam deeper into the substratum. (D) The shell adductor muscle relaxes to allow shell valves to push apart and create an anchorage in the new position. The foot is withdrawn. (E–I) Five bivalves in soft sediments; arrows indicate direction of water flow. (E) A deep burrower with long, fused siphons (*Tresus*). (F) A shallow burrower with very short siphons (*Clinocardium*). (G) A deep burrower with long, separate siphons (*Scrobicularia*). (H) The razor clam (*Tagelus*) lives in unstable sands and maintains a burrow into which it can rapidly escape. (I) The pen shell (*Atrina*) attaches its byssal threads to solid objects buried in soft sediments.

Most bivalves live in soft benthic habitats, where they burrow to various depths in the substratum (Figure 13.20E–I). In these infaunal species the foot is usually bladelike and laterally compressed (the word "Pelecypoda" means "hatchet foot"), as is the body in general, but the foot of protobranchs has a flattend surface or sole. The pedal retractor muscles in bivalves are somewhat different from those of gastropods, but they still run from the foot to the shell (Figure 13.8D). The foot is directed anteriorly and used primarily in burrowing and anchoring. It operates through a combination of muscle action and hydraulic pressure (Figure 13.20A–D). Extension of the foot is accomplished by engorgement with hemolymph, coupled with the action of the pedal protractor muscles. With the foot extended, the valves are

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pulled together by the shell adductor muscles. More hemolymph is forced from the visceral mass hemocoel into the foot hemocoel, causing the foot to expand and anchor in the substratum. Once the foot is anchored, the anterior and posterior pairs of pedal retractor muscles contract and pull the shell downward. Withdrawal of the foot into the shell is accomplished by contraction of the pedal retractors coupled with relaxation of the shell adductor muscles. Many infaunal bivalves burrow upward in this same manner, but others back out by using hydraulic pressure to push against the anchored end of the foot. Most motile bivalves possess well-developed anterior and posterior adductor muscles (the **dimyarian** condition).

There are several groups of bivalves that have epifaunal lifestyles and are permanently attached to the substratum. They do this either by cementing one valve to a hard surface, as in the true oysters such as the rock oysters (Ostreidae) and rock scallops (Spondylidae), or by using special anchoring threads (**byssal threads**), as in marine mussels (Mytilidae) (Figure 13.21A,B), ark shells, winged or pearl oysters (Pteriidae), and numerous other pteriomorphian bivalves, including the Pinnidae and many Pectinidae. While the juveniles of many heterodont bivalves produce one or a few temporary

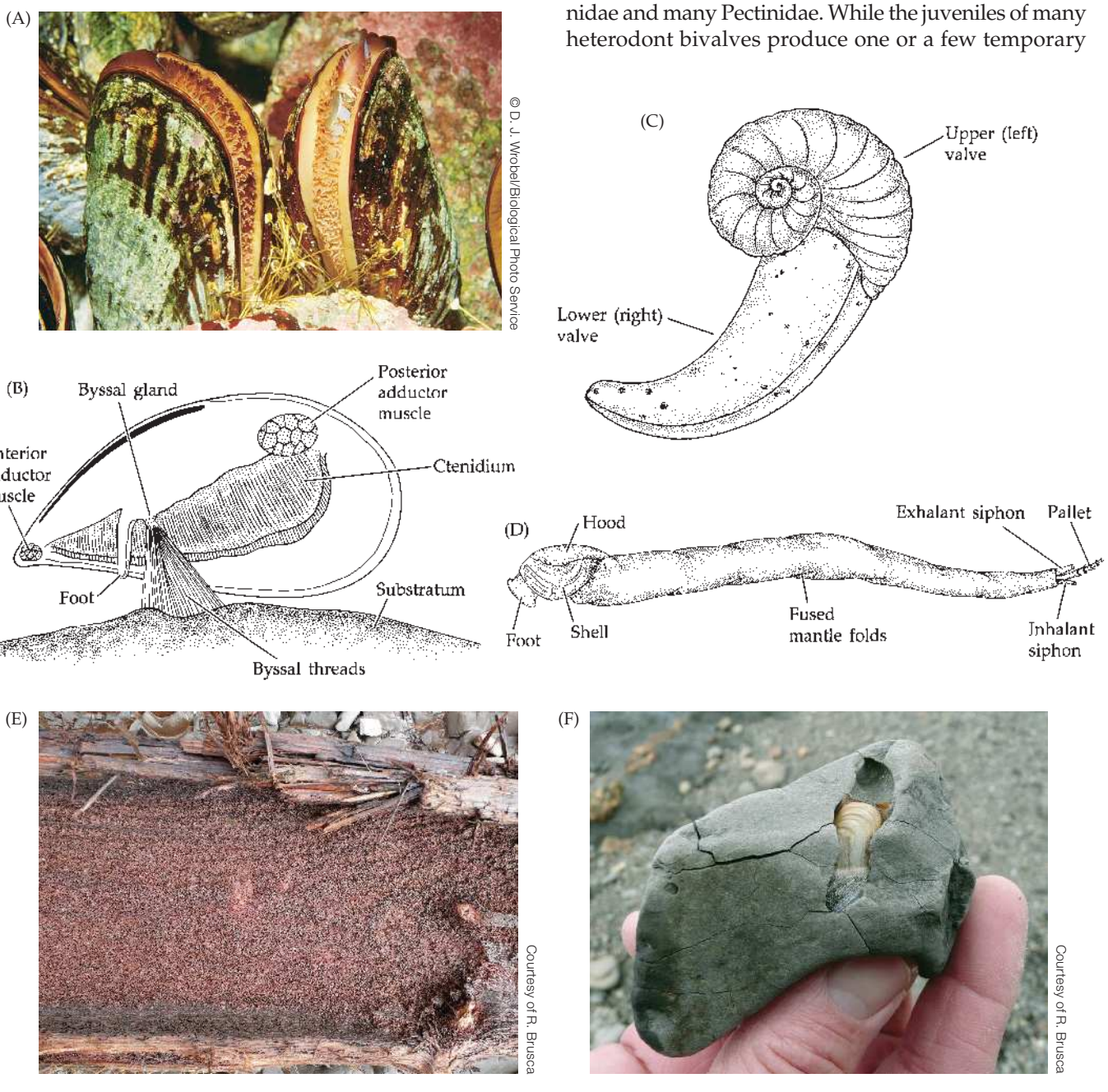

FIGURE 13.21 More bivalves. (A) A "bed" of mussels (*Mytilus californianus*) attached by byssal threads (close up of two mussels). (B) A mussel (lateral view, with left valve removed). (C) Shell of the Mesozoic rudist clam *Coralliochama*. (D) The wood-boring bivalve (shipworm) *Teredo*. The pallets (only one is shown) are a pair of shelly plates that close over the siphons when they are retracted. (E) A shipworm-bored piece of driftwood (notice the numerous small holes). (F) A pholad-bored rock. The pholad can be seen in its bore hole.

byssal threads, a few species, such as the zebra mussel (*Dreissena*), remain byssally attached as adults.

The true oysters (Ostreidae), including the edible oysters, initially anchor as a settling veliger larva (called a **spat** by oyster farmers) by secreting a drop of adhesive from the byssus gland. Adults, however, have one valve permanently cemented to the substratum, with the cement being produced by the mantle.

Byssal threads are secreted as a liquid by the **byssus gland** in the foot. The liquid flows along a groove in the foot to the substratum, where each thread becomes tightly affixed. The threads are placed by the foot; once attached, they quickly harden by a tanning process, whereupon the foot is withdrawn. A byssal thread retractor muscle may assist the animal in pulling against its anchorage. Mussels have a small, fingerlike foot whose principal function is generation and placement of the byssal threads. Giant clams (Cardiidae, Tridacninae) initially attach by byssal threads but usually lose these as they mature and become heavy enough not to be cast about by currents (Figure 13.1N). In jingle shells (Anomiidae), the byssal threads run from the upper valve through a hole in the lower valve to attach to the substratum, after which they become secondarily calcified. Byssal threads probably represent a primitive and persisting larval feature in those groups that retain them into adulthood, and many bivalves lacking byssal threads as adults utilize them for initial attachment during settlement.

In many families of attached bivalves, such as mussels and true oysters, the foot and anterior end are reduced. This often leads to a reduction of the anterior adductor muscle (**anisomyarian condition**) or its complete loss (**monomyarian condition**).

Great variation occurs in shell shape and size among attached bivalves. Some of the most remarkable were the Mesozoic rudists, in which the lower valve was hornlike and often curved, and the upper valve formed a much smaller hemispherical or curved lid (Figure 13.21C). Rudists were large, heavy creatures that often formed massive reeflike aggregations, either by somehow attaching to the substratum or by simply accumulating in large numbers on the seabed, in "logjams." These accumulations of fossil shells provide the spaces in which oil deposits formed in sediments in many parts of the Middle East, Gulf of Mexico, and Caribbean.

Some bivalves have evolved to live openly on the seafloor (e.g., some Pectinidae and Limidae) (Figure 13.1M). Some are capable of short bursts of "jet-propelled" swimming, which is accomplished by quickly clapping the valves together.

The habit of boring into hard substrata has evolved in several different bivalve lines. In all cases, excavation begins soon after larval settlement. As the animal bores deeper, it grows in size and soon becomes permanently trapped, with only the siphons protruding out of the original small opening. Boring is usually by a mechanical process; the animal uses serrations on the anterior region of the shells to abrade or scrape away the substratum. Some species also secrete an acidic mucus that partially dissolves or weakens hard calcareous substrata (limestone, coral, large dead shells). Some species bore into wood, such as *Martesia* (Pholadidae), *Xylophaga* (Xylophagaidae), and nearly all species in the family Teredinidae (*Bankia*, *Teredo*). Teredinids, with their long wormlike bodies, are known as shipworms because of the destruction that they can cause to the wooden hulls of ships (and wood pier pilings). In the teredinids the shells are reduced to small anterior bulblike valves that serve as the drilling apparatus (Figure 13.21D,E) and also have siphonal calcareous structures called pallets. Some pholadids bore into soft rock (e.g., *Pholas*; Figure 13.21F) or into other substrata (e.g., *Barnea*). Some species in the family Mytilidae are also borers, such as *Lithophaga* (which bores by mechanical and possibly chemical means into calcareous rocks, shells of various other molluscs including chitons, and corals), the genus *Adula* (which bores into soft rocks), and *Idas* (associated with whale falls).

Scaphopods are adapted to infaunal habitats, burrowing vertically by the same basic mechanism used by many bivalves (Figures 13.1L and 13.9). The elongate foot is projected downward into soft substrata, whereupon a rim in the distal part of the foot is expanded to serve as an anchoring device; contraction of the pedal retractor muscles pulls the animal downward.

Perhaps the most remarkable locomotory adaptation of molluscs is swimming, which has evolved in several different taxa in several different ways, including by valve flapping in scallops (Pectinidae) and some Limidae (e.g., flame scallops). In most other swimming molluscs the foot is modified as the swimming structure. In the unique caenogastropod group known as heteropods, the body is laterally compressed, the shell is greatly reduced, the foot forms a fin, and the animal swims upside down (Figure 13.7A–C). Swimming has evolved several times in the heterobranchs, including the pteropods (sea butterflies), where the parapodial extensions of the foot form two long lateral fins that are used like oars (Figure 13.7D,E). Some nudibranchs also swim by graceful undulations of flaplike parapodial folds along the body margin or by vigorous undulations of the body. Although not actually swimming, violet shells (*Janthina*) float about the ocean's surface on a raft of bubbles secreted by the foot, and some planktonic nudibranchs (e.g., *Glaucus*, *Glaucilla*) stay afloat by use of an air bubble held in the stomach!

The champion swimmers are, of course, the cephalopods (Figures 13.1J,K and 13.22). These animals have abandoned the generally sedentary habits of other molluscs and have become highly effective swimming predators. Virtually all aspects of their biology have evolved to exploit this lifestyle. Most cephalopods swim by rapidly expelling water from the mantle cavity. In

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FIGURE 13.22 Swimming cephalopods. (A) *Sepia*, the cuttlefish. (B) *Nautilus*. (C) *Grimpoteuthis*, a pelagic "dumbo octopus."

the coleoid cephalopods the mantle has both radial and circular muscle layers. Contraction of the radial muscles and relaxation of the circular muscles draws water into the mantle cavity, while reversal of this muscular action forces water out of the mantle cavity. The mantle edge is clamped tightly around the head to channel the escaping water through a ventral tubular **funnel**, or **siphon** (Figure 13.11B,C). The funnel is highly mobile and can be manipulated to point in nearly any direction, thus allowing the animal to turn and steer. Squid attain the greatest swimming speeds of any aquatic invertebrates, and several species can even leave the water and propel themselves many feet into the air. Most octopuses are benthic and lack the fins and streamlined bodies characteristic of squid. Although octopuses still use water-powered jet propulsion, they more commonly rely on their long suckered arms for crawling about the seafloor. Some octopuses even move about upright on only two tentacles—bipedal locomotion! Cuttlefish are slower than squid, and they often use their fins for forward swimming as well as stabilization and to assist in steering and propulsion.

Nautilus move up and down in the water column on a diel cycle, often traveling hundreds of meters in each direction. They can actively regulate their buoyancy by secretion and reabsorption of shell chamber fluid and gases (chiefly nitrogen) by the cells of the siphuncle. The unoccupied chambers of these shells are filled partly with gas and partly with a liquid called the **cameral fluid**. The septa act as braces, giving the shells strength to withstand external pressure at depth. As discussed earlier, each septum in nautiloid shells is perforated by a small hole, through which runs the siphuncle, which originates in the viscera and is enclosed in a porous calcareous tube. Various ions dissolved in the cameral fluid can be pumped through the porous outer layers into the cells of the siphuncular epithelium. When the cellular concentration of ions is high enough, the diffusion gradient thus created draws fluid from the shell chambers into the cells of the siphuncle while the fluid is replaced with gas. The result is an increase in buoyancy. By regulating this process, *Nautilus* may be able to remain neutrally buoyant at whatever depth they are. It was once thought that this gas-fluid "pump" mechanism allowed buoyancy changes sufficient to explain all the large-scale vertical movements of *Nautilus*, but density changes may not be the sole source of power for moving great distances up and down in the water column. *Nautilus* can move using jet propulsion by forcefully contracting its head, not by mantle muscle contraction, and move slowly by passing water out of the funnel by the action of funnel flaps.

Feeding

Two basic and fundamentally different types of feeding occur among molluscs: the first encompasses the feeding modes of most molluscs and includes micro- to macrophagy involving browsing and scraping, herbivory, carnivorous grazing, and predation, while the second is suspension feeding (suspension microphagy). The basic mechanics of these two feeding modes are examined in Chapter 3. Here we briefly summarize the ways in which these feeding behaviors are employed by molluscs. In this section we also discuss a uniquely molluscan structure, the radula, which is used in microphagy, herbivory, and predation and has

become modified in a variety of unusual and interesting ways. A few molluscs also supplement their diet with photosynthesis and chemosynthesis thanks to an array of symbionts.

The buccal cavity may contain a pair of lateral jaws (or a single dorsal jaw), muscularized regions with chitinous plates that can be solid or composed of multiple small units. Molluscan jaws are highly variable. For example, in some heterobranchs the jaws can be quite complex, with distinct "teeth." In some carnivorous caenogastropods the jaws can be large. In cephalopods the jaws are modified to form the beak, which has upper and lower elements. Some molluscs, including chitons and bivalves, have no jaws at all.

The radula is tipically a ribbon of recurved chitinous teeth (Figures 13.23, 13.24, 13.25, and 13.26). The teeth may be simple, serrate, pectinate, or otherwise modified. The radula often functions as a scraper to remove food particles for ingestion, although in many groups it has become adapted for other actions. A radula is present in the majority of living molluscan classes, though it is absent in all bivalves, and is assumed to have originated in the earliest stages of molluscan evolution. In the aplacophoran groups the teeth, when present, may be borne not on a ribbon per se but on a relatively thin cuticle covering the foregut epithelium—presumably a homologue of the ribbonlike radula. In some aplacophorans, the teeth form simple plates embedded in either side of the lateral foregut wall, while in others they form a transverse row, or up to 50 rows, with as many as 24 teeth per row.

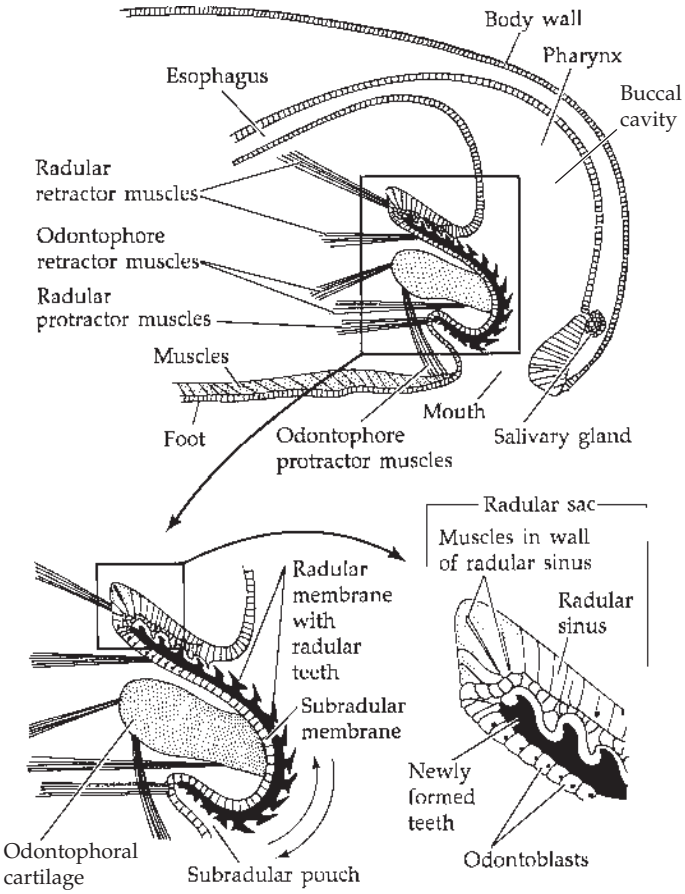

FIGURE 13.23 A generalized molluscan radula and associated buccal structures, at three "magnifications" (longitudinal section).

In gastropods and other molluscs (except bivalves) an **odontophore** projects from the floor of the buccal cavity (sometimes called the pharynx). It is a muscular structure bearing the complex tooth-bearing radular ribbon (Figure 13.23). The ribbon, called a **radular membrane**, is moved back and forth by sets of radular protractor and retractor muscles over cartilages encased in the odontophore (Figure 13.23). These cartilages are absent in many heterobranch gastropods. The radula originates in a **radular sac**, in which the radular membrane and new teeth are continually being produced by special cells called **odontoblasts**, to replace those lost by erosion during feeding. Measurements of radular growth indicate that up to five rows of new teeth may be added daily in some species. The odontophore itself is moved in and out of the buccal cavity during feeding by sets of odontophore protractor and retractor muscles, which also assist in applying the radula firmly against the substratum (Figure 13.24A).

The number of radular teeth ranges from a few to thousands and serves as an important taxonomic character in many groups. In some molluscs, the radular teeth are hardened with iron compounds, such as magnetite (in chitons) and goethite (in patellogastropods). Just as in many vertebrates, the radular teeth show adaptations to the type of food eaten. In vetigastropods (e.g., keyhole limpets, abalones, top shells), the **rhipidoglossate radulae** bear large numbers of fine marginal teeth in each row (Figures 13.25A and 13.26A). As the radula is pulled over the bending plane of the odontophore, these teeth act like stiff brushes, sweeping small particles to the midline, where they are caught on the recurved parts of the central teeth, which draw the particles into the buccal cavity. Most vetigastropods are intertidal foragers that live on diatoms and other algae and microbes on the substratum. In contrast, patellogastropods (e.g., lottiid and patellid limpets) possess a **docoglossate radula**, which is impregnated with iron and bears relatively few teeth in each transverse row. Lottiid radulae, for example, have only one, two, or no marginal teeth, and only three pairs of lateral teeth per row (Figure 13.26B). The lottiid radula is capable of powerful rasping and often leaves grooves on the substrate. Some homing species leave mucous trails that serve as adhesive traps for spores and diatoms and may enhance the densities of algae, thereby increasing their primary food resources.

The radula of many caenogastropods is the **taenioglossate type**, in which there are only two marginal

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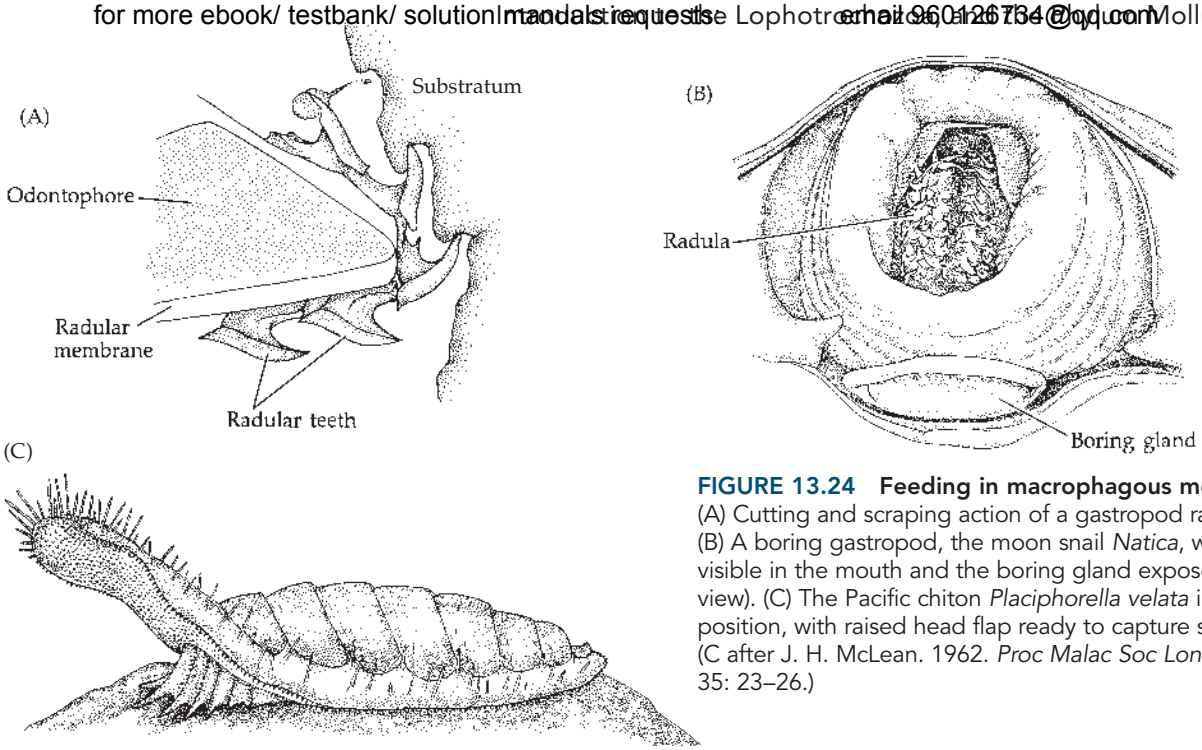

FIGURE 13.24 Feeding in macrophagous molluscs. (A) Cutting and scraping action of a gastropod radula. (B) A boring gastropod, the moon snail *Natica*, with radula visible in the mouth and the boring gland exposed (oral view). (C) The Pacific chiton *Placiphorella velata* in feeding position, with raised head flap ready to capture small prey. (C after J. H. McLean. 1962. *Proc Malac Soc London* 35: 23–26.)

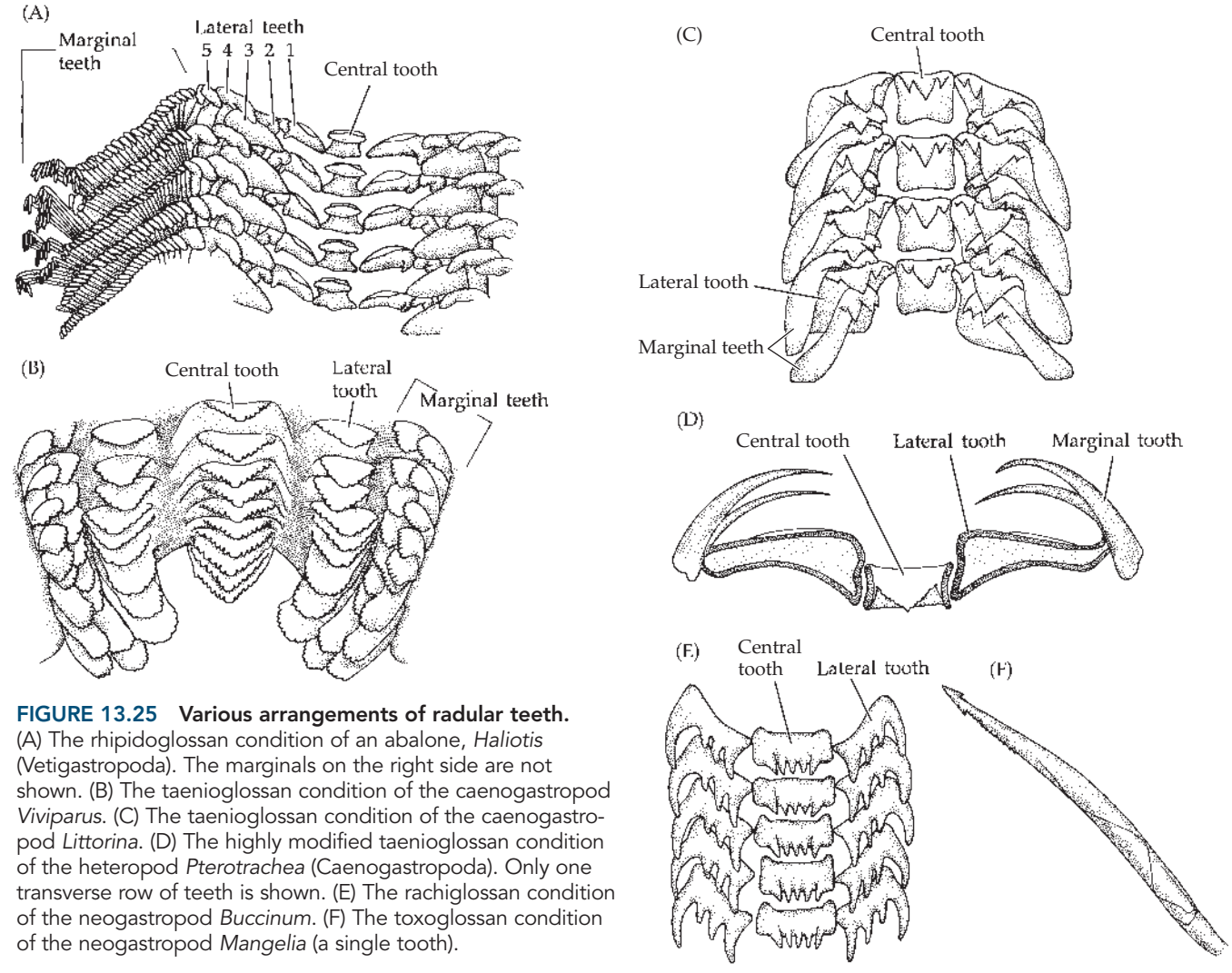

FIGURE 13.25 Various arrangements of radular teeth. (A) The rhipidoglossan condition of an abalone, *Haliotis* (Vetigastropoda). The marginals on the right side are not shown. (B) The taenioglossan condition of the caenogastropod *Viviparus*. (C) The taenioglossan condition of the caenogastropod *Littorina*. (D) The highly modified taenioglossan condition of the heteropod *Pterotrachea* (Caenogastropoda). Only one transverse row of teeth is shown. (E) The rachiglossan condition of the neogastropod *Buccinum*. (F) The toxoglossan condition of the neogastropod *Mangelia* (a single tooth).

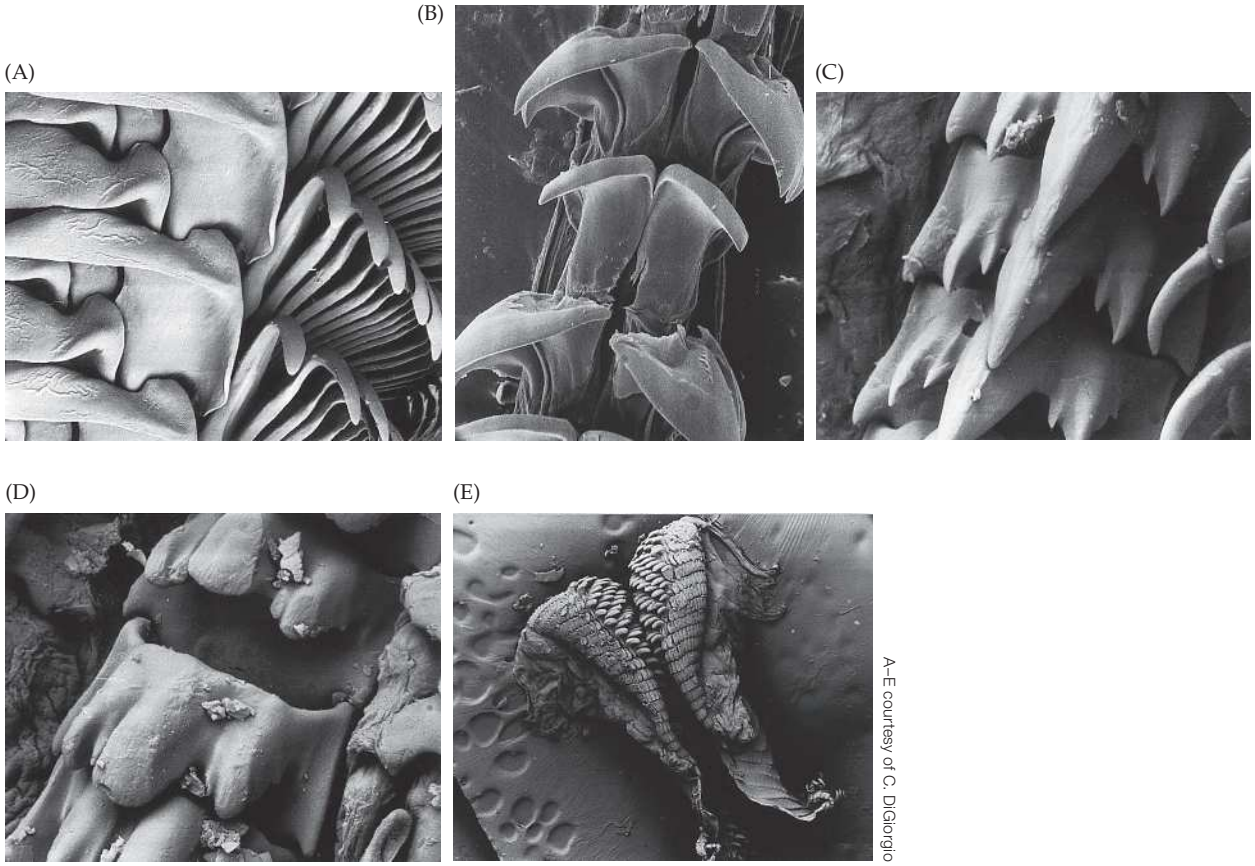

FIGURE 13.26 Gastropod radulae. (A) A closeup view of part of the rhipidoglossate radula of the abalone *Haliotis rufescens* (Vetigastropoda). Note the many hooklike marginal teeth. (B) The docoglossate radula of a lottiid limpet. (C) The serrated central teeth of a rachiglossate radula from the muricid whelk *Nucella emarginata*, a neogastropod (Caenogastropoda) that preys on small mussels and barnacles. (D) The worn radular teeth of *Nucella*. (E) The radula of the polycerid nudibranch *Triopha*, seen here in dorsal view as it rests in the animal.

teeth in each row, along with three other teeth (laterals and central) (Figure 13.25B–D). In conjunction with the elaboration of jaws, taenioglossate radulae are capable of powerful rasping, which enables some littorinid snails to feed by directly scraping off the surface cell layers of algae.

The most derived caenogastropods (Neogastropoda) usually have **rachiglossate radulae**, which lack marginal teeth altogether (Figures 13.25E and 13.26C,D). They use the remaining (one to three) teeth for rasping, tearing, or pulling. These snails are usually carnivores or carrion feeders, although some members of one family, the Columbellidae, are herbivores. Caenogastropods of the families Muricidae and Naticidae eat other molluscs by boring through the prey's calcareous shell to obtain the underlying flesh. This ability to bore has evolved entirely independently in the two groups. It is mainly mechanical, the predator boring with its radula while holding the prey with the foot. The boring activity is complemented by the secretion of an acidic chemical from a **boring gland** (also called the "accessory boring organ"); the chemical is periodically applied to the drill hole to weaken the calcareous matrix. The boring gland of the neogastropod muricids is located on the foot while that of the naticids is located on the anterior end of the proboscis (Figure 13.24B). Boring gastropods such as the Atlantic oyster drill (*Urosalpinx cinerea*) and the veined whelk (*Rapana venosa*) cause losses of millions of dollars annually for oyster farms.

Some carnivorous gastropods (e.g., *Janthina*) do not gnaw or rasp their prey, but swallow it whole. In these gastropods a **ptenoglossate radula** forms a covering of strongly curved spines over the buccal mass. The prey is seized by the quickly extruded buccal mass and simply pulled whole into the gut. A somewhat similar feeding method is seen in the carnivorous slug *Testacella*, where the hooked radula catches earthworms that the slug consumes whole. The nudibranch *Melibe* (Tethydidae) uses its large hood to sweep the water for copepods, amphipods, and other small planktonic prey.

A few gastropods have lost the radula altogether and feed by sucking body fluids from their prey, a habit seen, for example, in some nudibranchs. Pyramidellids do this with the aid of a hypodermic stylet (a modified jaw) on the tip of an elongate proboscis.

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One of the most specialized feeding modes in gastropods is seen in the cone snails (*Conus*) and their relatives (Neogastropoda). Their **toxoglossate radula** is formed from a few harpoonlike, venom-injecting teeth that are modified marginal teeth. The teeth (Figure 13.25F) are discharged from the end of a long proboscis that can be extended very rapidly to capture prey, usually a fish, a worm, or another gastropod, which is then pulled into the gut (Figure 13.27). The venom is injected through the hollow, curved radular teeth by contraction of a venom gland. A few Indo–West Pacific cones produce a potent neuromuscular toxin that has caused human deaths.

Among the most unusual gastropod feeding strategies are those that involve parasitism on fishes. For example, the neogastropod *Cancellaria cooperi* attaches to the Pacific electric ray and makes small cuts in the skin, through which the proboscis is inserted to feed on the ray's blood and cellular fluids. Several other neogastropods parasitize "sleeping" reef fishes by inserting their proboscides into the hosts and sucking out fluids, while the nudibranch *Gymnodoris nigricolor* (Polyceridae) attaches to the fins of gobiids on which it feeds. Some other gastropods are known to parasitize various invertebrate hosts, notably the Pyramidellidae on a variety of invertebrates (including other molluscs), and the Eulimidae on echinoderms; the Eulimidae include some internal parasites that have lost their shells and become wormlike.

Certain euthyneurans also show various radular modifications. Groups of "opisthobranchs" that feed on cnidarians, bryozoans, and sponges, as well as those that scrape algae (e.g., aplysiids), usually have typical rasping radulae. In sacoglossans, however, the radula is modified as a single row of lancelike teeth that can pierce the cellulose wall of filamentous algae, allowing the gastropod to suck out the cell contents. A similar type of feeding strategy is also seen in the microscopic lower heterobranch *Omalogyra*.

Aeolid nudibranchs (Figure 13.7G) have a well-deserved reputation for their particular mode of feeding, in which portions of their cnidarian prey are held by the jaws while the radula rasps off pieces for ingestion. A similar mode of feeding has also been observed in the caenogastropod family Epitoniidae.

Many aeolid nudibranchs engage in a remarkable phenomenon called **kleptocnidism**. Some of the prey's nematocysts are ingested unfired, passed through the nudibranch's gut, and eventually transported to lobes of the digestive gland in dorsal fingerlike extensions called **cerata** (singular, ceras) (see Figure 13.32D,E). How the nematocysts undergo this transport without firing is still a mystery. Popular hypotheses are that mucous secretions by the nudibranch limit the discharge, or that a form of acclimation occurs (like that suspected to occur between anemone fishes and their host anemones), or perhaps that only immature nematocysts survive, to later undergo maturation in the dorsal cerata. It may also be that, once the cnidocytes are digested, the nematocysts' firing threshold is raised, thereby preventing discharge. In any case, once in the cerata, the nematocysts are stored in structures called cnidosacs and presumably help the nudibranch to fend off attackers. Discharge might even be under the control of the host nudibranch, perhaps by means of pressure exerted by circular muscle fibers around each cnidosac.

Some doridid nudibranchs also utilize their prey in remarkable ways. Many doridids secrete complex toxic compounds incorporated into mucus released from the mantle surface. These noxious chemicals act to deter potential predators. While some of these chemicals may be manufactured in some doridids, in most cases

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FIGURE 13.27 Sequence of photographs of a cone snail (*Conus*) capturing and swallowing a small fish. The proboscis is extended and swept back and forth above the substratum in search of prey; when a fish is encountered, a poison-charged tooth of the toxoglossan radula is fired like a harpoon, and the prey is quickly paralyzed and ingested.

it appears that they are obtained from the sponges or bryozoans on which they feed. In some species, such as the "Spanish dancer" nudibranch (*Hexabranchus sanguineus*), the slug not only uses a chemical from its prey (in this case a sponge) for its own defense, but deposits some of the noxious chemical on its egg mass, helping to protect the embryos until they hatch.

In polyplacophorans there are generally 17 teeth in each transverse row of the radula (a central tooth flanked by eight on each side). Most chitons are herbivorous grazers. Notable exceptions are certain members of the order Chitonida (family Mopaliidae, e.g., *Mopalia*, *Placiphorella*), which are known to feed on both algae and small invertebrates. *Mopalia* consumes sessile invertebrates, such as barnacles, bryozoans, and hydroids. *Placiphorella* captures live microinvertebrates (particularly crustaceans) by trapping them beneath its head flap, a large anterior extension of the girdle (Figure 13.24C).

In monoplacophorans the radula consists of a ribbonlike membrane bearing a succession of transverse rows of 11 teeth each (a slender central tooth flanked on each side by 5 broader lateral teeth). Monoplacophorans are probably generalized deposit feeders that graze on minute organisms coating the substratum on which they live.

Cephalopods are predatory carnivores. Squid are some of the most voracious creatures in the sea, successfully competing with fishes. Octopuses are also active carnivores, preying primarily on crabs, bivalves, and gastropods. Some species of *Octopus* bore through the shells of molluscan prey in a fashion similar to that of gastropod drills. Some even drill and prey upon their close relatives, the chambered nautiluses. They do not use the radula to drill, but instead use a rasplike projection formed from the salivary papilla.

Using their impressive locomotor skills, most cephalopods hunt and catch active prey. Some octopuses, however, hunt "blindly," by tasting beneath stones with their highly sensitive suckers that are both mechano- and chemosensitive. In any event, once prey is captured and held by the arms, the cephalopod bites it with its horny beak (modified jaws) and injects a neurotoxin from modified salivary glands. This ability to quickly immobilize prey also helps prevent the soft-bodied cephalopod from being engaged in a potentially dangerous struggle.

Suspension feeding evolved in autobranch bivalves, and also several times in gastropods, and in most of these cases it involves modifications of the ctenidia that enabled the animal to trap particulate matter carried into the mantle cavity by the incoming respiratory water current. The lamellar nature of molluscan gills exapted them for extracting suspended food particles. Increasing the size of the gills and the degree of folding also increased the surface area available for trapping particulate material. In suspension feeders, at least some of the gill and mantle cilia, which otherwise serve to remove potentially clogging sediment from the mantle cavity (as pseudofeces), are preadapted to transport particulate matter from the gills to the mouth region.

While the collection of food on the gills has been adopted by autobranch bivalves and some groups of gastropods, other methods have also been employed. In the gill-less planktonic sea butterflies (pteropods), the ciliated "wings" or parapodia used for swimming (Figure 13.7D,E) also function as food-collecting surfaces or may cooperate with the mantle to produce large mucous sheets that capture small zooplankton. From the foot, ciliary currents carry mucus and food to the mouth. In some pteropods, the mucous sheet may be as large as 2 m across. Mucous sheet feeding is also employed by a few other gastropods, including the intertidal limpets Trimusculidae and the vermetids. Suspension-feeding gastropods include a few vetigastropods such as the sand-beach trochids (*Umbonium, Bankivia*), the hot-vent neomphalid (*Neomphalus*), some marine caenogastropods (Calyptraeidae, e.g., *Crepidula*; Vermetidae, e.g., *Vermetus*; Turritellidae, e.g., *Turritella*), and the freshwater Viviparidae (e.g., *Viviparus*). The ctenidial filaments in these filter feeders are much elongated, and the mantle waste rejection cilia have evolved into a food-collecting groove that runs to the mouth. The radula in suspension-feeding gastropods is somewhat reduced, serving mainly to pull mucus-bound food into the mouth. Some feed entirely by suspension feeding, others use browsing to supplement this method.

The wormlike shell of the vermetids is permanently affixed to the substratum, and while some adopt ciliary food collecting, others combine this with mucous net collecting or use the latter method exclusively. A special pedal gland in the reduced foot produces copious amounts of mucus that spreads into the water column as a sticky plankton trap. Periodically the net is hauled in by the foot and pedal tentacles, and a new one is quickly secreted. *Thylacodes arenarius*, a large Mediterranean vermetid, casts out individual threads up to 30 cm long, whereas the gregarious California species *Thylacodes squamigerus* forms a communal net shared by many individuals.

The radula apparently disappeared early in the course of bivalve evolution, and in living species there is no trace of this structure or even the buccal cavity that contained it. Most autobranch bivalves use their large ctenidia for suspension feeding, but the more primitive bivalves in the subclass Protobranchia are not suspension feeders but engage in a type of deposit-feeding microphagy. Protobranchs live in soft marine sediments and maintain contact with the overlying water either directly (e.g., *Nucula*) or by means of siphons (e.g., *Nuculana*, *Yoldia*). The two ctenidia are small, conforming to the primitive molluscan bipectinate plan of an elongated axis carrying a double row of lamellae (Figures 13.28A and 13.29). Protobranchs

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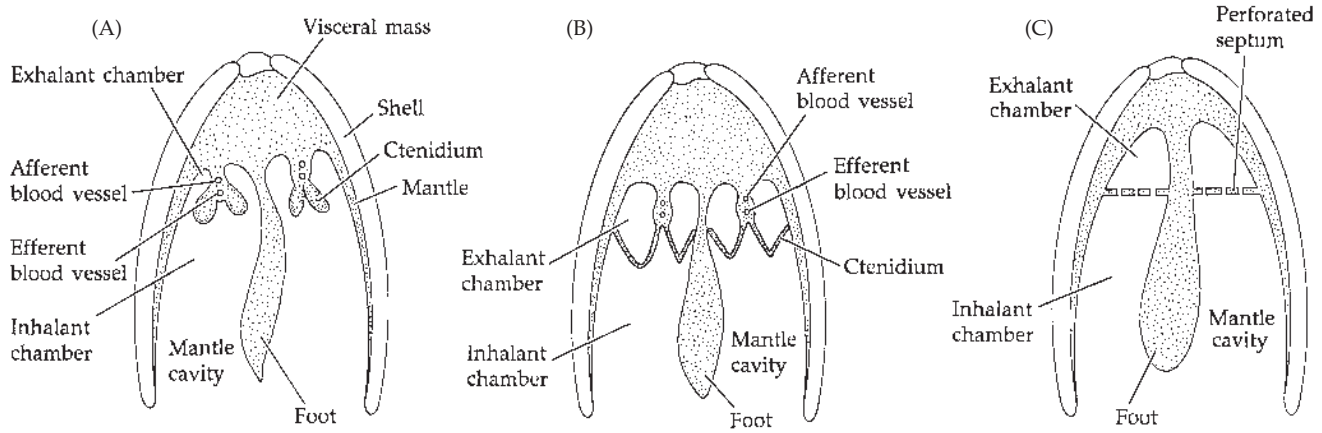


FIGURE 13.28 Arrangement of ctenidia in some bivalves (transverse sections) showing different conditions. (A) Protobranch condition. (B) Lamellibranch condition. (C) Septibranch condition.

feed by means of two pairs of large labial palps flanking the mouth. The two innermost palps are the short **labial palps**, and the two outermost palps are formed into tentacular processes called **proboscides** (each being called a **palp proboscis**), which can be extended beyond the shell (Figure 13.29). During feeding the proboscides are extended into the bottom sediments. Detrital material adheres to the mucus-covered surface of the proboscides and is then transported by cilia to the labial palps, which function as sorting devices. Low-density particles are carried to the mouth; heavy particles are carried to the palp margins and ejected into the mantle cavity.

In the suspension-feeding subclass Autobranchia, lateral cilia on the ctenidia generate a water current from which suspended particles are gleaned. Increased efficiency is achieved by various ctenidial modifications. The primary modification, seen in all living autobranch bivalves, has been the conversion of the original, small, triangular plates into V-shaped filaments with extensions on either side (Figures 13.28B and 13.30B). The arm of this V-shaped filament that is attached to the central axis of the ctenidium is called the descending arm; the arm forming the other half of the V is the ascending arm. The ascending arm is usually anchored distally by ciliary contacts or tissue junctions to the roof of the mantle, or to the visceral mass. Taken together, the two V-shaped filaments, with their double row of leaflets, form a W-shaped structure when seen in cross section.

Some pteriomorphian autobranch bivalves have **filibranch** ctenidia (e.g., mussels) wherein adjacent filaments are interlocked to one another by periodic clumps of specialized cilia, leaving long narrow slits in between (interfilament spaces) (Figure 13.30C,D). The spaces between the arms of the Ws are exhalant suprabranchial chambers, which merge with the exhalant area in the posterior mantle cavity to be discharged; the spaces ventral to the Ws are inhalant and communicate with the inhalant area of the mantle edge. Many other bivalves have **eulamellibranch** ctenidia, which are similar to the filibranch design but with neighboring filaments fused to one another by tissue junctions at numerous points along their length. This arrangement results in interfilament pores that are rows of ostia rather than the long narrow slits of filibranchs (Figure 13.30B,E,F). In addition, the ascending and descending halves of some filaments may be joined by tissue bridges that provide firmness and strength to the gill.

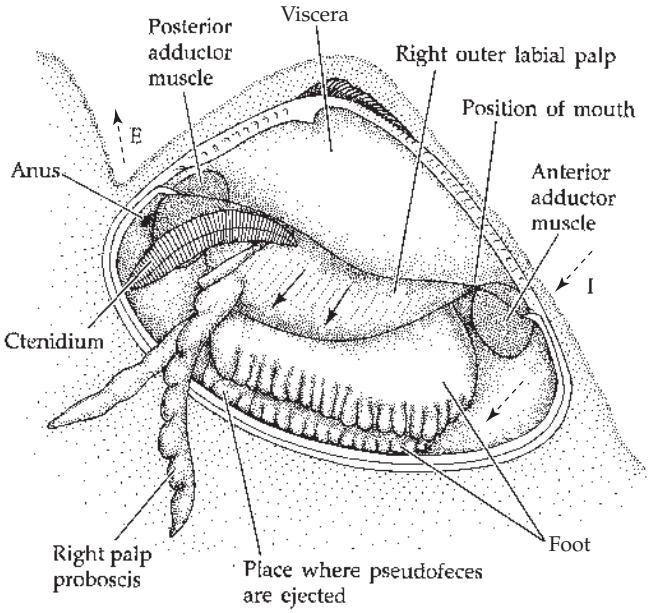
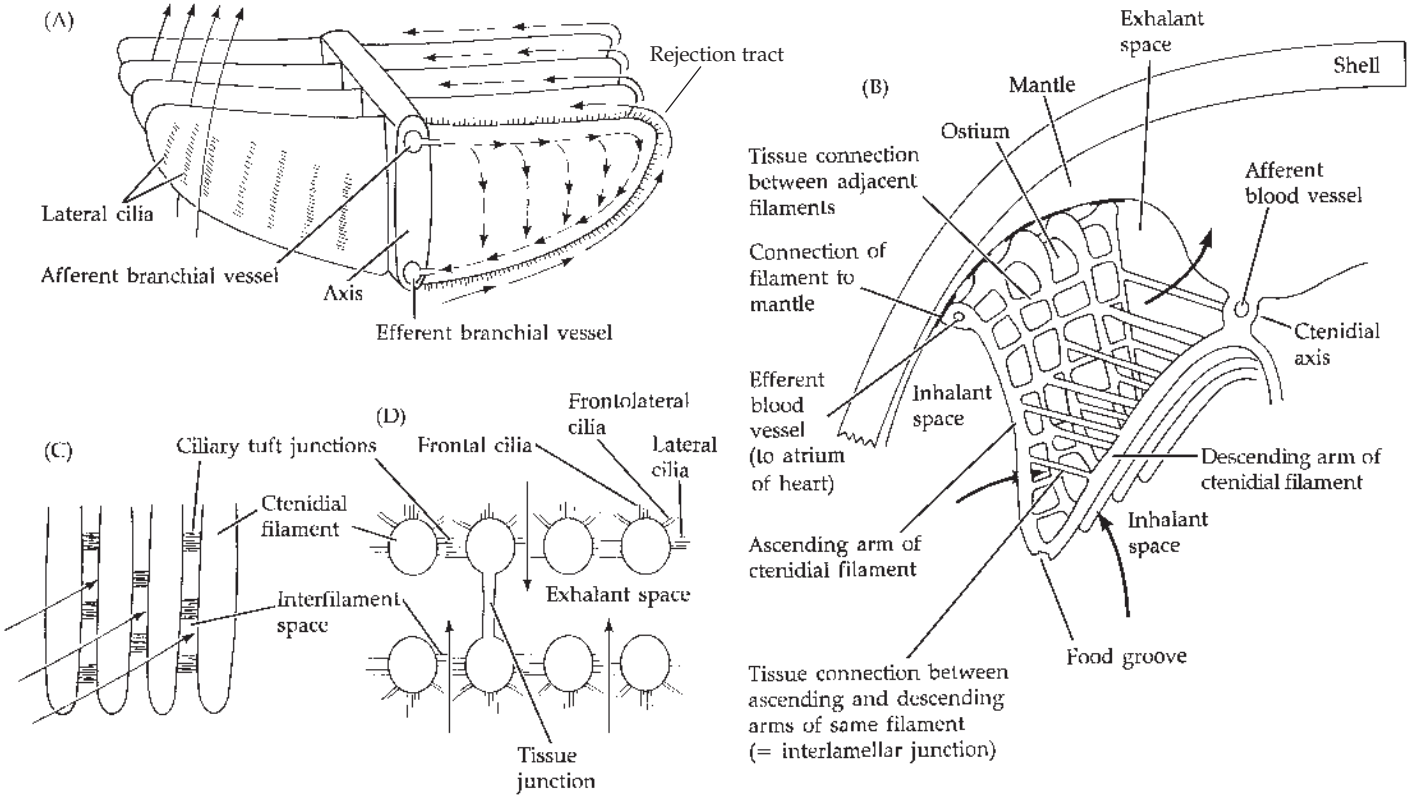
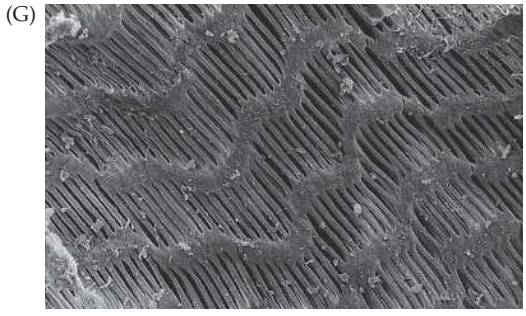
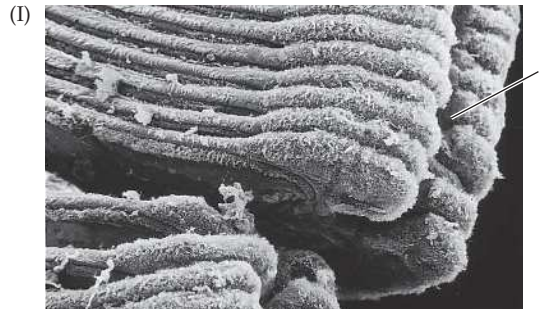


FIGURE 13.29 Feeding in the primitive bivalve *Nucula* (Protobranchia). The clam is seen from the right side, in its natural position in the substratum (right valve and right mantle skirt removed). Arrows show direction of ciliary currents in the mantle cavity and on the palps. Water currents are also shown in the (I) inhalant region and (E) exhalant region.







G–I courtesy of S. Hendrixson

FIGURE 13.30 Ctenidial structure in bivalve molluscs. In all drawings, solid arrows indicate the direction of water flow (from inhalant space, between ctenidial filaments, to exhalant space); solid arrows on right side indicate direction of rejection tract. (A) Section through part of the gill axis in a nuculanid protobranch, showing four alternating filaments (leaflets) on each side. Dashed arrows indicate direction of hemolymph flow in the filament. (B) Highly schematic cutaway view showing four ctenidial filaments, and their interconnections, on one side of the body of a eulamellibranch. (C) Lateral view of four ctenidial filaments of a filibranch. (D) Cross section through ascending and descending arms of four filibranch ctenidial filaments. (E) Lateral view of four filaments of a eulamellibranch. (F) Cross section through ascending and descending arms of four eulamellibranch ctenidial filaments. (G) Ctenidial filaments of the mussel *Mytilus californianus* showing ciliary junctions and interfilament spaces. (H) Frontal ciliary tracts on ctenidial filaments of *Mytilus*. (I) Ventral gill edge of *Mytilus* showing food groove.

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Both filibranch and eulamellibranch ctenidia are used to capture food. Water is driven from the inhalant to the exhalant parts of the mantle cavity by lateral cilia all along the sides of filaments in filibranchs, or by special lateral ostial cilia in eulamellibranchs (Figure 13.30E,F). As the water passes through the interfilament spaces, it flows through rows of frontolateral cilia, which flick particles from the water onto the surface of the filament facing into the current. These feeding cilia are called **compound cirri**; they have a pinnate structure that probably increases their catching ability. Mucus presumably plays some part in trapping the particles and keeping them close to the gill surface, although its precise role is uncertain. Bivalve ctenidia are not covered with a continuous sheet of mucus, as occurs in some other suspension-feeding invertebrates (e.g., certain gastropods, tunicates, amphioxus). Once on the filament surface, particles are moved by frontal cilia toward food groove on the free edges of the ctenidium, and then anteriorly to the labial palps. The palps sort the material by size and perhaps also by quality before passing the food to the mouth. Rejected particles fall off the gill or palp edges into the mantle cavity as **pseudofeces**. This "filtration" of water by bivalves is quite efficient. The American oyster (*Crassostrea virginica*), for example, can process up to 37 liters of water per hour (at 24°C) and can capture particles as small as 1 µm in size. Studies on the common mussels *Mytilus edulis* and *M. californianus* suggest that these bivalves maintain pumping rates of about 1 liter per hour per gram of (wet) body weight.

Members of the superfamily Tellinoidea (primarily Tellinidae and Semelidae) are deposit feeders, sucking up surface detritus with their long, mobile inhalant siphon (Figure 13.20G) and using the large labial palps to presort the particles before ingesting them.

Some members of the Anomalodesmata are known as septibranchs and are sessile predators, and unlike other autobranch bivalves, their gills are not used for feeding. Instead the ctenidia are very reduced and modified as a perforated but muscular septum that divides the mantle cavity into dorsal and ventral chambers (Figures 13.28C and 13.31A). The muscles are attached to the shell such that the septum can be raised or lowered within the mantle cavity. Raising the septum causes water to be sucked into the mantle cavity by way of the inhalant siphon; lowering the septum causes water to pass dorsally through the pores into the exhalant chamber. These movements also force hemolymph from mantle sinuses into the siphonal sinuses, thereby causing a rapid protrusion of the inhalant siphon, which can be directed toward potential prey (Figure 13.31B–D). In this fashion, small animals such as microcrustaceans are sucked into the mantle cavity, where they are grasped by muscular labial palps and thrust into the mouth; at the same time, the mantle tissue serves as the gas exchange surface.

While most pteriomorphians are restricted to epibenthic life, lacking siphons (Figure 13.21A,B), many heterodont bivalves live buried in soft sediments, where long siphons are utilized to maintain contact with the overlying water (Figures 13.8A and 13.20D–H).

Scaphopods consume foraminifera and other meiofaunal taxa, diatoms, zooplankton, and interstitial detritus. Two lobes flank the head, each bearing numerous (up to several hundred) long, slender tentacles called

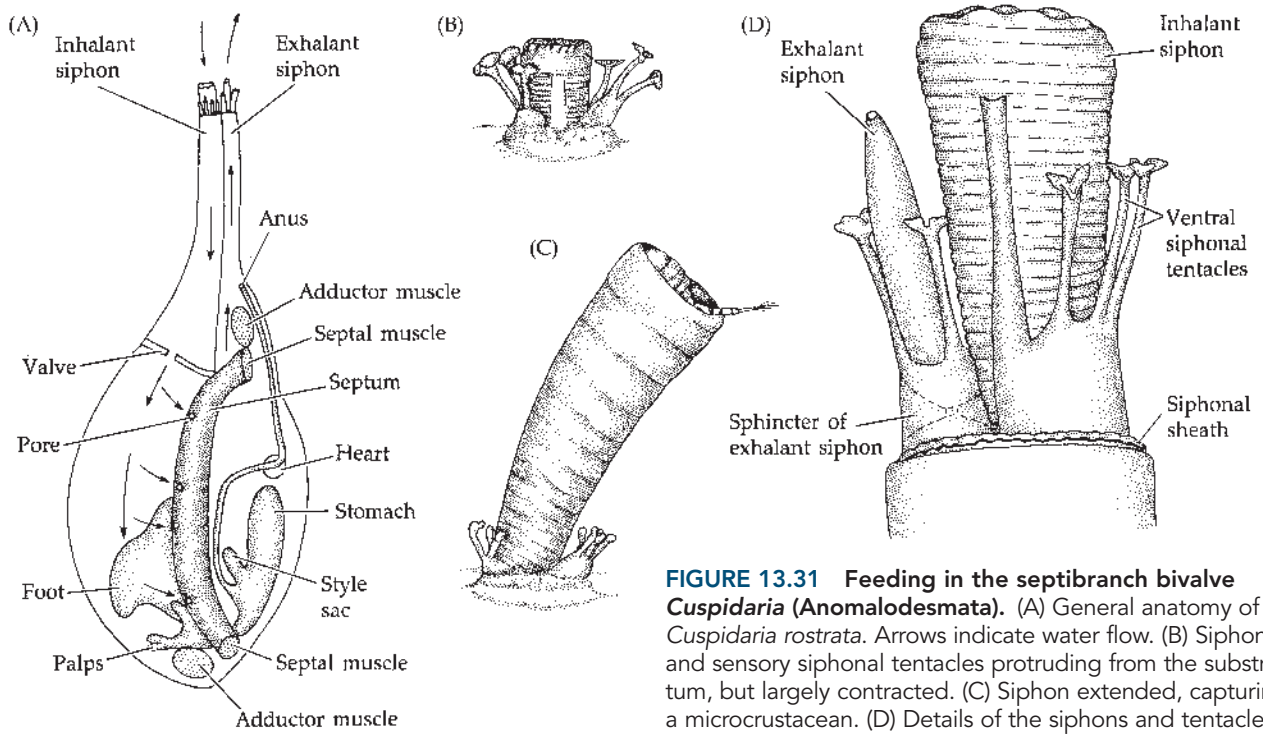

FIGURE 13.31 Feeding in the septibranch bivalve *Cuspidaria* (Anomalodesmata). (A) General anatomy of *Cuspidaria rostrata*. Arrows indicate water flow. (B) Siphon and sensory siphonal tentacles protruding from the substratum, but largely contracted. (C) Siphon extended, capturing a microcrustacean. (D) Details of the siphons and tentacles.

captacula (Figures 13.9 and 13.13F). The captacula are extended into the substratum by metachronal beating of cilia on the small terminal bulb. Within the sediment organic particles and microorganisms adhere to the sticky terminal bulb; small food particles are transported to the mouth by way of ciliary tracts along the tentacles, while larger food items are transported directly to the mouth by muscular contraction of the captacula. A well-developed, large radula pulls the food into the mouth, perhaps partially macerating it in the process.

Several forms of symbiotic relationships intimately tied to the host's nutritional biology have evolved within molluscs. One of the most interesting of these relationships exists between many molluscs and sulfur-reducing and sulfur-oxidizing bacteria. These molluscs appear to derive a portion of their nutritional needs from bacteria, which usually reside on the host mollusc's gills. In some monoplacophorans (*Laevipilina antarctica*) and gastropods (*Lurifax vitreus*, *Hirtopelta*) the bacteria are housed in special cavities called bacteriocytes in the mantle cavity. This mollusc-bacteria symbiosis has been documented from a variety of sulfide-rich anoxic habitats, including deep-sea hydrothermal vents, where geothermally produced sulfide is present, and from other reduced sediments, where microbial degradation of organic matter leads to the reduction of sulfate to sulfide (e.g., anoxic marine basins, sea grass bed and mangrove swamp sediments, pulp mill effluent sites, sewage outfall areas).

Members of some bivalve families, in particular the Solemyidae, Nucinellidae, and Lucinidae, harbor sulfur-reducing bacteria in their enlarged gills that have the ability to directly oxidize sulfide. They do this by means of a special sulfide oxidase enzyme in the mitochondria. These bivalves inhabit reduced sediments where free sulfides are abundant. The ability to oxidize sulfide not only provides the bivalves with a source of energy to drive ATP synthesis, but also enables them to rid their body of toxic sulfide molecules that accumulate in such habitats. The nutrients obtained by this symbiosis are sufficient for the bivalve, so in solemyids the gut is reduced or, in a few species, absent.

Another notable partnership exists between giant clams (*Tridacna*) and their symbiotic zooxanthellae (the dinoflagellate *Symbiodinium*, which is now known to be composed of at least seven distinct clades). These clams live with their dorsal side against the substratum, and they expose their fleshy mantle to sunlight through the large shell gape. The mantle tissues harbor the zooxanthellae and have special lenslike structures that focus light on zooxanthellae living in the deeper tissues. A few other bivalves and certain sea slugs also maintain a symbiotic relationship with *Symbiodinium*. Among nudibranchs, several species of *Melibe, Pteraeolidia*, and *Berghia* harbor colonies of these dinoflagellates in "carrier cells" associated with their digestive glands. Experiments indicate that when sufficient light is available, host nudibranchs utilize photosynthetically fixed organic molecules produced by the alga to supplement their usual diet of prey. The dinoflagellates are probably not transmitted with the zygotes of the nudibranchs, each new generation thus requiring reinfection from the environment. A number of aeolid nudibranchs accumulate zooxanthellae from their cnidarian prey. Some of the dinoflagellates end up inside cells of the nudibranch's digestive gland, but many others are released in the slug's feces, from where they may reinfect cnidarians. An even more remarkable phenomenon occurs in some members of another group of sea slugs, the Sacoglossa (e.g., *Plakobranchus*). These sea slugs obtain functional chloroplasts from the green algae upon which they feed and incorporate them into their own tissues; the chloroplasts remain active for a period of time and produce photosynthetically fixed carbon molecules that are utilized by the hosts.

Still another unusual symbiosis occurs between an aerobic bacterium and the wood-boring marine shipworm bivalves (Teredinidae) (Figure 13.21D). Shipworms are capable of living on a diet of wood alone by harboring this cellulose-decomposing, nitrogen-fixing bacterium. The bivalve cultures the bacterium in a special organ associated with ctenidial blood vessels called the **gland of Deshayes**. The bacterium breaks down cellulose and makes its products available to its host. Nitrogen-fixing bacteria occur as part of the gut flora in many animals whose diet is rich in carbon but deficient in nitrogen (e.g., termites). However, shipworms are the only animals known to harbor a nitrogen fixer as a pure (single species) culture in a specialized organ (similar to the host nodule–*Rhizobium* symbiosis of leguminous plants).

In addition to these and a myriad of other feeding strategies of molluscs, some species (notably some bivalves, cephalopods, and sea slugs) probably obtain a substantial portion of their nutritional needs by direct uptake of dissolved organic material, such as amino acids, from seawater.

Digestion

Molluscs possess complete guts, a few of which are illustrated in Figure 13.32. The mouth leads inward to a buccal cavity, within which the radular apparatus and jaws (when present) are located (Figure 13.23). The esophagus is generally a straight tube connecting the foregut to the stomach. Various glands are often associated with this anterior gut region; some produce enzymes, and other glands, usually called salivary glands, secrete a lubricant over the radula. In many herbivorous species (e.g., certain eupulmonates, aplysiidans, and some cephalaspideans), a muscular **gizzard** (unrelated to the jaws) may be present for grinding up tough vegetable matter. The

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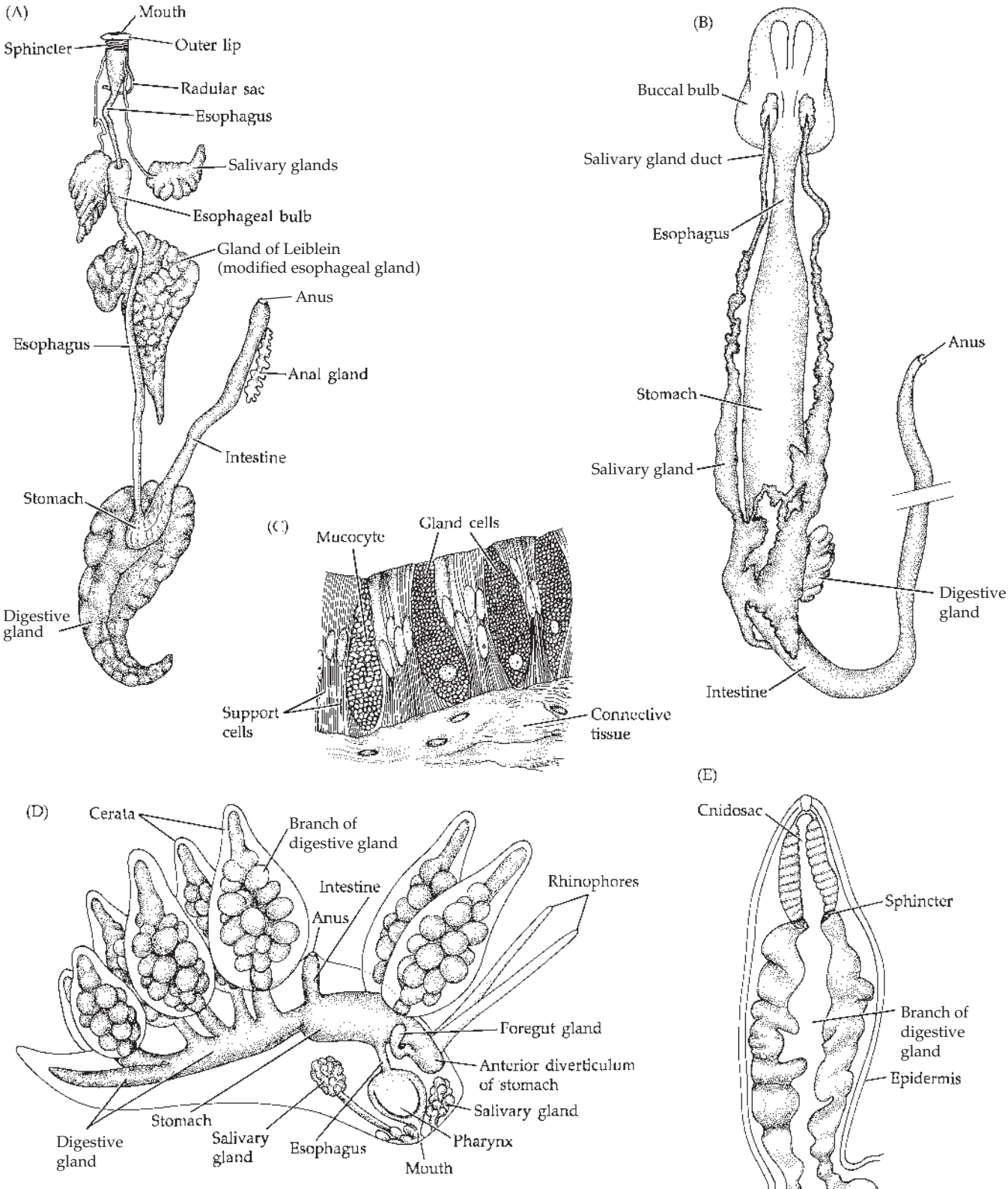

FIGURE 13.32 Molluscan digestive system. (A) The digestive system of a neogastropod (Muricidae). (B) The digestive system of the stylommatophoran land snail *Cornu*. (C) The histology of the intestinal wall of the caenogastropod *Tonna*. (D) A cladobranch nudibranch (*Embletonia*) in which large branches of the digestive gland fill the dorsal cerata. (E) A longitudinal section of the ceras of the aeolidid nudibranch *Trinchesia* showing the cnidosac where nematocysts (not shown) from this animal's cnidarian prey are stored.

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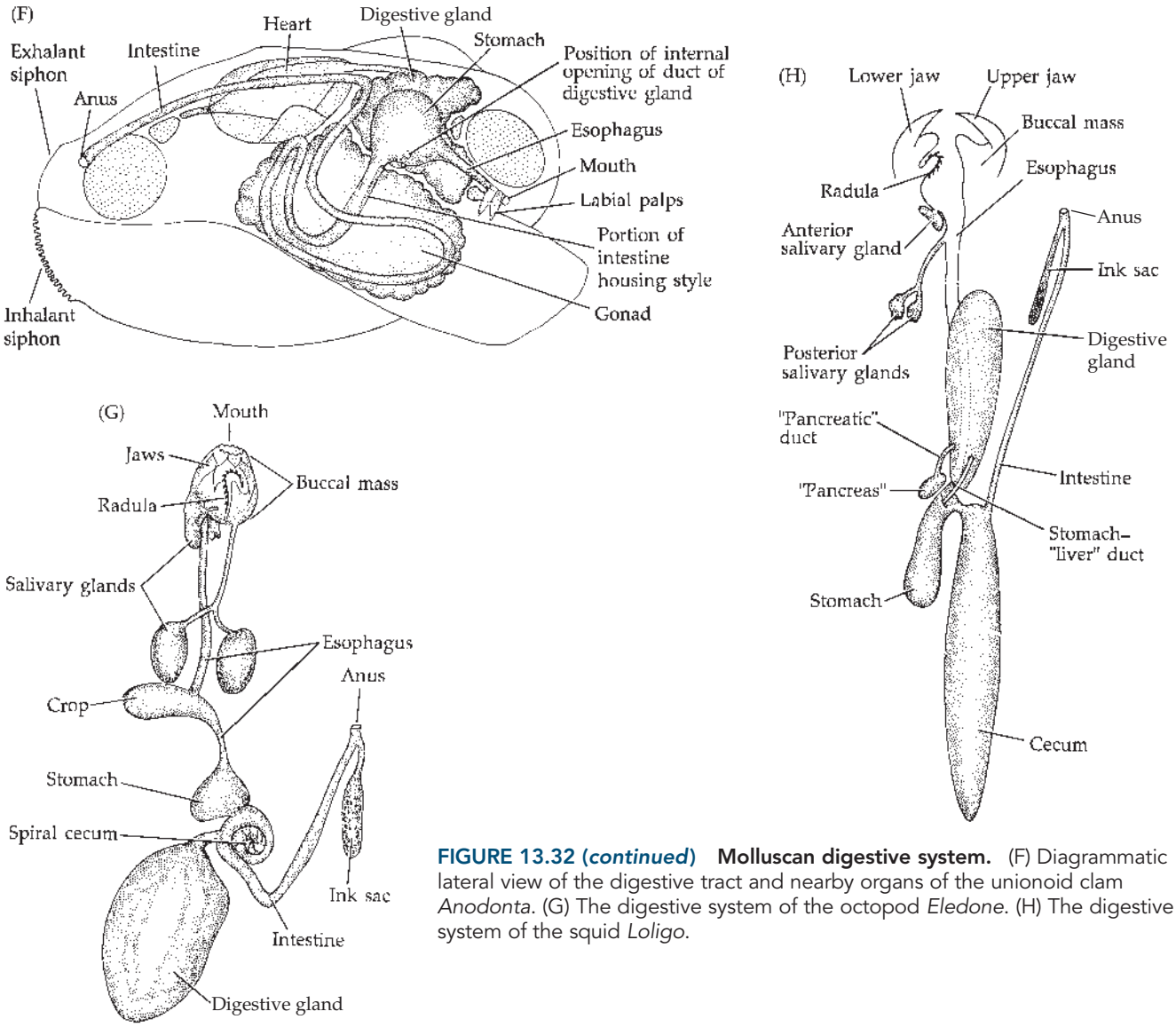

FIGURE 13.32 (*continued*) Molluscan digestive system. (F) Diagrammatic lateral view of the digestive tract and nearby organs of the unionoid clam *Anodonta*. (G) The digestive system of the octopod *Eledone*. (H) The digestive system of the squid *Loligo*.

gizzard may have chitinous, or even calcareous, plates or teeth. The stomach usually bears one or more ducts that lead to the large digestive gland (variously called the digestive diverticula, digestive caeca, midgut glands, liver, or other similar terms). Several sets of digestive glands may be present. The intestine leaves the stomach and terminates as the anus, which is typically located in the mantle cavity in or near the exhalant water flow.

Once food has entered the buccal cavity of most molluscs, it is carried in mucous strings into the esophagus and then to the stomach. In cephalopods and some predatory gastropods, chunks of food or whole prey are swallowed by muscular action of the esophagus. The food is stored in the stomach or in an expanded region of the esophagus called the "crop," as in octopuses and *Nautilus* and many gastropods. In many bivalves and gastropods, the stomach wall bears a chitinous **gastric shield** and a ciliated, ridged **sorting area** (Figure 13.33). The posterior stomach region (anterior in gastropods) is a **style sac**, which is lined with cilia and in autobranch bivalves and some gastropods contains a **crystalline style**. This structure, which functions to aid in digestion, is a rodlike matrix of proteins and enzymes (often amylase) that are slowly released as the projecting end of the style rotates and grinds against the gastric shield that protects the otherwise delicate stomach wall. The gastric cilia and rotating style wind up the mucus and food into a string and draw it along the esophagus to the stomach. The style is produced by special cells of the style sac. The style of some bivalves is enormous, one-third to one-half the length of the clam itself. Particulate matter is swept against the stomach's anterior sorting region, which sorts mainly by size. Small particles are carried into the digestive glands, which arise from the stomach wall. Larger particles are passed along ciliated grooves of the stomach to the intestine. In Protobranchia and in many gastropods, a crystalline

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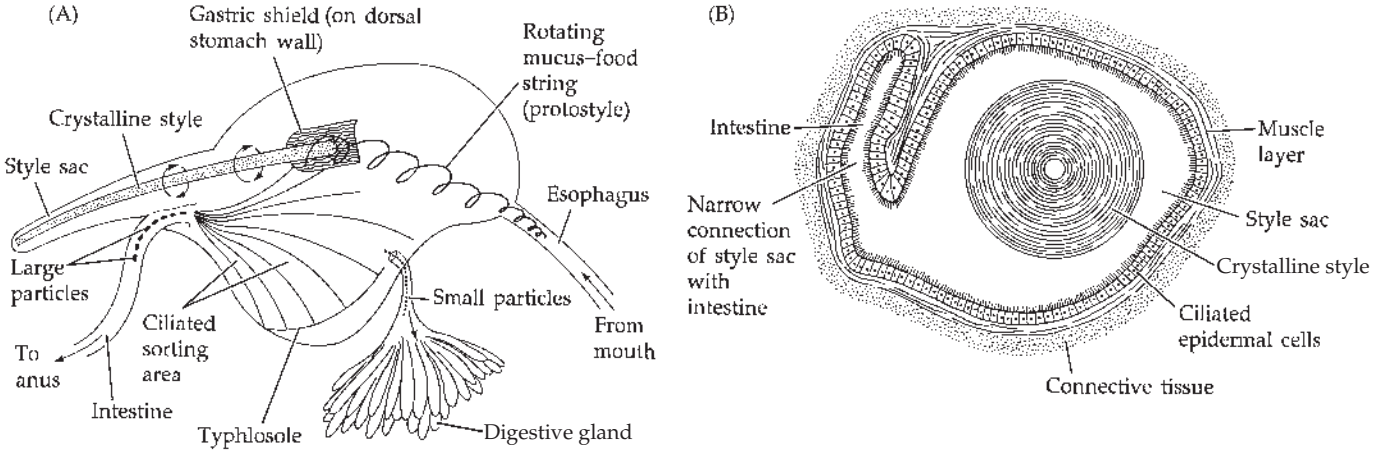

FIGURE 13.33 The molluscan stomach and style sac. (A) A generalized stomach and style apparatus of an autobranch bivalve. The crystalline style rotates against the gastric shield, releasing digestive enzymes and winding up the mucus-food string to assist in pulling it from the esophagus. Food particles are sorted in the ciliated, grooved sorting area: small particles are carried (in part by the typhlosole) to the digestive glands for digestion; large particles are carried to the intestine for eventual elimination. (B) A cross section of a style sac.

style is absent but there is often a style sac, which contains a rotating mass of mucus mixed with particles that is termed a **protostyle**.

Extracellular digestion takes place in the stomach and lumina of the digestive glands, while absorption and intracellular digestion occur in the digestive gland cells and the intestinal walls. Extracellular digestion is accomplished by enzymes produced in the foregut (e.g., salivary glands, esophageal pouches or glands, pharyngeal glands—sometimes called "sugar glands" because they produce amylase), the stomach, and the digestive glands. In primitive groups, intracellular digestion tends to predominate. In Solenogastres all digestive functions are accomplished in a uniform midgut lined by voluminous digestive and secretory cells. In most molluscs, ciliated tracts line the digestive glands and carry food particles to minute diverticula, where they are engulfed by phagocytic digestive cells of the duct wall. The same cells dump digestive wastes back into the ducts, to be carried by other ciliary tracts back to the stomach, from there to be passed out of the gut via the intestine and anus as fecal material. In most highly derived groups (e.g., cephalopods and many gastropods), extracellular digestion predominates. Enzymes secreted primarily by the digestive glands and stomach digest the food, and absorption occurs in the stomach, digestive glands, and intestine.

Circulation and Gas Exchange

Although molluscs are coelomate protostomes, the coelom is greatly reduced. The main body cavity is, in most species, an open circulatory space or hemocoel, which comprises several separate sinuses, and a network of vessels in the gills, where gas exchange takes place. The blood of molluscs contains various cells, including amebocytes, and is referred to as hemolymph. It is responsible for picking up the products of digestion from the sites of absorption and for delivering these nutrients throughout the body. It usually carries in solution the copper-containing respiratory pigment hemocyanin. Some molluscs use hemoglobin to bind oxygen, and many have myoglobin in the active muscle tissues, in particular those of the odontophore.

The heart lies dorsally within the **pericardial chamber** and includes a pair of atria (often called auricles) and a single ventricle. In monoplacophorans and in *Nautilus* there are two pairs of atria corresponding to two pairs of gills, while in many gastropods there is a single auricle (the left) that corresponds to the single gill. The atria receive the efferent branchial vessels, drawing oxygenated hemolymph from each ctenidium and passing it into the muscular ventricle, which pumps it anteriorly through a large anterior artery (the anterior or cephalic aorta). The anterior artery branches and eventually opens into various sinuses within which the tissues are bathed in oxygenated hemolymph. Return drainage through the sinuses eventually funnels the hemolymph back into the afferent branchial vessels. This basic pattern of molluscan circulation is shown diagrammatically in Figure 13.34, although it is modified to various degrees in different classes (Figure 13.35). In some cephalopods the circulatory system is secondarily closed (Figure 13.35C).

The majority of molluscs have ctenidia, but some have lost the ctenidia and rely either on secondarily derived gills or on gas exchange across the mantle or general body surface. In the primitive condition the ctenidium is built around a long, flattened axis projecting from the wall of the mantle cavity (Figure 13.30A). To each side of the axis are attached triangular or wedge-shaped filaments that alternate in position with filaments on the

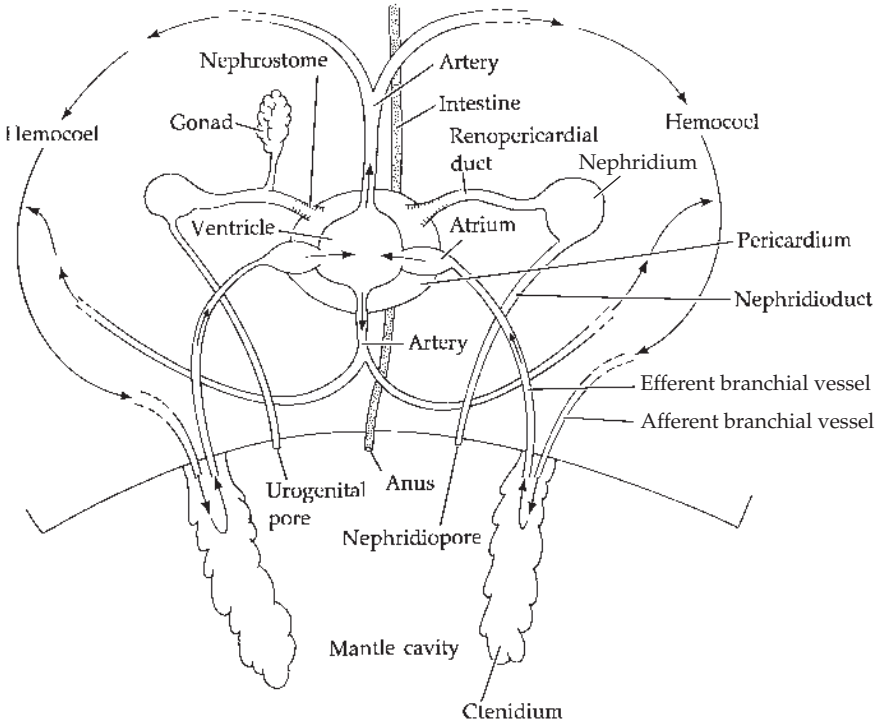

FIGURE 13.34 Hemolymph flow in a typical mollusc. Oxygenated hemolymph is pumped from the ventricle to the hemocoel, where it bathes the organs; eventually it drains into various channels and sinuses and then into the afferent branchial vessels, which enter the ctenidia. Oxygen is picked up in the ctenidia, and the hemolymph is then transported by the efferent branchial vessels to the left and right atria, through the ventricle, and then back to the hemocoel. Additional auxiliary pumping vessels occur in several taxa, particularly in active groups such as cephalopods.

opposite side of the axis. This arrangement, in which filaments project on both sides of the central axis, is called the **bipectinate condition**. There is one gill on each side of the mantle cavity, sometimes held in position by membranes that divide the mantle cavity into upper and lower chambers (Figure 13.28A,B). Lateral cilia on the gill draw water into the inhalant (ventral) chamber, from which it passes upward between the gill filaments to the exhalant (dorsal) chamber and then out of the mantle cavity (Figure 13.30A).

Two vessels run through each gill axis. The afferent vessel carries oxygen-depleted hemolymph into the gill, and the efferent vessel drains freshly oxygenated hemolymph from the gill to the atria of the heart, as noted above. Hemolymph flows through the filaments from the afferent to the efferent vessel. Ctenidial cilia move water over the gill filaments in a direction opposite to that of the flow of the underlying hemolymph in the branchial vessels. This countercurrent phenomenon enhances gas exchange between the hemolymph and water by maximizing the diffusion gradients of O_2 and CO_2 (Figure 13.30A). These presumed primitive bipectinate ctenidial gill conditions are expressed in several living groups, for example, in caudofoveates, chitons, protobranch bivalves, and some gastropods.

As a result of torsion, gastropods evolved novel ways to circulate water over the gills before it comes into contact with gut or nephridial discharges. Some vetigastropods with two bipectinate ctenidia may accomplish this by circulating water in across the gills, then past the anus and nephridiopore, and away from the body via slits or holes in the shell. This circulation pattern is used by the slit shells (Pleurotomariidae) and the minute Scissurellidae and Anatomidae (Figure 13.36), abalones (Haliotidae) (Figures 13.1D and 13.25A), and volcano (or keyhole) limpets (Fissurellidae) (Figure 13.16H,I). Some specialists regard the Pleurotomariidae as "living fossils" that reflect an early gastropod character state since gastropods bearing slits are found among early gastropod fossils. Most other gastropods have lost the right ctenidium and with it the right atrium; inhalant water enters on the left side of the head and then passes through the mantle cavity and straight out the right side, where the anus and nephridiopore open. Other gastropods have lost both ctenidia and utilize secondary respiratory regions—the mantle surface itself, expanded nephridial surfaces, or secondarily derived gills of one kind or another. Limpets of the genus *Patella* have rows of secondary gills in the mantle groove along each side of the body, superficially similar to the condition seen in chitons where multiple ctenidia are found.

In many gastropods one ctenidium is lost, e.g., in patellogastropods, some vetigastropods, and all neritimorphs and caenogastropods. In caenogastropods, the dorsal and ventral suspensory membranes seen in vetigastropod ctenidia are absent, and the gill is attached directly to the mantle wall by the gill axis. The gill filaments on the attached side have been lost, while those of the opposite side project freely into the mantle cavity. This arrangement of filaments on only one side of the central axis is referred to as the **monopectinate (or pectinobranch) condition** (Figure 13.14D). Some caenogastropods have evolved inhalant siphons by extension and rolling of the anterior mantle

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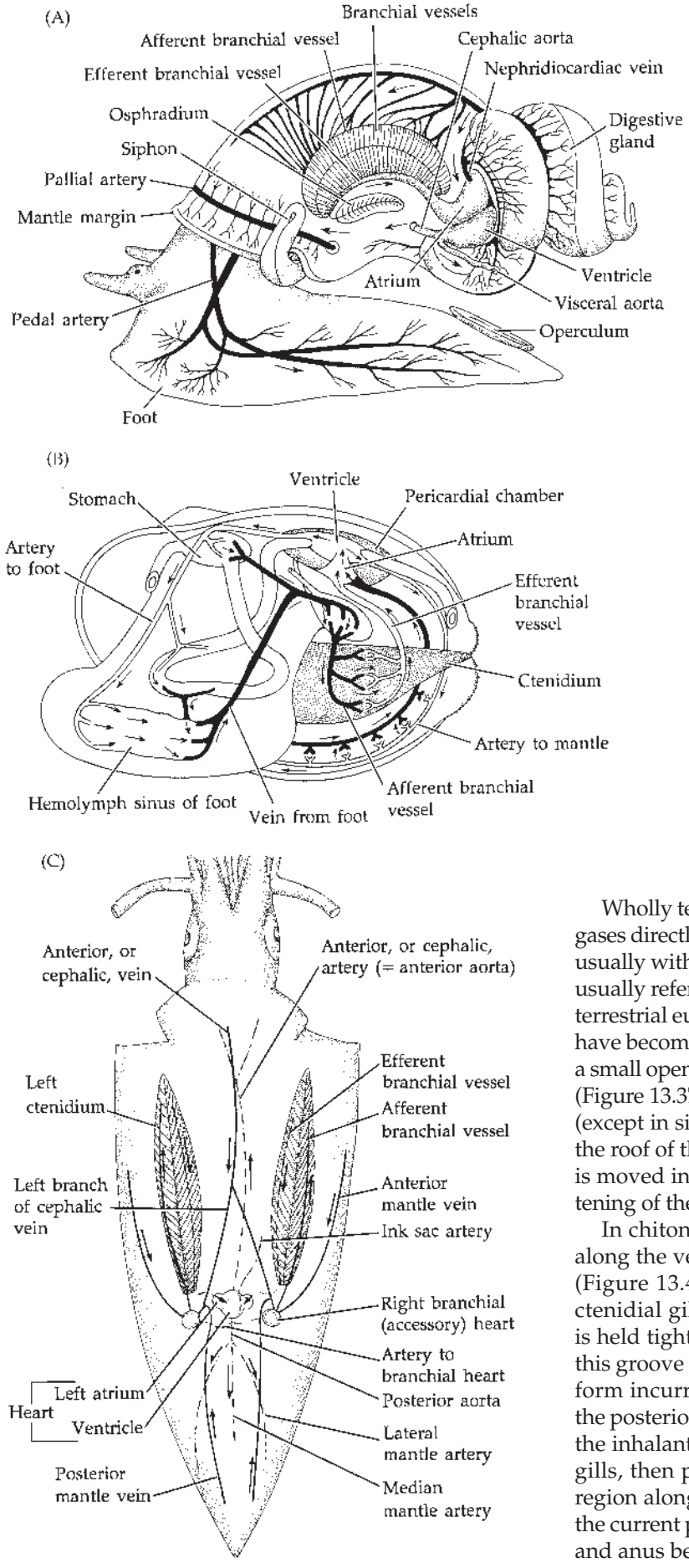

FIGURE 13.35 The circulatory system of three molluscs. (A) A neogastropod *Buccinum* (hemolymph sinuses not shown). (B) A eulamellibranch unionid bivalve (freshwater clam). (C) A squid, *Loligo*.

margin (Figures 13.1E and 13.40A). In these cases the margin of the shell may be notched or may be drawn out as a canal to house the siphon. The siphon provides access to surface water in burrowing species and may also function as a mobile, directional organ used in conjunction with the chemosensory osphradium.

All heterobranchs have lost the typical ctenidia, but some have a plicate, or folded, gill that is considered by some to be a reduced ctenidium and thought by others to be a secondary structure that has re-formed in much the same location as the original ctenidial gill. Trends toward detorsion, loss of the shell, and reduction of the mantle cavity occur in many heterobranchs, and the process has apparently occurred several times within this group. Some nudibranchs have evolved secondary dorsal gas exchange structures called **cerata** or, in others, secondary gills surrounding the anus (Figure 13.7F–J).

Wholly terrestrial gastropods lack gills and exchange gases directly across a vascularized region of the mantle, usually within the mantle cavity, the latter arrangement usually referred to as a **lung**. In marine, freshwater, and terrestrial eupulmonates, the edges of the mantle cavity have become sealed to the back of the animal except for a small opening on the right side called a **pneumostome** (Figure 13.37A) that is controlled by a sphincter muscle (except in siphonariid limpets). Instead of having gills, the roof of the mantle cavity is highly vascularized. Air is moved into and out of the lung by arching and flattening of the mantle cavity floor.

In chitons the mantle cavity is a groove extending along the ventral body margin and encircling the foot (Figure 13.4B). A large number of small bipectinate ctenidial gills lie laterally in this groove. The mantle is held tight against the substratum, largely enclosing this groove except on either side at the anterior end, to form incurrent channels, and in one or two places at the posterior end, to form excurrent areas. Water enters the inhalant region of the mantle groove lateral to the gills, then passes between the gills into the exhalant region along the sides of the foot. Moving posteriorly, the current passes over the gonopores, nephridiopores, and anus before exiting (Figure 13.4B).

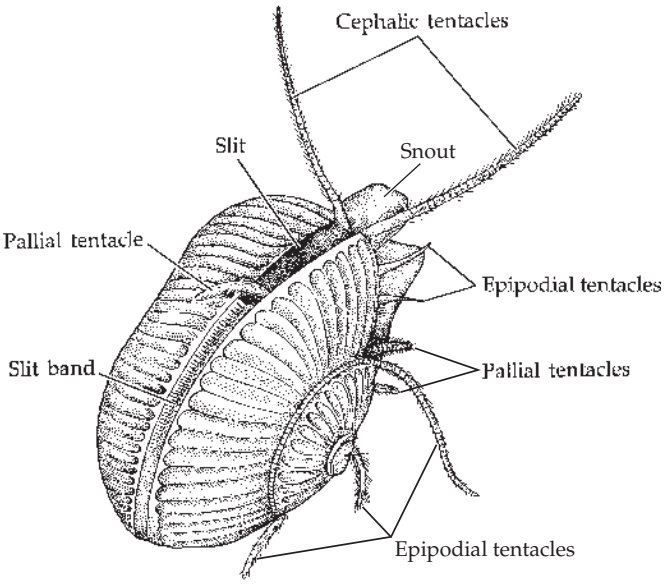

FIGURE 13.36 **The slit-bearing vetigastropod *Anatoma*.**

In bivalves the capacious mantle cavity allows the ctenidia to develop a greatly enlarged surface area, serving in most autobranch species for both gas exchange and feeding. Many of the morphological modifications of bivalve gills are described above. In addition to the folded, W-shaped ctenidial filaments seen in many bivalves (Figure 13.28B), some forms (e.g., oysters) have plicate ctenidia. A plicate ctenidium has vertical ridges or folds, each ridge consisting of several ordinary ctenidial filaments. So-called "principal filaments" lie in the grooves between these ridges, and their cilia are important in sorting particles from the ventilation and feeding currents. The plicate condition gives the ctenidium a corrugated appearance and further increases the surface area for feeding and gas exchange.

(A)

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FIGURE 13.37 **Land snails and slugs (Heterobranchia: Eupulmonata).** (A) A terrestrial slug (*Arion lusitanicus*), showing the pneumostome that opens to the "lung" (Stylommatophora: Limacidae). (B) Terrestrial helicid snails (Stylommatophora: Helicidae) during summer dormancy in Sicily.

In spite of these modifications, the basic system of circulation and gas exchange in bivalves is similar to that seen in gastropods (Figure 13.35B). In most bivalves, the ventricle of the heart folds around the gut, so the pericardial cavity encloses not only the heart but also a short section of the digestive tract. The large mantle lines the interior of the valves and provides an additional surface area for gas exchange, which in some groups may be as important as the gills in this regard. For example, in lucinid bivalves where the ctenidial gills are packed with symbiotic bacteria, folds on the mantle act as a secondary gill, and in septibranchs, which have very reduced gills or lack them, the mantle surface is the principal area of gas exchange.

Most autobranch bivalves lack respiratory pigments in the hemolymph, although hemoglobin occurs in a few families and hemocyanin is found in protobranchs.

Scaphopods have lost the ctenidia, heart, and virtually all vessels. The circulatory system is reduced to simple hemolymph sinuses, and gas exchange takes place mainly across the mantle and body surface. A few ciliated ridges occur in the mantle cavity that may assist in maintaining water flow. A few tiny gastropods and at least one small monoplacophoran species lack a heart altogether.

(B)

Courtesy of R. Brusca

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No doubt associated with their large size and active lifestyle, cephalopods have a more developed circulatory system than other molluscs, and in the highly active decapodiforms (squid and cuttlefish) it is effectively closed, with many discrete vessels, secondary pumping structures, and capillaries (Figures 13.11C, 13.12B, and 13.35C). The result is increased pressure and efficiency of hemolymph flow and delivery. In most cephalopods, the pumping of blood into the ctenidia is assisted by muscular accessory branchial hearts, which boost the low venous pressure as the hemolymph enters the gills. The gills are not ciliated and their surface is highly folded, increasing their surface area for the greater gas exchange necessary to meet the demands of their high metabolic rate.

In the Solenogastres, gills are absent but the mantle cavity surface may be folded or form respiratory papillae. Caudofoveates have a single pair of bipectinate ctenidia in the mantle cavity. Monoplacophoran gills are well developed but weakly muscular and ciliated, with lamellae on only one side of the gill axis; they occur as three to six pairs, aligned bilaterally within the mantle groove. The gills of monoplacophorans are thought to be modified ctenidia that vibrate and ventilate the groove where gas exchange occurs.

Excretion and Osmoregulation

The basic excretory structures of adult molluscs are paired tubular metanephridia (often called kidneys or simply nephridia) that are primitively similar to those of annelids, but some larval forms have protonephridia. Typical nephridia are absent in aplacophorans. Three, six, or seven pairs of nephridia occur in monoplacophorans, two pairs in nautiloids, and a single pair in all other molluscs (although one is lost in all higher gastropods) (Figure 13.14). The nephrostome typically opens into the pericardial coelom via a renopericardial duct, and the nephridiopore discharges into the mantle cavity, often near the anus (Figures 13.14 and 13.34). The pericardial fluids ("primary urine") pass through the nephrostome and into the nephridium, where selective resorption occurs along the tubule wall until the final urine is ready to pass out the nephridiopore. The pericardial sac and heart wall act as selective barriers between the open nephrostome and the hemolymph in the surrounding hemocoel and in the heart. Mollusc nephridia are rather large and saclike, and their walls are often greatly folded. In many species, afferent and efferent nephridial vessels carry hemolymph to and from the nephridial tissues (Figure 13.38). Sometimes a bladder is present just before the nephridiopore, or a ureter may form a duct to carry urine well beyond the nephridiopore.

In many molluscs urine formation involves pressure filtration, active secretion, and active resorption. Aquatic molluscs excrete mostly ammonia, and most marine species are osmoconformers. In freshwater species the nephridia are capable of excreting a hyposmotic urine by resorbing salts and by passing large quantities of water. Terrestrial gastropods conserve water by converting ammonia to uric acid. Land snails are capable of surviving a considerable loss of body water, which is brought on in large part by evaporation and the production of the metabolically expensive slime trail. They often absorb water from the urine in the ureter. In many gastropods (e.g., neritimorphs, caenogastropods, and heterobranchs), torsion is accompanied by loss of the adult right nephridium; in neritimorphs and caenogastropods, a small remnant contributes to part of the gonoduct. Some gastropods have lost the direct connection of the nephrostome to the pericardial coelom. In such cases the nephridium is often very glandular and served by afferent and efferent hemolymph vessels, and wastes are removed from the circulatory fluid.

In bivalves, the two nephridia are located beneath the pericardial cavity and are folded in a long U shape. In autobranch bivalves, one arm of the U is glandular and opens into the pericardial cavity; the other arm often forms a bladder and opens through a nephridiopore in the suprabranchial cavity. In protobranchs, the unfolded walls of the tube are glandular throughout. The nephridiopores may be separate from or joined with the ducts of the reproductive system. In the latter case, the openings are called urogenital pores.

In patellogastropods, vetigastropods, and some other molluscs, the gonoduct fuses with the renopericardial canal, and the nephridiopore functions as a

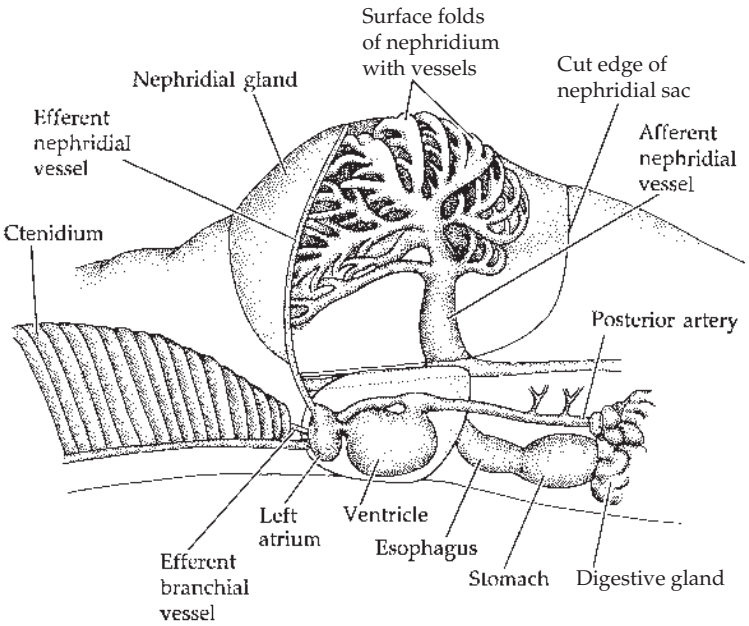

FIGURE 13.38 The nephridium and nearby organs of *Littorina* (cutaway view). The nephridial sac has been slit open.

urogenital pore discharging both excretory wastes and gametes. In some cases, as in one monoplacophoran, a few bivalves, and some vetigastropods, the urogenital pore may become glandular. In many bivalves and chitons the nephridium and gonad have separate ducts.

In monoplacophorans and chitons, the nephridia open into the exhalant regions of the mantle grooves; in scaphopods, the paired nephridia open near the anus. In most gastropods the nephridiopores open directly into the mantle cavity, but in some, such as stylommatophoran eupulmonates, there is an elongate ureter that in some opens outside the enclosed lung (mantle cavity).

Cephalopods retain the basic nephridial plan, in which the nephridia drain the pericardial coelom by way of renopericardial canals and empty via nephridiopores into the mantle cavity. However, the nephridia bear enlarged regions called **renal sacs**. Before reaching the branchial heart, a large vein passes through the renal sac, wherein numerous thin-walled evaginations, called **renal appendages**, project off the vein. As the branchial heart beats, hemolymph is drawn through the renal appendages, and wastes are filtered across their thin walls into the nephridia. The overall result is an increase in excretory efficiency over the simpler arrangement present in other molluscs.

The fluid-filled nephridia of cephalopods are inhabited by a variety of commensals and parasites. The epithelium of the convoluted renal appendages provides an excellent surface for attachment, and the renal pores provide a simple exit to the exterior. Symbionts identified from cephalopod nephridia include viruses, fungi, ciliate protists, dicyemids (all the members of this phylum live exclusively in the renal sac of benthic cephalopods—see Chapter 10), trematodes, larval cestodes, and juvenile nematodes.

Nervous System

The molluscan nervous system is derived from the basic protostome plan of an anterior circumenteric arrangement of ganglia and paired ventral nerve cords. In molluscs, the more ventral and medial of the two pairs of nerve cords are called the **pedal cords** (or ventral cords); they innervate the muscles of the foot. The more lateral pair of nerves are the **visceral cords** (or lateral cords); they serve the mantle and viscera. Transverse commissures interconnect these longitudinal nerve cord pairs, creating a ladderlike nervous system. This basic plan is seen in the aplacophorans and polyplacophorans (Figure 13.39). The molluscan nervous system lacks any trace of segmentally arranged ganglia.

In aplacophorans, monoplacophorans, and polyplacophorans, ganglia are poorly developed (Figure 13.39). A simple nerve ring surrounds the anterior gut, often with small cerebral ganglia on either side. Each cerebral ganglion, or the nerve ring itself, issues small nerves to the buccal region and gives rise to the pedal and the visceral nerve cords. Most other molluscs have more well-defined ganglia. Their nervous system is built around three pairs of large ganglia that interconnect to form a partial or complete nerve ring around the gut (Figures 13.40 and 13.41). Two pairs, the cerebral and pleural ganglia, lie dorsal or lateral to the esophagus, and one pair, the pedal ganglia, lies ventral to the gut, in the anterior part of the foot. In cephalopods, bivalves, and some neogastropods and heterobranch gastropods, the cerebral and pleural ganglia are often fused. From the cerebral ganglia, peripheral nerves innervate, when present, the tentacles, eyes, statocysts, and general head surface, as well as buccal ganglia, with special centers of control for the buccal region, radular apparatus, and esophagus. The pleural

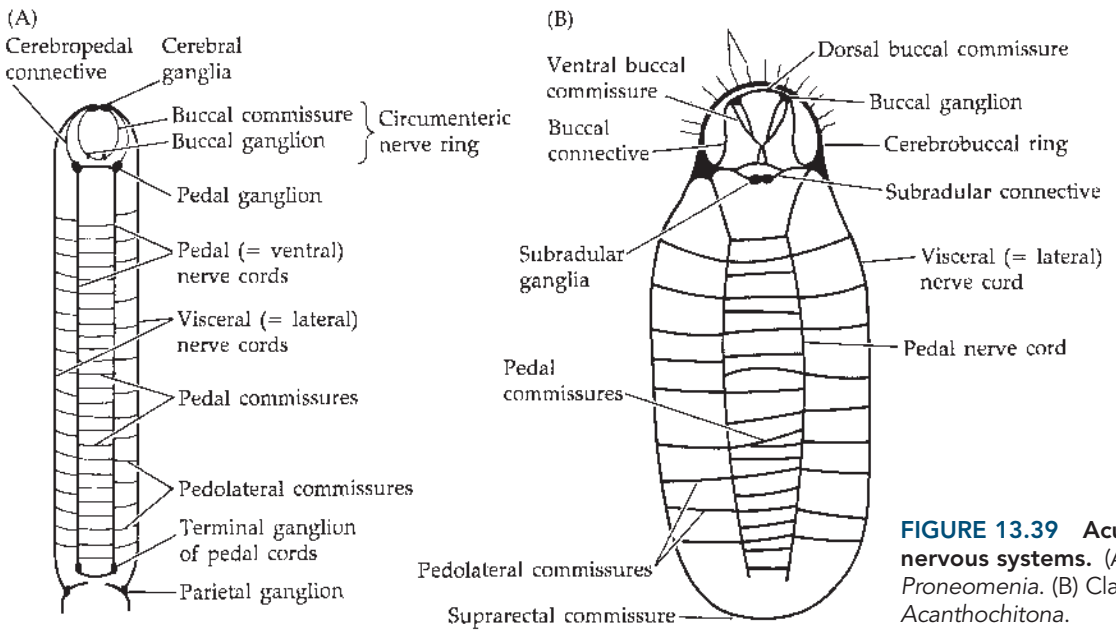

FIGURE 13.39 Aculiferan molluscan nervous systems. (A) Class Solenogastres, *Proneomenia*. (B) Class Polyplacophora, *Acanthochitona*.

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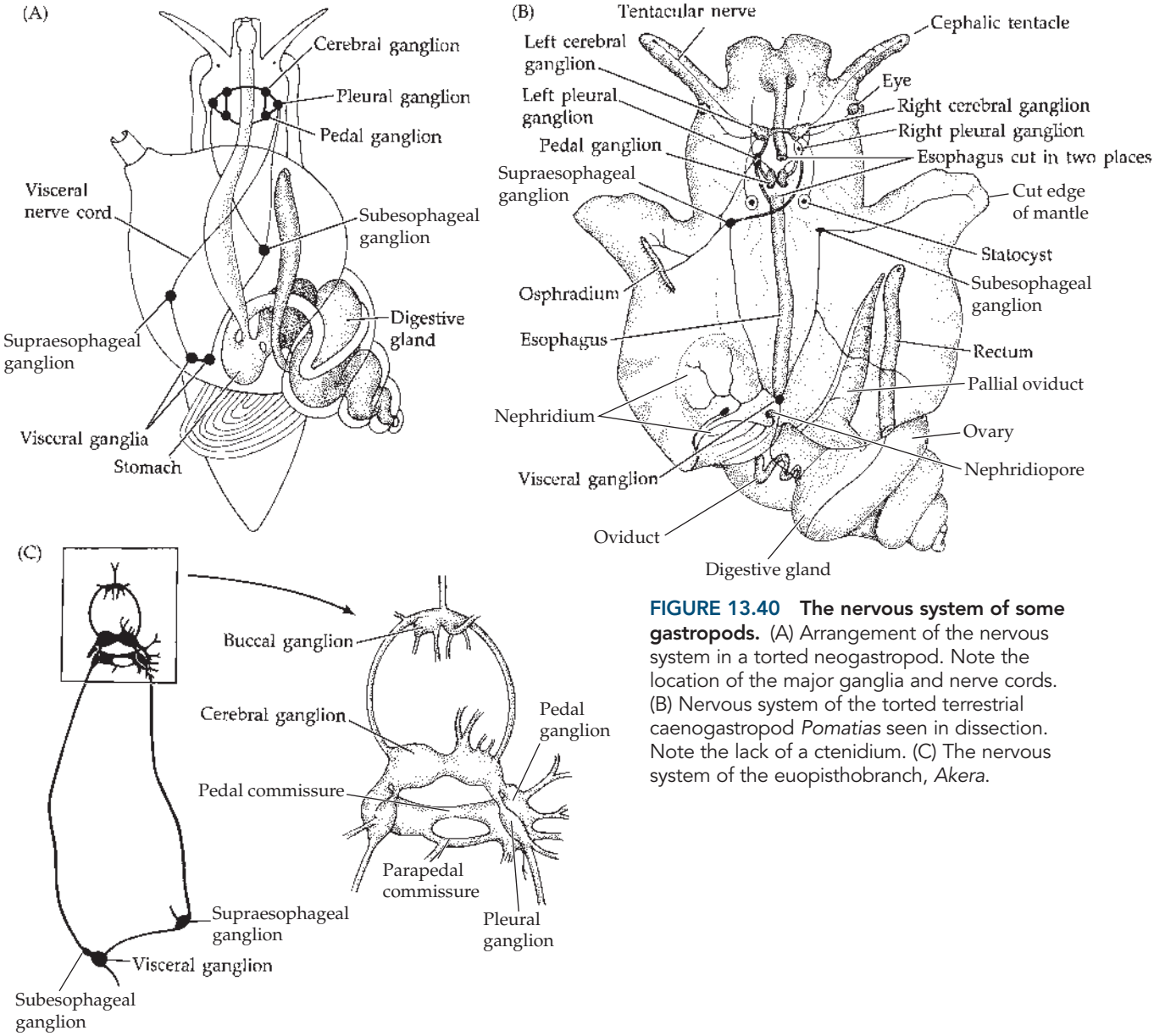

FIGURE 13.40 The nervous system of some gastropods. (A) Arrangement of the nervous system in a torted neogastropod. Note the location of the major ganglia and nerve cords. (B) Nervous system of the torted terrestrial caenogastropod *Pomatias* seen in dissection. Note the lack of a ctenidium. (C) The nervous system of the euopisthobranch, *Akera*.

ganglia give rise to the visceral cords, which extend posteriorly, supplying peripheral nerves to the viscera and mantle. The visceral cords eventually join a pair of esophageal (= intestinal, = pallial) ganglia and from there continue to terminate in paired visceral ganglia. The esophageal ganglia or associated nerves innervate the gills and osphradium, and the visceral ganglia serve organs in the visceral mass. The pedal ganglia also give rise to a pair of pedal nerve cords that extend posteriorly and provide nerves to muscles of the foot.

As described previously, due to torsion, the posterior portion of the gastropod nervous system is twisted into a figure eight, the condition known as **streptoneury** (Figure 13.40). In addition to twisting the nervous system, torsion brings the posterior ganglia forward. In many advanced gastropods this

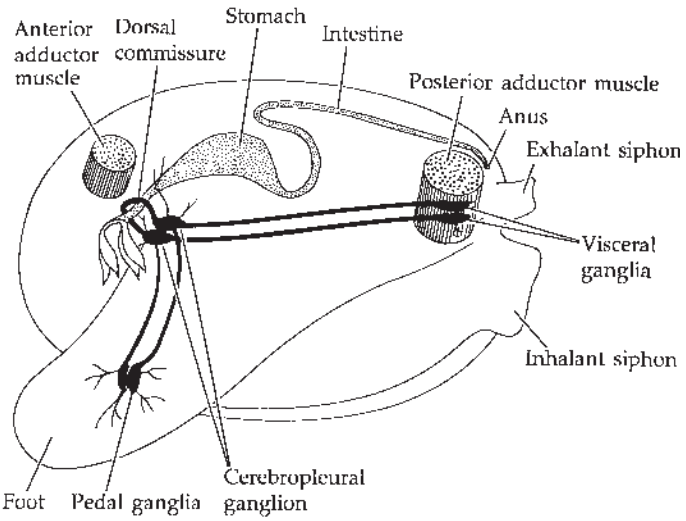

FIGURE 13.41 The reduced and concentrated nervous system of a typical autobranch bivalve.

anterior concentration of the nervous system is accompanied by a shortening of some nerve cords and fusion of ganglia. In most detorted gastropods the nervous system displays a secondarily derived bilateral symmetry and more or less untwisted visceral nerve cords—the condition known as **euthyneury** (Figure 13.40).

In bivalves, the nervous system is clearly bilaterally symmetrical, and fusion has usually reduced it to three large, distinct pairs of ganglia. Anterior cerebropleural ganglia give rise to two pairs of nerve cords, one extending posterodorsally to the visceral ganglia, the other leading ventrally to the pedal ganglia (Figure 13.41). The two cerebropleural ganglia are joined by a dorsal commissure over the esophagus. The cerebropleural ganglia send nerves to the palps, anterior adductor muscle, and mantle. The visceral ganglia issue nerves to the gut, heart, gills, mantle, siphon, and posterior adductor muscle.

The degree of nervous system development within the Cephalopoda is unequaled among invertebrates. The paired ganglia seen in other molluscs are not recognizable in cephalopods, where extreme cephalization has concentrated ganglia into lobes of a large brain encircling the anterior gut (Figure 13.42A). In addition to the usual head nerves originating from the dorsal part of the brain (more or less equivalent to the cerebral ganglia), a large optic nerve extends to each eye via a massive optic lobe. In most cephalopods, much of the brain is enclosed in a cartilaginous cranium. The pedal lobes supply nerves to the funnel, and anterior divisions of the pedal ganglia (called brachial lobes) send nerves to each of the arms and tentacles, an arrangement suggesting that the funnel and tentacles are derived from the molluscan foot. Octopuses may be the "smartest" living invertebrates, for they can quickly learn complex memory-dependent tasks. Squid and cuttlefish (Decabrachia) have a rapid escape behavior that depends on a system of giant motor fibers that control powerful and synchronous contractions of the mantle muscles. The command center of this system is a pair of very large first-order giant neurons in the lobe of the fused visceral ganglia. Here, connections are made to second-order giant neurons that extend to a pair of large stellate ganglia. At the stellate ganglia, connections are made with third-order giant neurons that innervate the circular muscle fibers of the mantle (Figure 13.42D). Other nerves extend posteriorly from the brain and terminate in various ganglia that innervate the viscera and structures in the mantle cavity.

For several decades neurobiologists have utilized the giant axons of loliginid squid as an experimental system for the study of nerve physiology and mechanics, and much of our fundamental knowledge of how nerve cells work is based on squid neurobiology. The sea hare *Aplysia* and some eupulmonate snails have also been used in the same fashion, and although they lack giant axons, they possess exceptionally large neurons and ganglia that can be easily impaled with microelectrodes to discover the physiological secrets of such systems.

Sense Organs

With the exception of aplacophorans, molluscs possess various combinations of sensory tentacles, photoreceptors, statocysts, and osphradia. **Osphradia** are patches of sensory epithelium, located on or near the base of the gills or on the mantle wall (Figures 13.40B and 13.43A,B). They are chemoreceptors, and their cilia can also assist in mantle cavity ventilation in some caenogastropods. Little is known about the biology of osphradia, and their morphology and histology differ markedly within the phylum and even within some classes such as the gastropods.

In vetigastropods, a small osphradium is present on the base of each gill; in those gastropods that possess one gill, there is only one osphradium, and it lies on the mantle cavity wall anterior and ventral to the attachment of the gill itself. Osphradia are reduced or absent in gastropods that have lost ctenidial gills, that possess a highly reduced mantle cavity, or that have taken up a strictly pelagic existence. Osphradia are best developed in benthic predatory and scavenging neogastropods and some other caenogastropods.

Most gastropods have one pair of sensory cephalic tentacles, but eupulmonates and many sea slugs possess two pairs. Many vetigastropods also have epipodial tentacles on the margin of the foot or mantle, and epipodial sense organs may also be present on the margin of the foot (Figure 13.5A,C). The cephalic tentacles may bear eyes as well as tactile and chemoreceptor cells. Many nudibranchs have a pair of branching or folded anterior dorsal chemoreceptors called **rhinophores** (Figure 13.7F,G) that are modified cephalic tentacles.

The patellogastropod limpets have simple pigment-cup eyes, while the remaining gastropods have more complex eyes with a lens and often a cornea (Figure 13.44A,B,D). Most gastropods have a small eye at the base of each cephalic tentacle, but in some, such as the conch *Strombus* and some neogastropods, the eyes are enlarged and elevated on long stalks. The stylommatophoran and systellommatophoran pulmonates have eyes placed on the tips of optic tentacles and, in stylommatophorans, these tentacles are also olfactory organs.

Gastropods typically produce a mucopolysaccharide slime trail as they crawl. In many species the trail contains chemical messengers that other members of the species "read" by means of their excellent chemoreception. These chemical messengers may be simple trail markers, so one animal can follow or locate another, or they may be alarm substances that serve to warn others of possible danger on the path ahead. For example, when the carnivorous cephalaspidean sea slug *Navanax*

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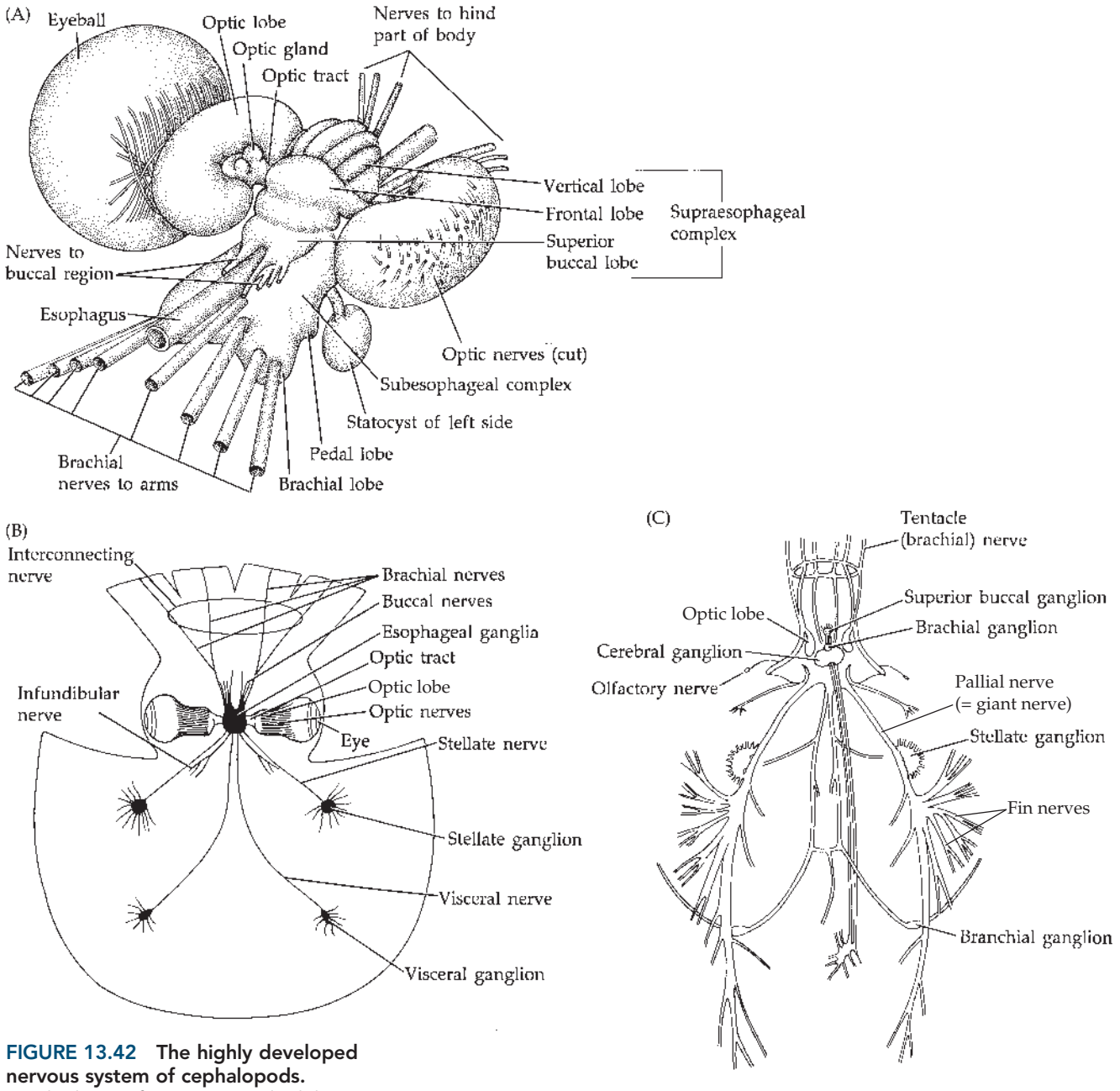

FIGURE 13.42 The highly developed nervous system of cephalopods.
(A) The brain of an octopus. The lobes of the supraesophageal complex approximately correspond to the cerebral and buccal ganglia of other molluscs, while the subesophageal complex comprises the fused pedal and pleurovisceral ganglia. About 15 structurally and functionally distinct pairs of lobes have been identified in the brain of octopuses. (B) Nervous system of an octopus. (C) Nervous system of a squid (*Loligo*). (D) Giant fiber system of a squid. Note that the first-order giant neurons possess an unusual cross connection and that the third-order giant neurons are arranged so that motor impulses can reach all parts of the mantle-wall musculature simultaneously (because impulses travel faster in thicker axons).

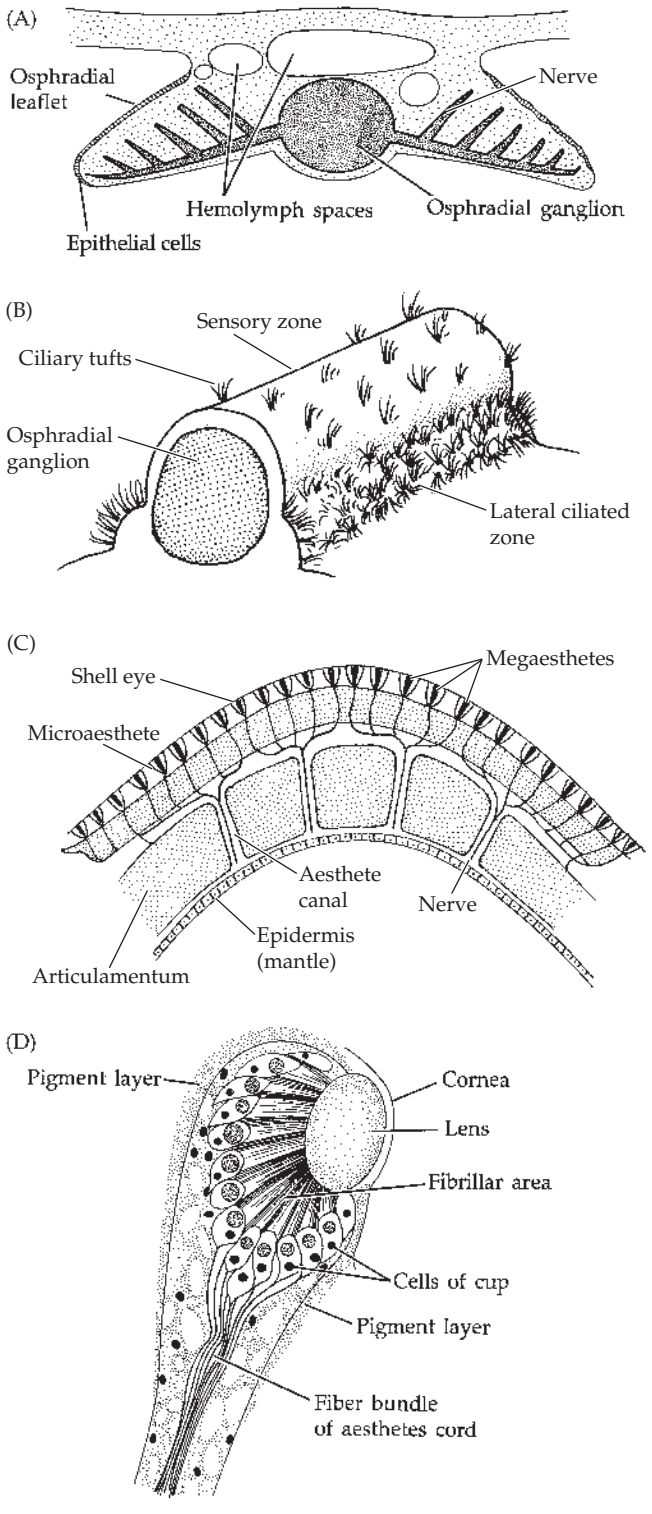

FIGURE 13.43 Two sensory organs of molluscs: osphradia and aesthetes. (A) Cross section of a bipectinate osphradium of the caenogastropod *Ranella* showing two leaflets. (B) Part of the osphradium of a littorinimorph caenogastropod such as *Littorina*. (C) One valve of a polyplacophoran (*Tonicia*). The aesthetes extend to the shell surface through megapores and micropores. (D) Eye-bearing aesthetes (longitudinal section) in a megapores of a chiton (*Acanthopleura*).

is attacked by a predator, it quickly releases a yellow chemical mixture on its trail that causes other members of the species to abort their trail-following activity. Laboratory experiments have shown that at least one nudibranch (*Tritonia tetraquetra*) possesses geomagnetic orientation to the Earth's magnetic field.

Motile gastropods usually possess a pair of closed statocysts near the pedal ganglia in the anterior region of the foot that contain either a single large **statolith** or several **statoconia** (much smaller particles).

Scaphopods lack the eyes, tentacles, and osphradia typical of the epibenthic and motile molluscan groups. The captacula may function as tactile (as well as feeding) structures. Sense organs are found on the anterior mantle edge surrounding the ventral aperture and at the dorsal water intake opening.

Bivalves have most of their sensory organs along the middle lobe of the mantle edge where they are in contact with the external environment (Figure 13.15C). These receptors may include mantle tentacles, which can contain both tactile and chemoreceptor cells. Such tentacles are commonly restricted to the siphonal areas, but in some swimming clams (e.g., *Lima*, *Pecten*) they may line the entire mantle margin. Paired statocysts usually occur in the foot near the pedal ganglia and are of particular importance in georeception by burrowing bivalves. Mantle eyes may also be present along the mantle edge or on the siphons and have evolved independently in a number of bivalve groups. In spiny oysters (*Spondylus)* and pectinid scallops, these eyes are "mirror eyes" with a reflective layer (the **tapeum**) behind paired retinas. This layer reflects light back into the eye, giving these bivalves a separate focal image on each retina—one from the lens and the other from the mirror (Figure 13.44C). The bivalve osphradium lies in the exhalant chamber, beneath the posterior adductor muscle.

Chitons lack statocysts, cephalic eyes, and tentacles. Instead, they rely largely on three special sensory structures. These are the anterior **Schwabe organs** in lepidopleuridan chitons, the **adanal sensory structures** in the posterior portion of the mantle cavity, and the **aesthetes**, which are a specialized system of photoreceptors unique to the class Polyplacophora. Aesthetes typically occur in high numbers across the dorsal surface of the shell plates. They are mantle cells that extend into the minute vertical canals (megapores and micropores) in the upper tegmentum of the shell (Figure 13.43C,D). The canals and sensory endings terminate beneath a cap on the shell surface. Little is known about the functioning of aesthetes, although the megaesthetes are known to mediate light-regulated behavior. In some (e.g., Chitonidae), they may be modified as simple lensed image-forming eyes; the lenses are made of aragonite, the same mineral that makes up chiton

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shells. The outer mantle surface of the girdle of many chitons is liberally supplied with tactile and photoreceptor cells (Figure 13.43D).

Like the rest of their nervous systems, the sense organs of cephalopods are highly developed. The eyes are superficially similar to those of vertebrates (Figure 13.44E), and these two types of eyes are often cited as a classic example of convergent evolution. The eye of a coleoid cephalopod such as *Octopus* sits in a socket associated with the cartilaginous cranium. The cornea, iris, and lens arrangement is much like that of vertebrate eyes. Also, as in vertebrates, the lens is suspended by ciliary muscles, but it has a fixed shape and focal length. An iris diaphragm controls the amount of light entering the eye, and the pupil is a horizontal slit. The

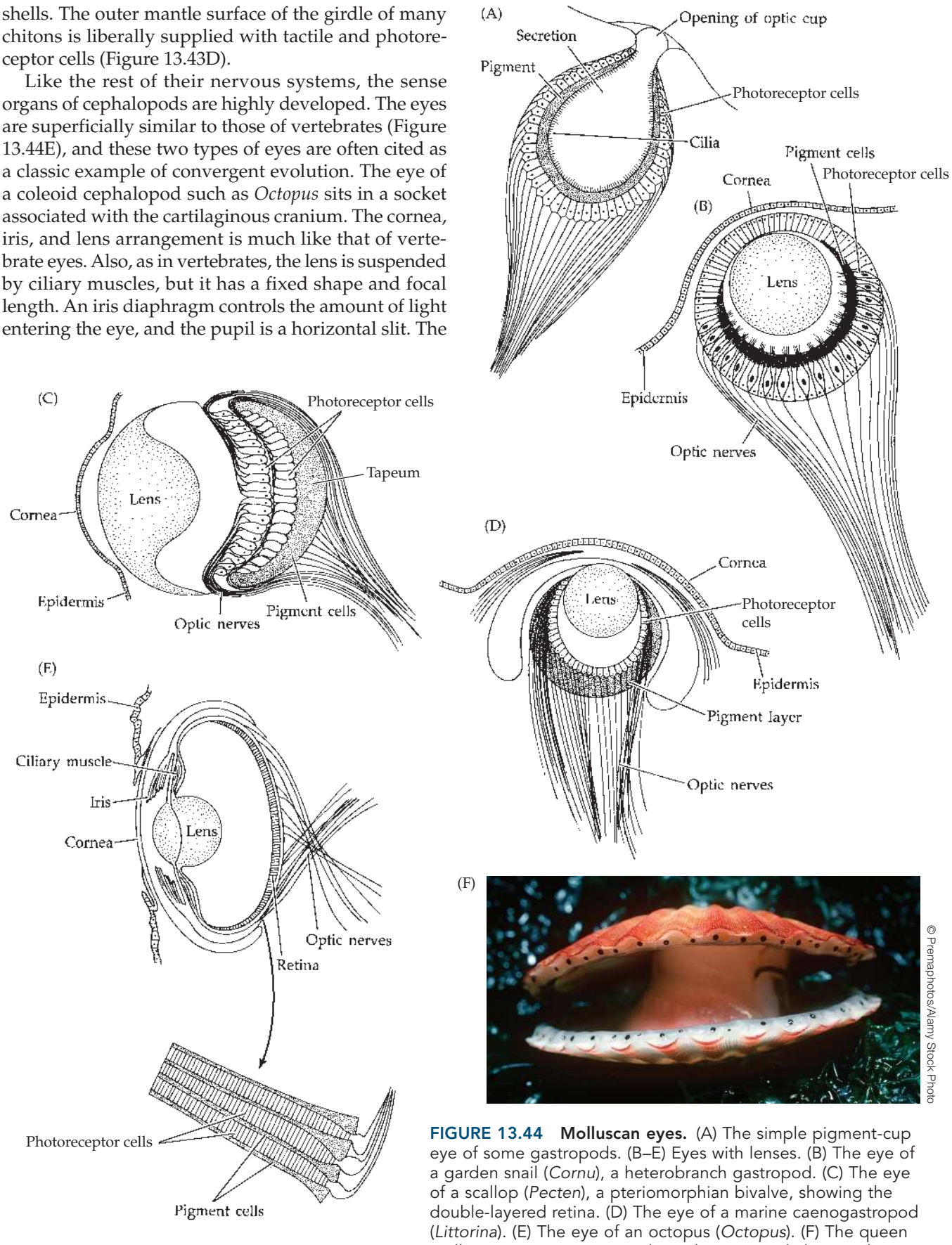

FIGURE 13.44 Molluscan eyes. (A) The simple pigment-cup eye of some gastropods. (B–E) Eyes with lenses. (B) The eye of a garden snail (*Cornu*), a heterobranch gastropod. (C) The eye of a scallop (*Pecten*), a pteriomorphian bivalve, showing the double-layered retina. (D) The eye of a marine caenogastropod (*Littorina*). (E) The eye of an octopus (*Octopus*). (F) The queen scallop *Aequipecten opercularis*, showing its dark eyes along the mantle edges.

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retina comprises closely packed, long, rodlike photoreceptors whose sensory ends point toward the front of the eye; hence the cephalopod retina is of the direct type rather than the indirect type seen in vertebrates. The rods connect to retinal cells that supply fibers to the large optic ganglia at the distal ends of the optic nerves. Unlike the corneas of vertebrates, the coleoid cornea probably contributes little to focusing, because there is almost no light refraction at the corneal surface. The coleoid eye accommodates to varying light conditions by changes in the size of the pupil and by migration of the retinal pigment. Coleoid eyes form distinct images (although octopuses are probably quite nearsighted), and experimental work suggests that they do not see colors other than as different shades of gray, although they can detect polarized light. In addition, coleoids can discriminate among objects by size, shape, and vertical versus horizontal orientation. The eyes of *Nautilus* are rather primitive relative to the eyes of coleoids. They lack a lens and are open to the water through the pupil. They are thought to function in the same way that a pinhole camera does.

Coleoids have complex statocysts that provide information on static body position and on body motion. Those of *Nautilus* are relatively simple. In addition, the arms of coleoids are well supplied with chemosensory and tactile cells, especially on the suckers of benthic octopuses, which have extremely good chemical and textural discrimination capabilities. Nautilidae are the only cephalopods with osphradia.

Cephalopod Coloration and Ink

Coleoid cephalopods are noted for their striking pigmentation and dramatic color displays. In nature, their highly dynamic skin coloration (and texture) changes, to allow rapid camouflage and intraspecies communication. The integument contains many pigment cells, or chromatophores, most of which are under nervous control. Such chromatophores can be rapidly expanded or contracted individually by means of tiny muscles attached to the periphery of each cell. Contraction of these muscles pulls out the cell and its internal pigment into a flat plate, thereby displaying the color; relaxation of the muscles causes the cell and pigment to concentrate into a tiny, inconspicuous dot. Because these chromatophores are displayed or concealed by muscle action, their activity is extremely rapid, and coleoid cephalopods can change color (and pattern) almost instantaneously. Chromatophore pigments are of several colors—black, yellow, orange, red, and blue. The chromatophore color may be enhanced by deeper layers of iridocytes that both reflect and refract light in a prismatic fashion. Some species of cuttlefish and many octopuses are capable of closely mimicking their background coloration (Figure 13.12E) as well as producing vivid contrasting colors (Figure 13.12F,G). Many epipelagic squid show a dark-above, light-below countershading similar to that seen in pelagic fishes. Most coleoids also undergo color changes in relation to behavioral rituals, such as courtship and aggression. In octopuses, many color changes are accompanied by modifications in the surface texture of the body, mediated by muscles beneath the skin—something like elaborate, controlled "gooseflesh."

In addition to the color patterns formed by chromatophores, some coleoids are bioluminescent. When present, the light organs, or photophores, are arranged in various patterns on the body, and in some cases they even occur on the eyeball. The luminescence is sometimes produced by symbiotic bacteria, but in other cases it is autogenic. The photophores of some species have a complex reflector and focusing-lens arrangement, and some even have an overlying color filter or chromatophore shutter to control the color or flashing pattern. Most luminescent species are deep-sea forms, and little is known about the role of light production in their lives. Some shallow-water sepiolids appear to use the photophores to create countershading, so as to appear less visible to predators (and prey) from below and above. Others living below the photic zone may use their glowing or flashing patterns as a means of communication, the signals serving to keep animals together in schools or to attract prey. The flashing may also play a role in mate attraction and in avoiding predation. The fire squid, *Lycoteuthis*, can produce several colors of light: white, blue, yellow, and pink. The members of at least one genus of squid, *Heteroteuthis*, secrete a luminescent ink. The light comes from luminescent bacteria cultured in a small gland near the ink sac, from which ink and bacteria are ejected simultaneously.

In most coleoid cephalopods, a large ink sac is located near the intestine (Figure 13.32H). An ink-producing gland lies in the wall of the sac, and a duct runs from the sac to a pore into the rectum. The gland secretes a brown or black fluid that contains a high concentration of melanin pigment and mucus; the fluid is stored in the ink sac. When alarmed, the animal releases the ink through the anus and mantle cavity and out into the surrounding water. The cloud of inky material hangs together in the water, forming a "dummy" image that serves to confuse predators. It may also serve as an "ink screen" obscuring the squid or its bioluminescence trail in the deep sea. The alkaloid nature of the ink may also act to deter predators, particularly fishes, and may interfere with their chemoreception.

Like virtually all other aspects of coleoid biology, the abilities to change color and to defend against predators are part and parcel of their active hunting lifestyles. In the course of their evolution, coleoid cephalopods abandoned the protection of an external shell, becoming more efficient swimmers but also exposing their fleshy bodies to predators. The evolution of camouflage and ink production, coupled with

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high mobility and complex behavior, played a major role in the success of these animals in their radical modification of the basic molluscan body plan.

Reproduction

Primitively, molluscs are mostly gonochoristic, with a pair of gonads that discharge their gametes to the water, either through the nephridial plumbing or through separate ducts. In these free-spawnning species, fertilization is external and development is indirect. Many molluscs with separate gonoducts that store and transport the gametes also have various means of internal fertilization. In these forms, direct and mixed life history patterns have evolved.

Caudofoveata are gonochoristic, and Solenogastres are hermaphroditic (Figure 13.45). In both aplacophoran groups the paired gonads discharge gametes by way of short gonopericardial ducts into the pericardial chamber, from which they pass through gametoducts to the mantle cavity. In the Solengastres fertilization is internal and the young are sometimes brooded, while in the Caudofoveata the gametes are discharged into the surrounding seawater, where fertilization occurs.

Monoplacophorans possess two pairs of gonads, each with a gonoduct connected to a nephridium (Figures 13.3D and 13.14E). One tiny monoplacophoran species, *Micropilina arntzi,* is a hermaphrodite and broods its embryos in its mantle cavity.

Most chitons are gonochoristic, although a few hermaphroditic species are known. In chitons, the two gonads are fused and situated medially in front of the pericardial cavity (Figure 13.4F). Gametes are transported directly to the outside by two separate gonoducts. The gonopores are located in the exhalant region of the mantle groove, one in front of each nephridiopore. Fertilization is external but can occur in the mantle cavity of the female. The eggs are enclosed within a spiny, buoyant membrane (hull)—with a striking case of coevolution in which the sperm head has elongated to be able to reach the egg surface—and are released into the sea individually or in strings. A few chitons brood their embryos in the mantle groove, and in one species (*Calloplax vivipara*) development takes place entirely within the ovary.

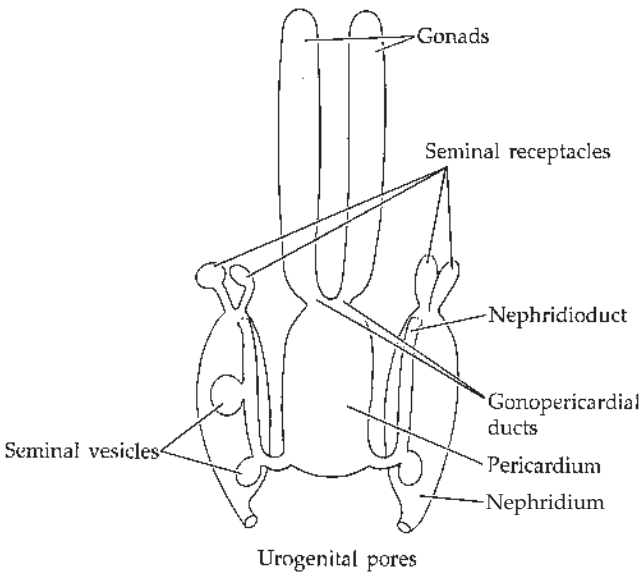

FIGURE 13.45 **A solenogaster urogenital system.**

In living gastropods, one gonad has been lost and the remaining one is usually located with the digestive gland in the visceral mass. The gonoduct is developed in association with the right nephridium in patellogastropods and vetigastropods (Figure 13.46A), while in neritimorphs and caenogastropods a vestige of the right nephridium is incorporated in the oviduct. In cases where the right nephridium is still functional in transporting excretory products, as in the patellogastropods and vetigastropods, the gonoduct is properly called a urogenital duct, because it discharges both gametes and urine.

Gastropods may be gonochoristic or hermaphroditic, but even in the latter case usually only a single gonad (an ovotestis) exists, although a few heterobranchs have separate male and female gonads (e.g., *Omalogyra* and the mathildid *Tuba valkyrie*), while others are protandric. The commitment of the right nephridial plumbing entirely to serving the reproductive system was a major event in gastropod evolution. The isolation of the reproductive tract allowed its independent evolution, without which the great variety of reproductive and developmental patterns in gastropods may never have been possible.

In many gastropods with isolated reproductive tracts, the female system bears a ciliated fold or tube that forms a vagina and oviduct (or pallial oviduct). During development, the tube extends inward from the mantle wall and connects with the genital duct. The oviduct may bear specialized structures for sperm storage or egg case secretion. An organ for storing received sperm, the seminal receptacle, often lies near the ovary at the proximal end of the oviduct. Eggs are fertilized at or near this location prior to entering the long secretory portion of the oviduct. Many female systems also have a copulatory bursa, usually at the distal end of the oviduct, where sperm are received during mating. In such cases the sperm are later transported along a ciliated groove in the oviduct to the seminal receptacle, near where fertilization takes place. The secretory section of the oviduct may be modified as an albumin gland and a mucous or capsule gland. Many heterobranchs lay fertilized eggs in jellylike mucopolysaccharide masses or strings produced by these glands. Most terrestrial eupulmonates produce a small number of large, individual, yolky eggs, which are often provided with calcareous shells. Other eupulmonates brood their embryos internally and give birth to juveniles. Many

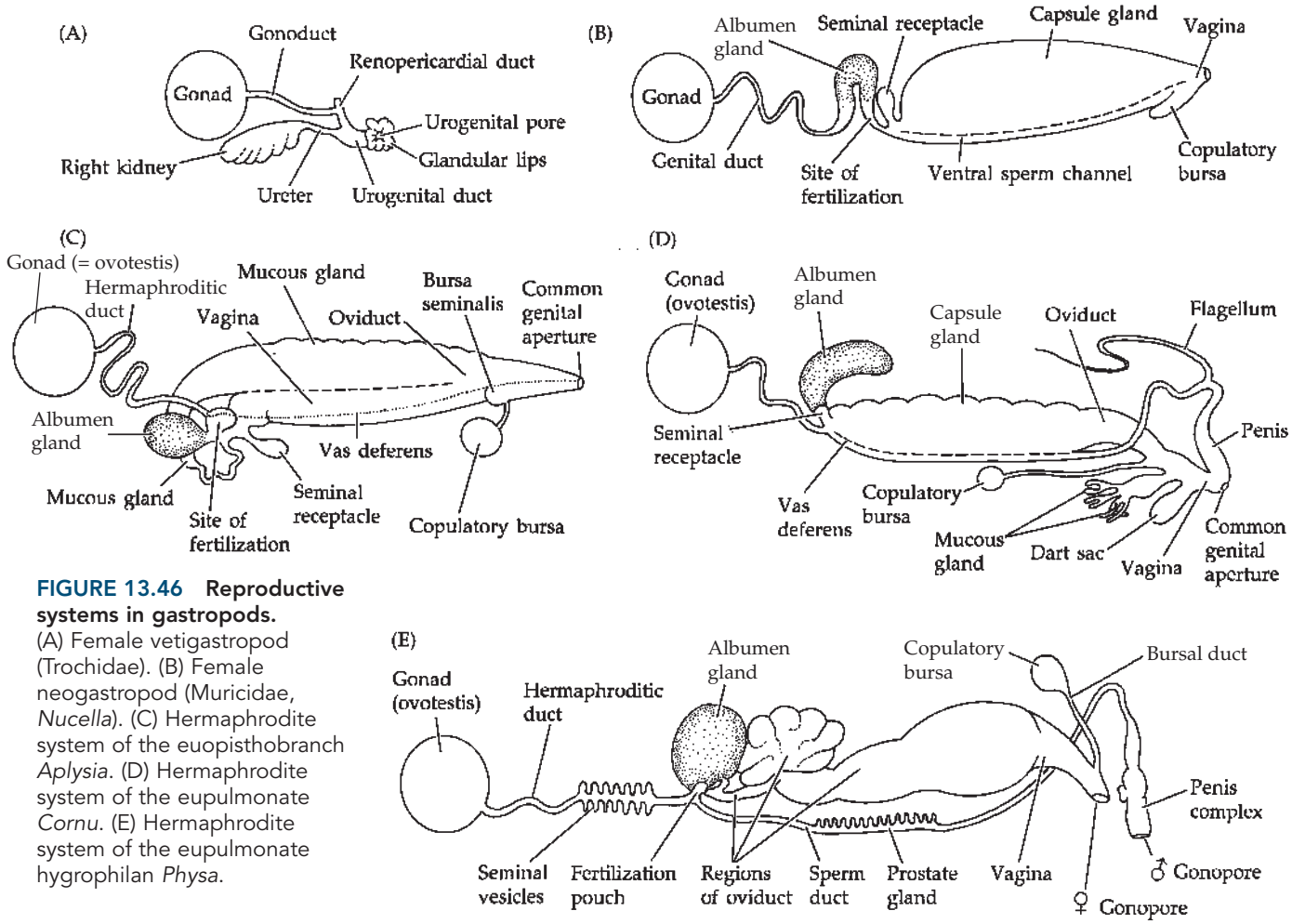

FIGURE 13.46 Reproductive systems in gastropods. (A) Female vetigastropod (Trochidae). (B) Female neogastropod (Muricidae, *Nucella*). (C) Hermaphrodite system of the euopisthobranch *Aplysia*. (D) Hermaphrodite system of the eupulmonate *Cornu*. (E) Hermaphrodite system of the eupulmonate hygrophilan *Physa*.

caenogastropods produce egg capsules in the form of leathery or hard cases that are attached to objects in the environment, thereby protecting the developing embryos. A ciliated groove is often present to conduct the soft egg capsules from the female gonopore down to a gland in the foot, where they are molded and attached to the substratum.

The male genital duct, or vas deferens, often includes a prostate gland for production of seminal secretions. In many gastropods the proximal region of the vas deferens functions as a sperm storage area, or seminal vesicle. In many caenogastropods, neritimorphs, and the so-called "lower heterobranchs," the males have an external penis to facilitate transfer of sperm (Figures 13.6 and 13.47), and internal fertilization takes place prior to formation of the egg case. The penis is a long extension of the body wall, usually arising behind the right cephalic tentacle. In these groups with a cephalic penis, most of the glandular parts of the reproductive system lie within the mantle cavity or may extend back alongside the nephridium. In most euthyneurans, these parts of the reproductive system have migrated into the body cavity and the penis has become a retractile, internal structure. Sperm transfer in some gastropods involves the use of **spermatophores**, either involving a penis or without one, as in the cerithiomorph groups and some others. In some, large sterile parasperm are used to transport the normal sperm.

With both simultaneous and sequential hermaphrodite gastropods, copulation is the rule—either with one individual acting as the male and the other as the female, or with a mutual exchange of sperm between the two. Sedentary species, such as territorial limpets and slipper shells, are often protandric hermaphrodites. In slipper shells (e.g., *Crepidula fornicata*), individuals may stack one atop the other (Figure 13.48), with the more recently settled individuals being males on top of the stack, females on the bottom. Each male (Figure 13.47B) uses its long penis to inseminate the females (Figure 13.47C) below. Males that are in association with females tend to remain male for a relatively long period of time. Eventually, or if isolated from a female, the male develops into a female. Female slipper shells cannot switch back to males, because the masculine reproductive system degenerates during the sex change.

Most eupulmonates are simultaneous hermaphrodites, although protandric hermaphrodites sometimes occur. In most simultaneous hermaphrodite euthyneurans a single complex gonad, the ovotestis, produces both eggs and sperm (Figures 13.46C–E and 13.47D),

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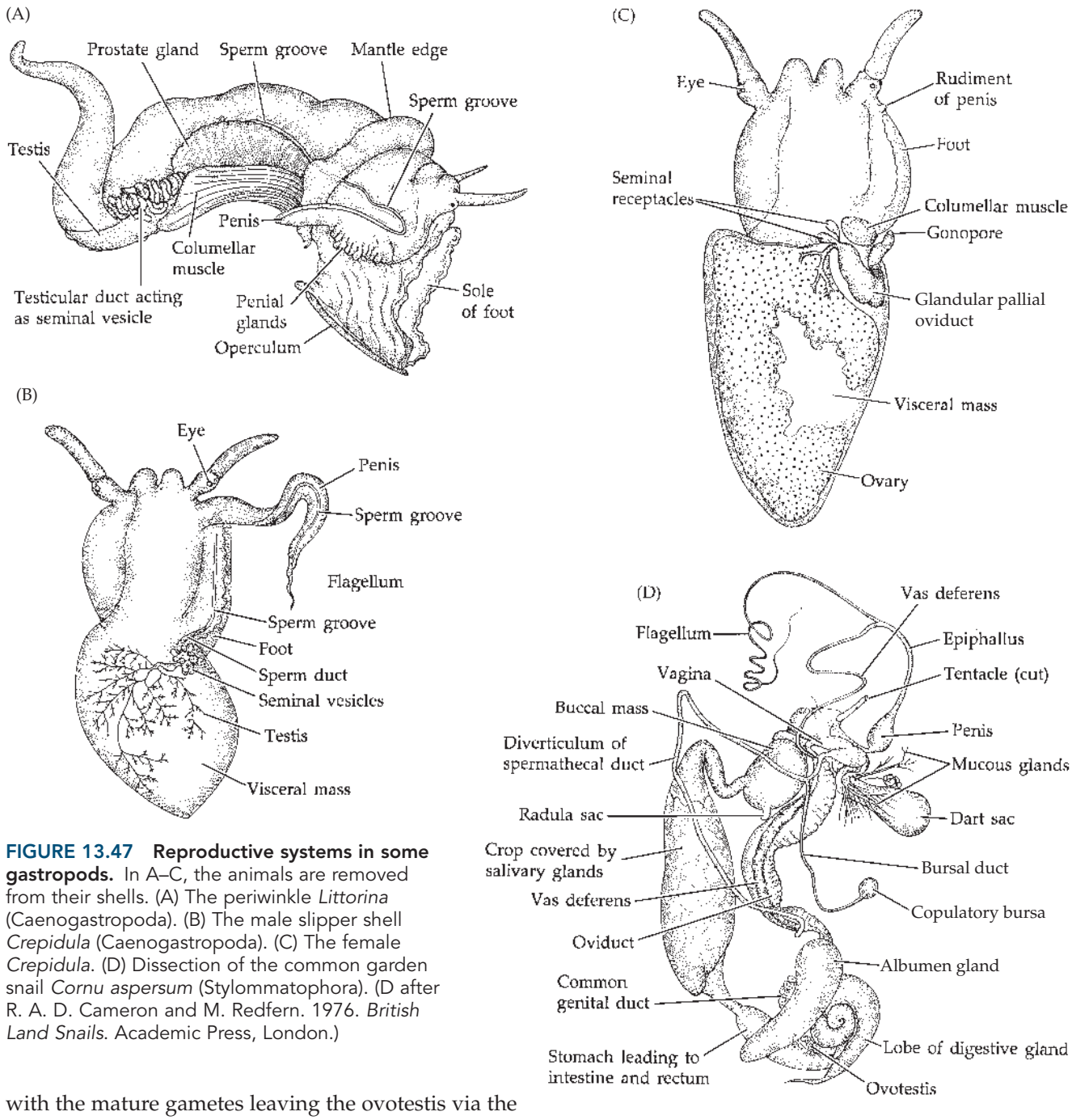

FIGURE 13.47 Reproductive systems in some gastropods. In A–C, the animals are removed from their shells. (A) The periwinkle *Littorina* (Caenogastropoda). (B) The male slipper shell *Crepidula* (Caenogastropoda). (C) The female *Crepidula*. (D) Dissection of the common garden snail *Cornu aspersum* (Stylommatophora). (D after R. A. D. Cameron and M. Redfern. 1976. *British Land Snails*. Academic Press, London.)

with the mature gametes leaving the ovotestis via the hermaphroditic duct. Euthyneuran reproductive systems are amazingly complex and varied in their plumbing and structure; they may have separate male and female gonopores or only a single common gonopore (Figure 13.46D,E).

Distinct precopulatory behaviors occur in a few groups of gastropods. These courtship routines are best documented in land eupulmonates and include behaviors such as oral and tentacular stroking, and intertwining of the bodies. In some eupulmonates (e.g., the common garden snail, *Cornu*, formerly *Helix*) the vagina contains a dart sac, which secretes a calcareous harpoon. As courtship reaches its crescendo and a pair of snails is intertwined, one will drive its dart into the body wall of the other. The dart is coated with mucus that contains a hormonelike substance that enhances the shooter's paternity.

Most bivalves are gonochoristic and retain the primitively paired gonads. However, the gonads are large and closely invested with the viscera and with each other, so an apparently single gonadal mass results. The gonoducts are simple tubes, and fertilization is usually external, although some marine and most freshwater species brood their embryos for a time. In protobranch bivalves, the gonoducts join the nephridia, and gametes are released through urogenital pores. In autobranch bivalves, the gonoducts open into the

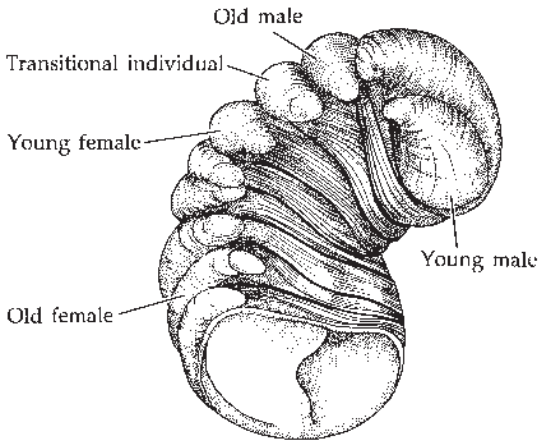

Photo courtesy of David McIntyre

FIGURE 13.48 **A stack of *Crepidula fornicata*, a slipper shell (Caenogastropoda), displaying sequential hermaphroditism.**

mantle cavity separately from the nephridiopores. Hermaphroditism occurs in some bivalves, including shipworms and some species of cockles, oysters, scallops, anomalodesmatans, and others. Oysters of the genus *Ostrea* are sequential hermaphrodites, and most are capable of switching sex in either direction. Shipworms (Teredinidae) remain confined to the wood they colonize as larvae, and this has led to some interesting reproductive strategies, from broadcast spawning to spermcasting, larval brooding, and extreme sexual size dimorphism with male dwarfism. Some shipworms engage in pseudocopulation, a form of direct fertilization where groups of neighboring individuals simultaneously inseminate one another via their siphons (the only part of the animal extending beyond the burrow), and they are the only bivalves known to do so. This has led to copulatory behaviors such as siphon wrestling and the removal of a rival's spermatozoa from the siphons of a recipient.

Cephalopods are almost all gonochoristic, with a single gonad in the posterior region of the visceral mass (Figures 13.11C, 13.12B, and 13.49). The testis releases sperm to a coiled vas deferens, which leads anteriorly to a seminal vesicle. Here various glands assist in packaging the sperm into elaborate spermatophores, which are stored in a large reservoir called **Needham's sac**. From there the spermatophores are released into the mantle cavity via a sperm duct. In females the oviduct terminates in one oviducal gland in squid, and two in octopuses. This gland secretes a protective membrane around each egg.

The highly developed nervous system of cephalopods has facilitated the evolution of some very sophisticated precopulatory behaviors, which culminate in the transfer of spermatophores from the male to the female. Because the oviducal opening of females is deep within the mantle chamber, male coleoids use one of their arms as an intromittent organ to transfer the spermatophores. These modified arms are called **hectocotyli** (Figures 13.12D and 13.49B). In squid and cuttlefish the right or left fourth arm is used; in octopuses it is the right third arm. In *Nautilus* four small arms form a conical organ, the **spadix**, that functions in sperm transfer. Hectocotylus arms have special suckers, spoonlike depressions, or superficial chambers for holding spermatophores during the transfer, which may be a brief or a very lengthy process.

Each spermatophore comprises an elongate sperm mass, a cement body, a coiled and "spring-loaded" ejaculatory organ, and a cap. The cap is pulled off as the spermatophore is removed from the Needham's sac in squid or by uptake of seawater in octopuses. Once the cap is removed, the ejaculatory organ everts, pulling the sperm mass out with it. The sperm mass adheres by means of the cement body to the seminal receptacle or mantle wall of the female, where it disintegrates and liberates sperm for up to two days.

Precopulatory rituals in coleoid cephalopods usually involve striking changes in coloration, as the male tries to attract the female (and discourage other males in the

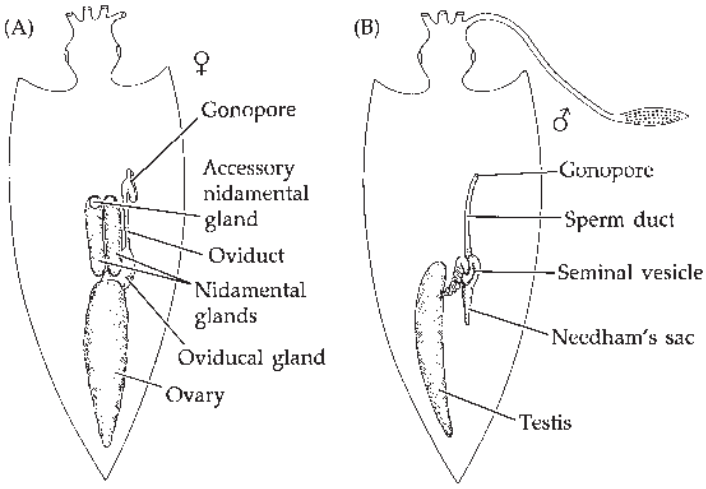

FIGURE 13.49 **Reproductive systems in a coleoid cephalopod, the squid *Loligo*.** (A) Female. (B) Male.

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area). Male squid often seize the female partner with the tentacles, and the two swim head-to-head through the water. Eventually the male's hectocotylus grabs a spermatophore and inserts it into the mantle chamber of his partner, near or in the oviducal opening. Mating in octopuses can be a savage affair. The exuberance of the copulatory embrace may result in the couple tearing at each other with their sharp beaks, or even strangulation of one partner by the other as the former's arms wrap around the mantle cavity of the latter, cutting off ventilation. In many octopuses (e.g., *Argonauta*, *Tremoctopus*) the tip of the hectocotylus arm may break off and remain in the female's mantle chamber.[8]

As the eggs pass through the oviduct, they are covered with a capsulelike membrane produced by the oviducal gland. Once in the mantle cavity, various kinds of **nidamental glands** may provide additional layers or coatings on the eggs. In squid like *Doryteuthis*, which migrate to shallow water to breed, the nidamental glands coat the eggs within an oblong gelatinous mass, each containing about 100 eggs. The female holds these egg cases in her arms and fertilizes them with sperm ejected from her seminal receptacle. The egg masses harden as they react with seawater and are then attached to the substratum. The adults die after mating and egg laying. Cuttlefish deposit single eggs and attach them to seaweed or other substrata. Many open-ocean pelagic coleoids have floating eggs, and the young develop entirely in the plankton. Octopuses usually lay grapelike egg clusters in dens in rocky areas, and many species care for the developing embryos by protecting them and by aerating and cleaning them by flushing the egg masses with jets of water. Octopuses and squid tend to grow quickly to maturity, reproduce, and then die, usually within a year or two. The chambered nautilus, however, is long-lived (perhaps to 25–30 years), slow growing, and able to reproduce for many years after maturity.

One of the most astonishing reproductive behaviors among invertebrates occurs in members of the pelagic octopod genus *Argonauta*, known as the paper nautiluses. Female argonauts use two specialized arms to secrete and sculpt a beautiful, coiled, calcareous shell-like egg case into which eggs are deposited (Figure 13.17B). The thin-walled, delicate shell is carried by the female and serves as her temporary home and as a brood chamber for the embryos. The much smaller male often cohabits the egg case with the female.

Development

Development in molluscs is similar in many fundamental ways to that of the other spiralian protostomes. Most molluscs undergo typical spiral cleavage, with the mouth and stomodeum typically developing from the blastopore, and the anus forming as a new opening on the gastrula wall (protostomous). Cell fates are also typically spiralian, including a 4d mesentoblast.

By the end of the 64-cell stage, the distinctive molluscan cross is typically formed by a group of apical micromeres ($1a^{12}$–$1d^{12}$ cells and their descendants, with cells $1a^{112}$–$1d^{112}$ forming the angle between the arms of the cross) (Figure 13.50). This configuration of blastomeres appears to be just one of several patterns found in lophotrochozoans. As detailed studies are conducted on more and more species, the phylogenetic implications of these variations are being evaluated.

Development may be direct, mixed, or indirect. During indirect development, the free-swimming trochophore larva that develops is remarkably similar to that seen in annelids (Figure 13.51). Like the annelid larva, the molluscan trochophore bears an apical sensory plate with a tuft of cilia and a girdle of ciliated cells—the prototroch—just anterior to the mouth.

In some free-spawning molluscs (e.g., Polyplacophora and Caudofoveata), the trochophore is the only larval stage, and it metamorphoses directly into the juvenile (Figure 13.51C). Solenogasters and protobranch bivalves usually have a so-called "test cell larva," or pericalymma where a bell-shaped larval test encloses parts of the developing embryo. But in other groups (e.g., gastropods and autobranch bivalves), the trochophore is followed by a uniquely molluscan larval stage called a veliger (Figure 13.52). The **veliger larva** may possess a foot, shell, operculum, and other adult-like structures. The most characteristic feature of the veliger larva is the swimming organ, or **velum**, which consists of two large ciliated lobes developed from the trochophore's prototroch. In some species the velum is also a feeding organ

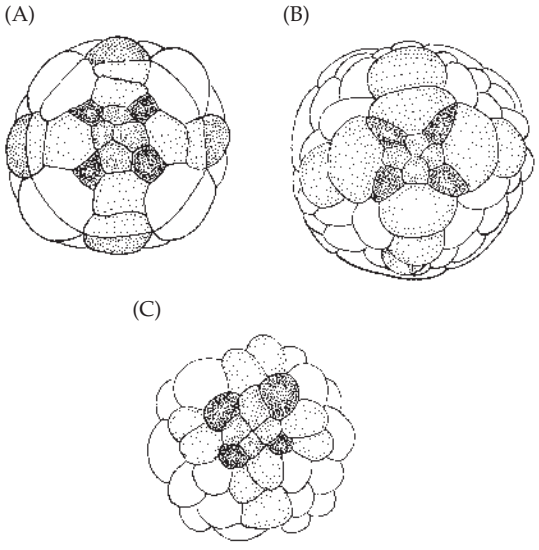

FIGURE 13.50 The "molluscan cross" of developing embryos. (A) Gastropoda (*Lymnaea*). (B) Polyplacophora (*Stenoplax*). (C) Solenogastres (*Epimenia*).

[8]The detached arm was mistakenly first described as a parasitic worm and given the genus name *Hectocotylus* (hence the origin of the term)

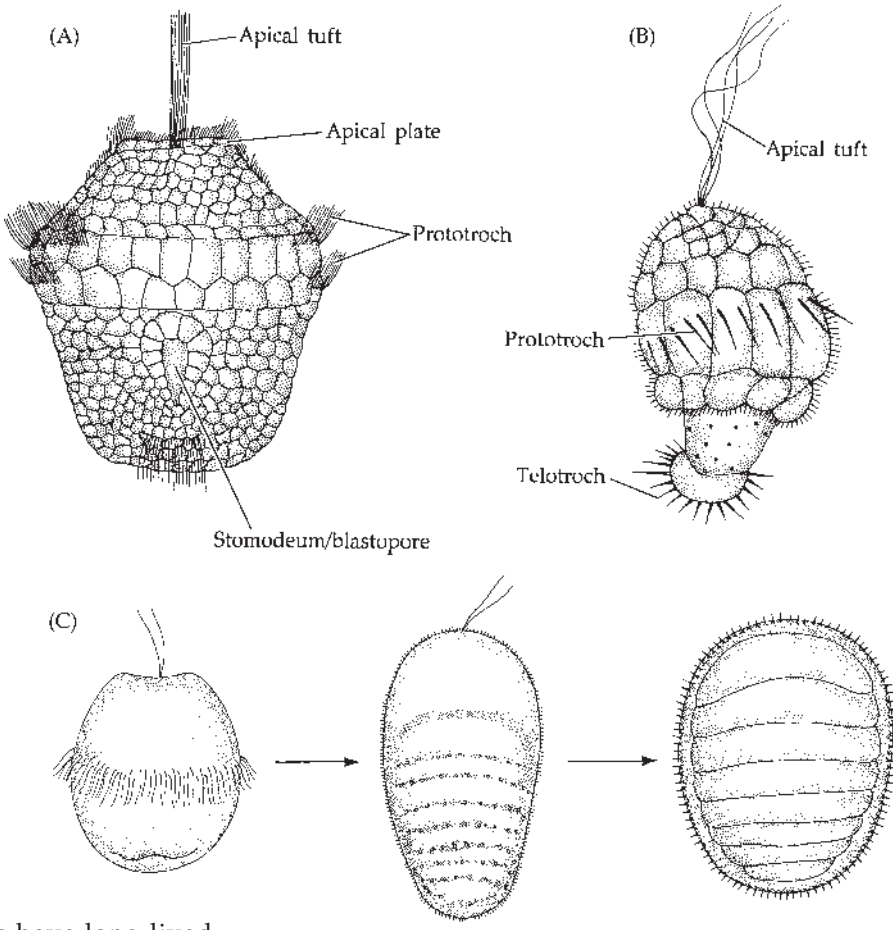

FIGURE 13.51 Molluscan trochophore larvae. (A) Generalized molluscan trochophore larva. (B) Trochophore of a solengaster aplacophoran. (C) Metamorphosis of a polyplacophoran from trochophore to juvenile.

and is subdivided into four, five, or even six separate lobes (Figure 13.52C). Feeding (planktotrophic) veligers capture particulate food between opposed prototrochal and metatrochal bands of cilia on the edge of the velum, others are non-feeding (lecithotrophic) and live on yolk reserves. Eventually eyes and tentacles appear, and the veliger transforms into a juvenile, settles to the bottom, and assumes an adult existence.

Like gastropods, some bivalves have long-lived planktotrophic veligers, whereas others have short-lived lecithotrophic veligers. Many widely distributed species have very long larval lives that allow dispersal over great distances. A few bivalves have mixed development and brood the developing embryos in the suprabranchial cavity through the trochophore period; then the embryos are released as veliger larvae. Some marine and freshwater clams have direct development, as for example in the freshwater family Sphaeriidae where embryos are brooded between the gill lamellae and juveniles shed into the water when development is completed. Several unrelated marine groups have independently evolved a similar brooding behavior (e.g., philobryids such as *Lissarca miliaris*, some archiheterodonts and galeommatoideans, etc.).

In the freshwater clams (Unionidae), the embryos are also brooded between the gill lamellae, where they develop into highly modified veligers adapted for a parasitic phase on fishes, thereby facilitating dispersal. These parasitic larvae are called **glochidia** (Figure 13.52E). They attach to the skin or gills of the host fish by a sticky mucus, hooks, or other attachment devices. Most glochidia lack a gut and absorb nutrients from the host by means of special phagocytic mantle cells. The host tissue often forms a cyst around the glochidium. Eventually the larva matures, breaks out of the cyst, drops to the bottom, and assumes its adult life.

Among gastropods, only patellogastropods and vetigastropods rely on external fertilization and retain a free-swimming trochophore larva. All other gastropods suppress the trochophore or pass through it quickly before hatching. In many groups embryos hatch as veligers (e.g., many neritimorphs, caenogastropods and heterobranchs). Some of these gastropods have planktotrophic veligers that may have brief or extended (to several months) free-swimming lives. Others have lecithotrophic veligers that remain planktonic only for short periods (sometime less than a week). Planktotrophic veligers feed by use of the velar cilia, whose beating drives the animal forward and draws minute planktonic food particles into contact with the shorter cilia of a food groove. Once in the food groove, the particles are trapped in mucus and carried along ciliary tracts to the mouth.

Almost all eupulmonates and many caenogastropods have direct development, and the veliger stage is passed in the egg case, or capsule. Upon hatching, tiny snails crawl out of the capsule into their adult habitat. In some neogastropods (e.g., certain species of *Nucella*), the encapsulated embryos cannibalize their siblings, a phenomenon called **adelphophagy**; consequently, only one or two juveniles eventually emerge from each capsule.

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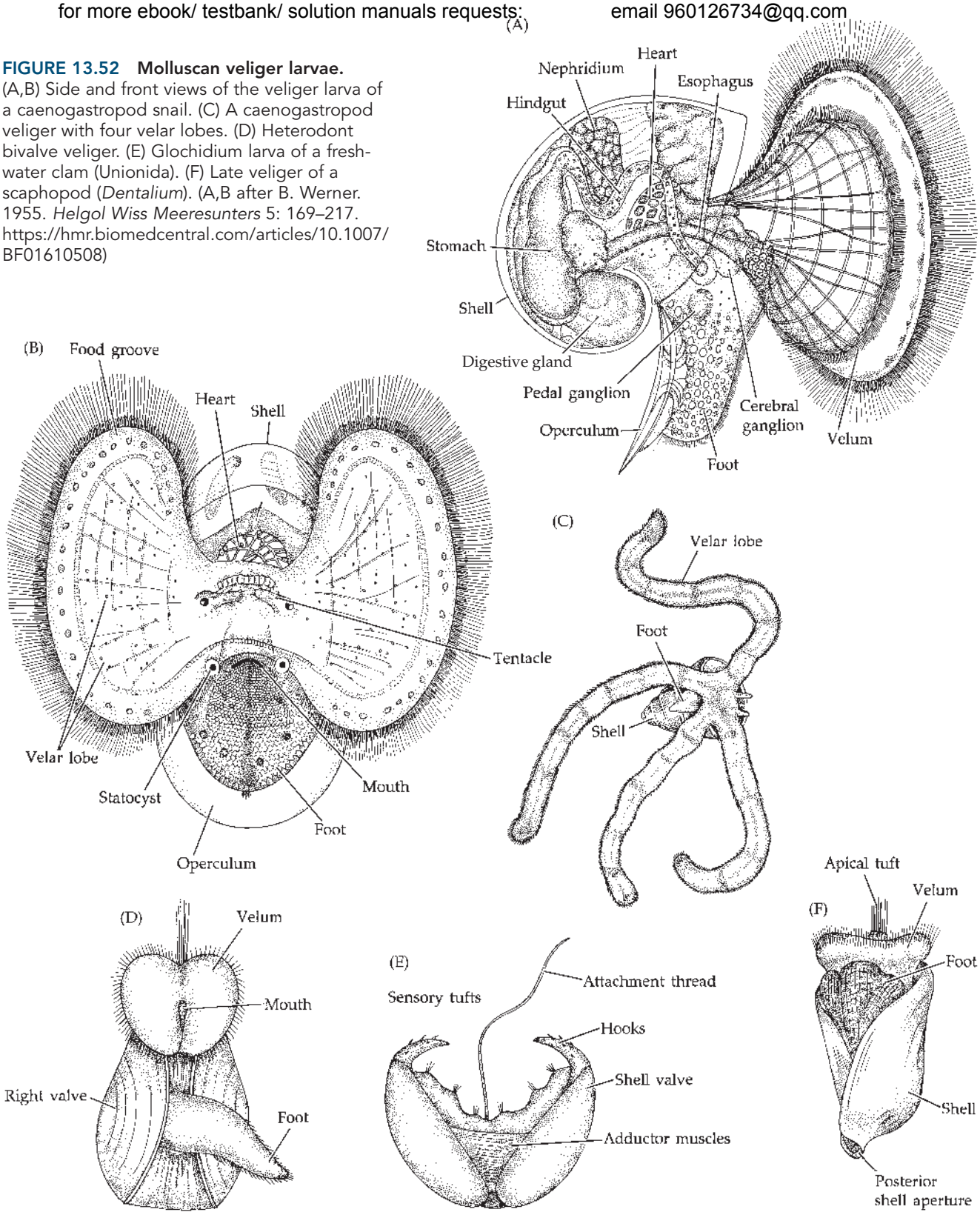

FIGURE 13.52 Molluscan veliger larvae. (A,B) Side and front views of the veliger larva of a caenogastropod snail. (C) A caenogastropod veliger with four velar lobes. (D) Heterodont bivalve veliger. (E) Glochidium larva of a freshwater clam (Unionida). (F) Late veliger of a scaphopod (*Dentalium*). (A,B after B. Werner. 1955. *Helgol Wiss Meeresunters* 5: 169–217. https://hmr.biomedcentral.com/articles/10.1007/BF01610508)

It is usually during the veliger stage that gastropods undergo torsion (see the previous section Torsion, or "How the Gastropod Got its Twist"), when the shell and visceral mass twist relative to the head and foot (Figures 13.18 and 13.53). As we have seen, this phenomenon is still not fully understood, but it has most probably played a major role in gastropod evolution.

Cephalopods produce large, yolky, telolecithal eggs. Development is always direct, the larval stages having been lost entirely during evolution of the yolk-laden

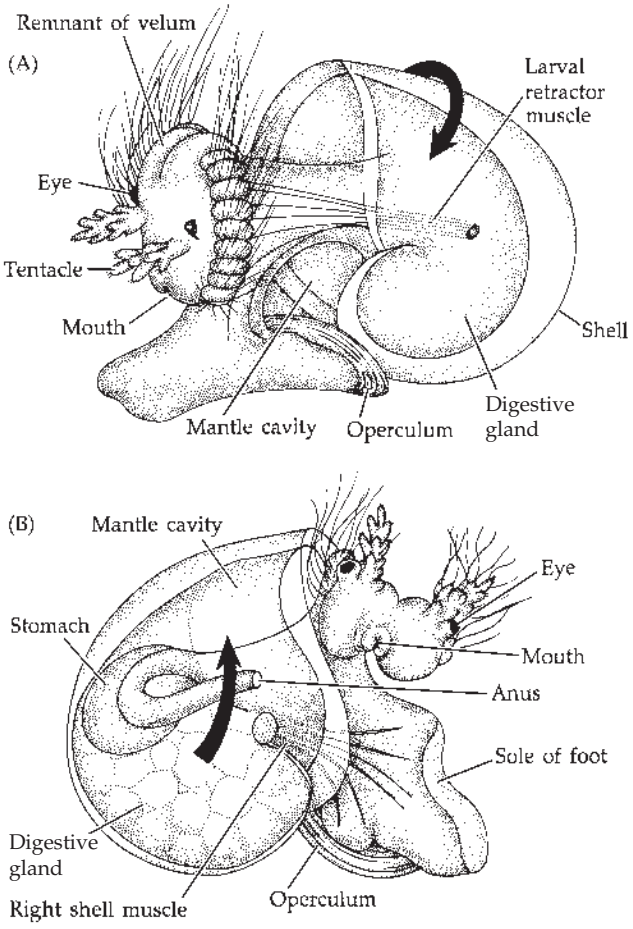

FIGURE 13.53 Settled larva of the abalone (*Haliotis*) undergoing torsion. (A) Left-side view after about 90° of torsion, with mantle cavity on the right side. (B) Torsion continues as the mantle cavity and its associated structures twist forward over the head.

embryo that develops within the egg case. Early cleavage is meroblastic and eventually produces a cap of cells (a discoblastula) at the animal pole, without remnants of the spiral cleavage typical of other molluscs. The embryo grows in such a way that the mouth opens to the yolk sac, and the yolk is directly "consumed" by the developing animal (Figure 13.54).

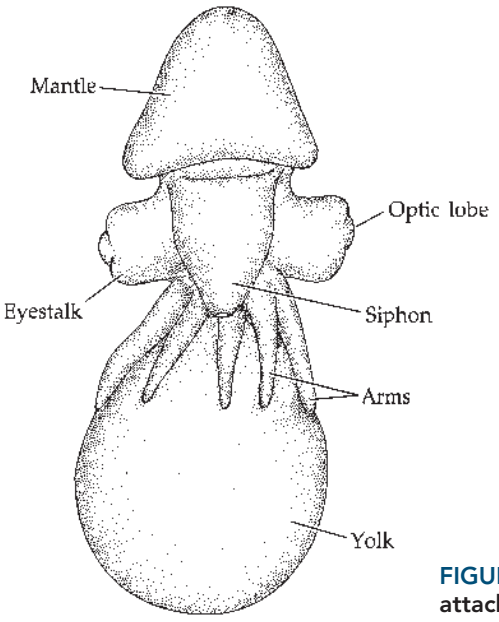

FIGURE 13.54 Juvenile coleoid cephalopod attached to and consuming its sac of yolk.

Molluscan Evolution and Phylogeny

The phylogenetic details of molluscan evolution have yet to be thoroughly elucidated. The phylum is highly diverse, and many named taxa below the class level are known to be polyphyletic or paraphyletic. The existence of a good fossil record (primarily of shells) has been both a blessing and a curse, as efforts to trace the evolutionary history of molluscs have often been frustrated by the limited and sometimes confusing data molluscan shells have provided.

Until fairly recently, the idea of a "hypothetical ancestral mollusc" (HAM) was popular, the nature of which derived largely from early work of the eminent British biologist and "Darwin's Bulldog," T. H. Huxley. Detailed and sometimes highly imaginative descriptions of this hypothetical ancestral mollusc were proposed by various workers, even including speculations on its physiology, ecology and behavior (see Lindberg and Ghiselin 2003). The usefulness of HAM in molluscan evolutionary studies was questioned as zoology moved into an era of explicit phylogenetic analysis (i.e., cladistics). Thus, most workers now avoid the pitfalls of a priori construction of a hypothetical ancestor and instead analyze the evolutionary history of molluscs by phylogenetic inference. Although morphological analyses of molluscan relationships have differed in some details, the phylogenetic relationships resulting from this work have been similar. In contrast, more recent molecular analyses of molluscan relationships have produced several alternative trees depending on the molecular data type and analytical methods.. The phylogeny summarized here (Figure 13.55) is one of the possible scenarios of molluscan evolution. The characters used to construct the cladogram are enumerated in the figure legend and briefly summarized in the following discussion. The nodes on the cladogram have been lettered to facilitate the discussion.

Exactly where the molluscs arose within the lophotrochozoan clade, along with their kinship to the other phyla, are still matters of debate. While some workers treat them as descendant from a segmented ancestor, most do not. We support the idea that molluscs arose from a nonsegmented precursor. Some molecular studies (see the References) have suggested the Brachiozoa (Brachiopoda and Phoronida) as the sister group of the molluscs, with the annelids nested outside of the Mollusca + Brachiozoa. This placement is

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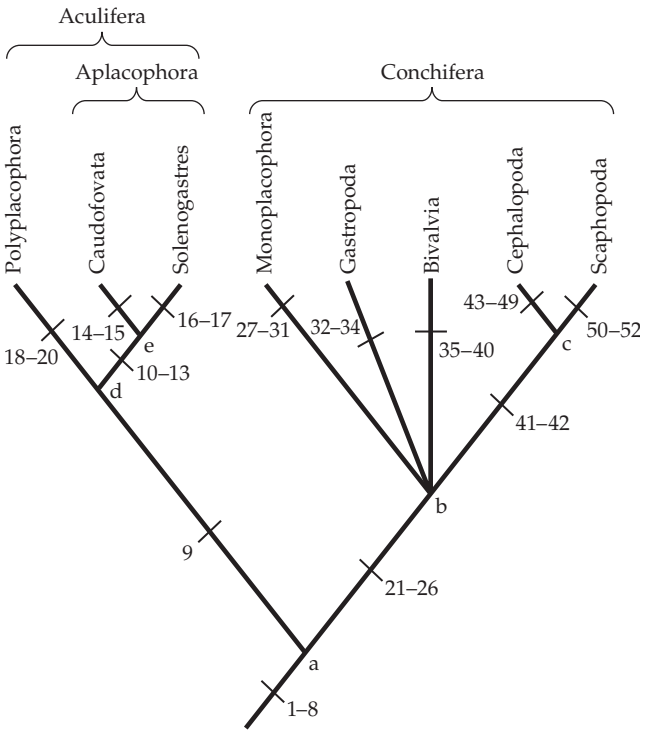

FIGURE 13.55 A cladogram depicting a conservative view of the phylogeny of the Mollusca. This cladogram is based on current hypotheses; see Sigwart and Lindberg (2015) and Ponder et al. (2020) for alternative molluscan phylogenies. The numbers on the cladogram indicate suites of synapomorphies for each hypothesized line or clade.

Phylum Mollusca at node a: (1) reduction of the coelom and development of an open hemocoelic circulatory system; (2) dorsal body wall forms a mantle; (3) extracellular production of calcareous sclerites (and/or shell) by mantle shell glands; (4) ventral body wall muscles develop as muscular foot (or foot precursor); (5) radula; (6) chambered heart with separate atria and ventricle; (7) increase in gut complexity, with large digestive glands; (8) ctenidia.

Aculifera (Aplacophora + Polyplacophora) node d: (9) sclerites.

Aplacophora (Caudofoveata + Solenogastres) node e: (10) vermiform body; (11) foot reduced; (12) gonads empty into pericardial cavity, exiting to mantle cavity via U-shaped gametoducts; (13) without nephridia.

Caudofoveata: (14) calcareous sclerites of the body wall form imbricating scales; (15) complete loss of foot.

Solenogastres: (16) posterior end of reproductive system with copulatory spicules; (17) loss of ctenidia.

Polyplacophora: (18) shell with 8 plates (and with 8 shell gland regions), articulamentum layer, and aesthetes; (19) multiple ctenidia; (20) expanded and highly cuticularized mantle girdle that "fuses" with shell plates.

Conchifera node b: (21) presence of a well-defined single shell gland region and larval shell (protoconch); (22) shell univalve (of a single piece; note that the bivalve shell is derived from the univalve condition); (23) shell of basically 3 layers (periostracum, prismatic layer, lamellar or crossed layer); (24) mantle margin of 3 parallel folds, each specialized for specific functions; (25) statocysts; (26) viscera concentrated dorsally.

Monoplacophora: (27) 3–6 pairs of ctenidia; (28) 3–7 pairs of nephridia; (29) 8 pairs of pedal retractor muscles; (30) 2 pairs of gonads; (31) 2 pairs of heart atria.

Gastropoda: (32) torsion; (33) cephalic tentacles; (34) operculum.

Bivalvia: (35) bivalve shell and its associated mantle and (in autobranch bivalves) ctenidial modifications; (36) loss of radula; (37) byssus (autobranchs); (38) lateral compression of body; (39) adductor muscles; (40) ligament.

Cephalopod-scaphopod lineage node c: (41) ano-pedal flexure; (42) new neuroanatomical features, including cerebral ganglia fusion and position.

Cephalopoda: (43) expansion of the coelom and closure of the circulatory system; (44) septate shell; (45) ink sac (in coleoids); (46) siphuncle; (47) beaklike jaws; (48) foot modified as prehensile arms/tentacles and funnel (= siphon); (49) development of large brain.

Scaphopoda: (50) tusk-shaped, shell open at both ends; (51) loss of heart and ctenidia; (52) captacula.

surprising, as molluscs have spiral cleavage while the brachiopods have radial cleavage; however both radial and spiral cleavage patterns are present in phoronids—see Chapter 16. In addition, the molluscan coelom is formed through schizocoely, while the brachiopods are characterized by enterocoely.

The major steps in the evolution of what we generally think of as a "typical" mollusc—that is, a shelled mollusc—also remain controversial. Previous scenarios have often argued that the first step took place after the origin of the aplacophorans, perhaps as molluscs adapted to active epibenthic lifestyles. These steps centered largely on the elaboration of the mantle and mantle cavity, the refinement of the ventral surface as a well-developed muscular foot, and the evolution of a consolidated dorsal shell gland and solid shell(s) in place of independent calcareous sclerites.

The description of a solenogaster larva by Pruvot in 1890, in which the dorsal surface was said to bear seven transverse bands of sclerites (described as "composite plates," reminiscent of chitons), led some workers to postulate that aplacophorans and polyplacophorans might be sister groups; this relationship was confirmed by several phylogenomic studies (e.g., Kocot et al. 2011, Smith et al. 2011). However, the discovery from Silurian deposits in England of a possible aplacophoran fossil having seven dorsal shell plates (*Acaenoplax hayae*), as well as "footless" chitons (*Kulindroplax perissokomos* and *Phthipodochiton thraivensis*), has further confused the polarity of the aplacophoran-chiton character transformation. Adding to the confusion, there are fundamental differences between the shells of polyplacophorans and those of all other molluscs, an observation suggesting that the chitons and aplacophorans may stand alone as a unique radiation off the early

molluscan line. Three hypotheses have been offered to explain this "shell problem" in molluscan evolution: (1) The multiplate shell may have been ancestral, the single-shell condition having evolved by coalescence of plates. (2) The single shell may have been ancestral, and the multiplate forms arose by subdivision of the single shell. (3) The single-shell and multishell designs arose independently from a shell-less ancestor, perhaps by way of sclerite consolidation. The presence of eight pairs of pedal retractor muscles in both polyplacophorans and monoplacophorans has been taken as evidence in favor of the first explanation. Acceptance of the first hypothesis suggests that the ancestor at node *a* in the cladogram in Figure 13.55 was a multivalved chitonlike creature. Acceptance of the second hypothesis implies that the ancestor at node *a* was a univalved, monoplacophoran-like ancestor. The third hypothesis postulates that the ancestor at node *a* lacked a solid shell altogether.

The primitive mantle and foot arrangement was probably somewhat similar to that in living polyplacophorans or monoplacophorans—that is, a large flattened sole was surrounded by a mantle groove. Because of their small size, the first molluscs probably did not require specialized respiratory structures, and gas exchange was through the dorsal epidermis. However, with the origin of the cuticle-covered mantle or dorsal shell covering this surface, posterior, specialized respiratory structures (ctenidia) originated and became associated with excretory and reproductive pores in a posterior mantle cavity. This arrangement would have been modified at least twice; in both the polyplacophorans and monoplacophorans, the mantle cavity became continuous with the expanded mantle groove alongside the foot, and the ctenidia multiplied and extended anteriorly in the mantle groove. Secondary modifications of the shape of the foot and other features in bivalves and scaphopods allowed most of these animals to exploit infaunal life in soft sediments, and both of these taxa are highly adapted to sediment burrowing. However, these modifications are clearly convergent, and scaphopods share other characters, including ano-pedal flexure, with cephalopods. Gastropods also undergo ano-pedal flexure, but according to some molecular studies this could be convergent. Scaphopods are also the last class of molluscs to appear in the fossil record (about 427 Ma, Silurian).

Monoplacophorans share the character of a single (univalve) shell with other molluscs (other than bivalves and chitons). They also share a similar shell structure and a host of other features. The only synapomorphies defining the monoplacophorans seem to be their repetitive organs (multiple gills, nephridia, pedal muscles, gonads, and heart atria). The question of whether this multiplicity arose uniquely in the monoplacophorans or represents a symplesiomorphic retention of ancestral features from some unknown metameric ancestor (below node *a* on the cladogram) has not been resolved and will likely require developmental studies on monoplacophorans to finally settle the question.

The bivalve line in the cladogram is defined by the presence of two shell valves, adductor muscles, reduction of the head region, decentralization of the nervous system and associated reduction or loss of certain sensory structures, and expansion of the mantle cavity.

Cephalopods are highly specialized molluscs and possess a number of complex synapomorphies. Primitive shelled cephalopods are represented today by about six species of *Nautilus* and *Allonautilus*, although thousands of fossil species of shelled cephalopods have been described. This highly successful molluscan class probably arose about 497 million years ago. The palcephalopods underwent a series of radiations during the Paleozoic but were largely replaced by the ammonites after the Devonian period (358 Ma). The ammonites, in turn, became extinct around the Cretaceous-Tertiary boundary (66 Ma). The origin of the coleoid cephalopods (octopuses, squid, and cuttlefish) is obscure, possibly dating back to the Devonian. They diversified mainly in the Mesozoic and became a highly successful group by exploiting a very new lifestyle, as we have seen.

The issue of ancestral metamerism in molluscs has been debated since the discovery of the first living monoplacophoran (*Neopilina galatheae*) in 1952. However, monoplacophorans are not the only molluscs to express serial replication or to have repeated organs reminiscent of metamerism (or "pseudometamerism," as some prefer to call it). Polyplacophorans have many serially repeated gills in the mantle groove and also typically possess eight pairs of pedal retractor muscles and eight shell plates. The two pairs of heart atria, nephridia, and ctenidia in *Nautilus* (and two pairs of retractor muscles in some fossil forms) have also been regarded by some workers as primitive metameric features.

The presence of organ repetition in some molluscs has been used to argue a close relationship to annelids. Recent molecular studies have included an unresolved relationship between molluscs, annelids, nemerteans, and brachiozoans (Dunn et al. 2014), while Kocot et al. (2017) suggested a resolved clade of brachiozoans, annelids, and nemerteans as the sister taxon of the molluscs. Laumer et al. (2019) also recovered a clade of brachiozoans, annelids, and nemerteans; this was also the first analysis to include the bryozoans, which grouped with the brachiozoans, thus supporting the monophyly of the lophophorates. The analysis of brachiopod, mollusc, and annelid genomes by Luo et al. (2015) placed the brachiopods as the sister taxon of the molluscs; this analysis did not include nemertean or bryozoan genomes. These molecular analyses suggest that organ repetition in molluscan groups is the result of independent convergent evolution, and is not

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ancestral, and that the genetic/evolutionary potential for serial repetition of organs is not uncommon and occurs in other nonannelid bilaterian phyla as well, e.g., Nemertea and Chordata. We regard organ repetition in the molluscs as independent convergent evolution of this characteristic.

The origin of molluscs themselves remains enigmatic. The excellent fossil record of this phylum extends back some 500 million years and suggests that the origin of the Mollusca probably lies in the Precambrian. Indeed, the late Precambrian fossil *Kimberella quadrata*, once thought to be a cnidarian, has been argued to have molluscan features, including perhaps a shell and muscular foot. However, recent examination of hundreds of specimens now suggests that *Kimberella* more likely belongs to an extinct lophotrochozoan group.

Chapter Summary

The phylum Mollusca is probably the most morphologically diverse of all animal phyla, and with ~73,000 described living species it is second only to the phylum Arthropoda in diversity. Molluscs are spiralian protostomes, with species ranging in size from microscopic, to giant squid reaching at least 13 m in length (including the tentacles), to octopuses weighing over 40 kg. The classification of Mollusca is complex, with eight classes that include two classes of spiculate, wormlike aplacophorans; the deep-sea, limpet-shaped monoplacophorans; eight-plated chitons (polyplacophorans); limpets, snails, and slugs (gastropods); clams, mussels, and their relatives (bivalves); tusk shells (scaphopods); and octopuses, squid, and nautiluses (cephalopods). Molluscs have radiated in every environment on Earth, from the deepest seas to high mountains. But despite this enormous diversity, all molluscs share a suite of defining characters that include (but are not limited to) bilateral symmetry (lost in gastropods), reduced coelom (the principal body cavity being the hemocoel), viscera concentrated dorsally as a "visceral mass," body covered by a cuticular epidermal sheet called the mantle (which has shell glands that secrete sclerites or shells), distinctive gills known as ctenidia (which may be lost or modified), a buccal feeding structure called the radula (except in bivalves), and spiral cleavage (except in cephalopods), and some groups have a trochophore larva, while bivalves and gastropods have a unique veliger larva.

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Courtesy of G. Giribet

CHAPTER 14

Phylum Nemertea

The Ribbon Worms

Members of the phylum Nemertea (Greek, "a sea nymph"), or Rhynchocoela (Greek *rhynchos*, "snout"; *coel*, "cavity"), are commonly called ribbon worms. Figure 14.1 illustrates a variety of body forms within this taxon and the major features of their anatomy. These unsegmented vermiform animals are usually flattened dorsoventrally and are moderately cephalized; they possess highly extensible bodies and strong regeneration powers. Many ribbon worm species are rather drab in appearance, but others are brightly colored or distinctively marked (e.g., the tropical eastern Pacific species *Baseodiscus punnetti*, above).

There are about 1,300 accepted, described species of nemerteans. They range in length from a few millimeters to several meters. Many can stretch easily to several times their contracted lengths (one specimen of *Lineus longissimus* reportedly measured 30 m in length). They are predominately benthic marine animals. A few, however, are planktonic, and some are symbiotic in molluscs, ascidians, or other marine invertebrates. A few freshwater and terrestrial species are known, the latter having some species distributed mostly on islands around the world.

Many features of the nemertean body plan (Box 14A) are similar to the conditions seen in flatworms (Platyhelminthes), and historically the two taxa were often grouped together as triploblastic acoelomate Bilateria. However, we now understand that nemerteans are truly coelomate and that they are closely related to annelids, molluscs, and the lophophorate phyla. Similarities with the flatworms are reflected in the overall architecture of the nervous systems, the types of sense organs, and the protonephridial excretory structures. However, in other respects ribbon worms are more similar to the previously mentioned spiralian phyla. Nemerteans possess a through gut with an anus

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

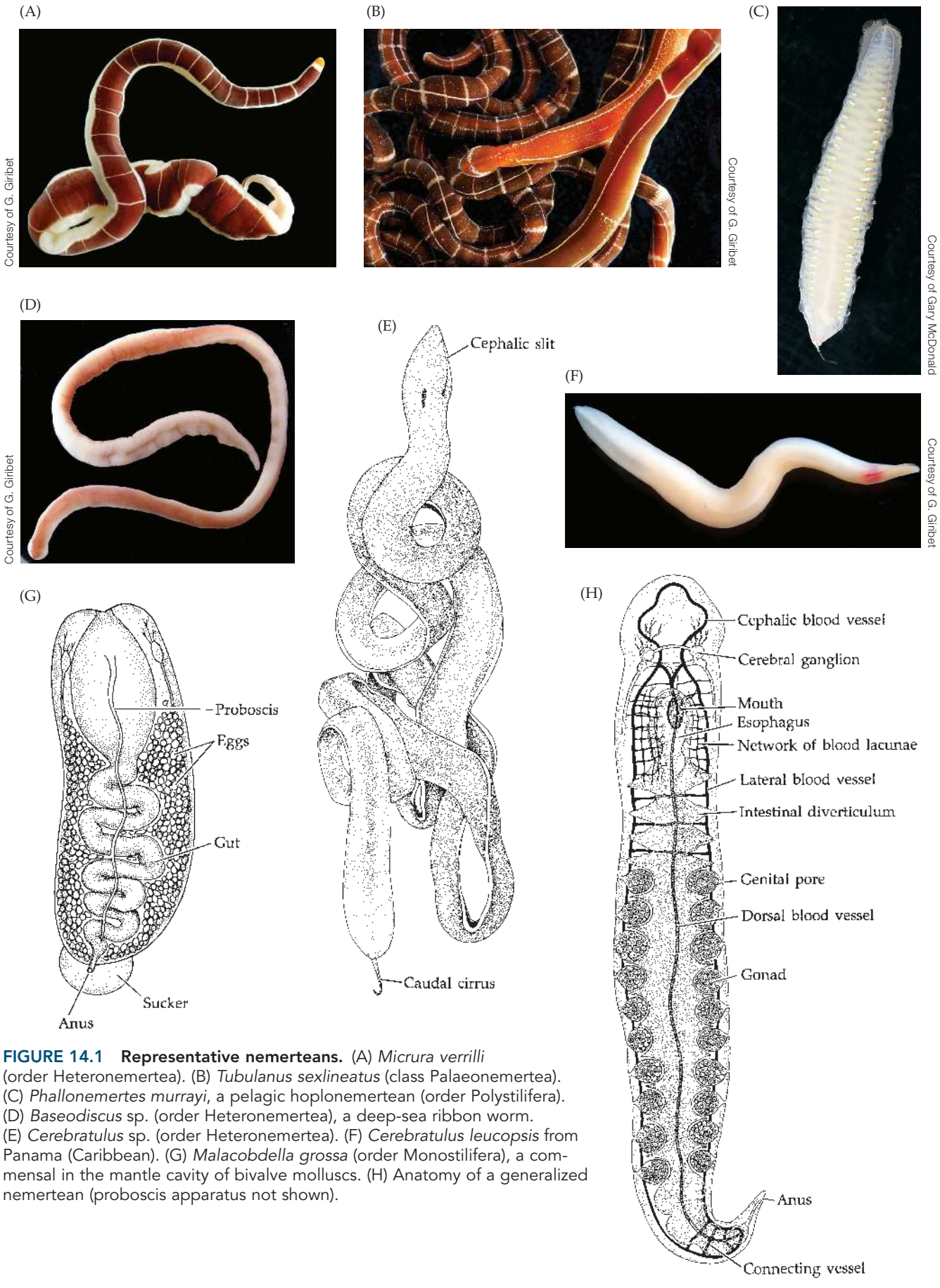

FIGURE 14.1 Representative nemerteans. (A) *Micrura verrilli* (order Heteronemertea). (B) *Tubulanus sexlineatus* (class Palaeonemertea). (C) *Phallonemertes murrayi*, a pelagic hoplonemertean (order Polystilifera). (D) *Baseodiscus* sp. (order Heteronemertea), a deep-sea ribbon worm. (E) *Cerebratulus* sp. (order Heteronemertea). (F) *Cerebratulus leucopsis* from Panama (Caribbean). (G) *Malacobdella grossa* (order Monostilifera), a commensal in the mantle cavity of bivalve molluscs. (H) Anatomy of a generalized nemertean (proboscis apparatus not shown).

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BOX 14A Characteristics of the Phylum Nemertea

1. Marine, freshwater, or terrestrial
2. Triploblastic, coelomate, bilaterally symmetrical unsegmented worms (one species externally "segmented")
3. Digestive tract complete, with anterior mouth and posterior anus
4. With protonephridia (a few deep-sea pelagic species lacking excretory systems)
5. With a bilobed cerebral ganglion that surrounds proboscis apparatus (not the gut), and two or more longitudinal nerve cords connected by transverse commissures
6. With two or three layers of body wall muscles arranged in various ways
7. With a unique proboscis apparatus lying dorsal to the gut and surrounded by a coelomic hydrostatic chamber called the rhynchocoel
8. With a closed circulatory system; some species with hemoglobin
9. Most gonochoristic; cleavage holoblastic; early development typically spiralian, and either direct or indirect, some with a pilidium larva
10. Asexual reproduction by fragmentation not uncommon

(a complete, one-way digestive tract), a closed circulatory system that is coelomic in nature, and an eversible proboscis surrounded by a hydrostatic cavity called the rhynchocoel. The circulatory system and the rhynchocoel are both coelomic cavities. The structure of the proboscis apparatus is unique to nemerteans and represents a novel synapomorphy that distinguishes the Nemertea from all other invertebrate taxa.

Taxonomic History and Classification

The earliest report of a nemertean was that of William Borlase (1758), who described his specimen as "the sea long-worm" and categorized it "among the less perfect kind of sea animals." For nearly a century, most authors placed the ribbon worms with the turbellarian flatworms, although other writers suggested that they were allied to annelids (including sipunculans), nematodes, and even molluscs and insects. It was during this period that Georges Cuvier (1817) described a particular ribbon worm and called it *Nemertes*, from which the phylum name was eventually derived. However, it was not until 1851 that substantial evidence for the distinctive nature of the ribbon worms was published by the German zoologist Max Schultze, who described the functional morphology of the proboscis, established the presence of nephridia and an anus, and discussed many other features of these animals. Schultze even proposed the basis for classifying these worms, which is still largely employed today by most authorities. Interestingly, he persisted in considering them to be turbellarians (today a paraphyletic grouping of the free-living Platyhelminthes), but he coined the names Nemertina and Rhynchocoela. The American anatomist Charles Minot separated the nemerteans from the flatworms in 1876, but it was not until the mid-twentieth century that the unique combination of characters displayed by the ribbon worms was fully accepted. Since that time they have been treated as a valid phylum. Then it took until the mid-1980s for James M. Turbeville, who studied their ultrastructure, to determine that nemerteans are more closely related to the coelomate protostomes than to platyhelminths, a result later corroborated by molecular sequence data and by their early cleavage pattern.

Classification

Since the publication of Schultze's classic accounts, the primary effort of nemertean taxonomists has been to refine the details of his scheme, which has generated surprisingly few controversies. The classification scheme used here is mostly based on the traditional one established by Wesley Coe in 1943 and refined with molecular phylogenetic analyses.

For most of the last 100 years, the classification system of nemerteans has largely followed that of the Dutch biologist Gerarda Stiasny-Wijnhoff (1936), which accepted as classes Schultze's (1851) division of nemerteans into Anopla and Enopla. Stiasny-Wijnhoff further divided Anopla into Palaeonemertea and Heteronemertea, and Enopla into Hoplonemertea and Bdellonemertea. Hoplonemertea was further subdivided into Monostilifera and Polystilifera. Recent molecular phylogenetic studies of nemerteans found a basal division between Palaeonemertea and Neonemertea, but Hubrechtiidae, formerly in Palaeonemertea, appears nested within Neonemertea, as the sister group of the remaining Heteronemertea. This extended Heteronemertea, including Hubrechtiidae, constitute the clade Pilidiophora (see the Classification section). Furthermore, all molecular analyses have contradicted the ordinal status of Bdellonemertea (*Malacobdella*), which is deeply nested within Hoplonemertea (and in the order Monostilifera).

We therefore follow a system in which the phylum is subdivided into two main clades, Palaeonemertea and Neonemertea (which we rank as classes), the latter divided into two subclasses, Pilidiophora (including the traditional order Heteronemertea and the family Hubrechtiidae) and Hoplonemertea (= Enopla of older classifications). The principal anatomical features used to distinguish between these clades include proboscis armature, mouth location relative to the position of the cerebral ganglion, gut shape, layering of the body wall

muscles, position of the longitudinal nerve cords, and several larval features. We rely on a recent proposal by nearly all active workers on nemerteans for this taxonomy (Strand et al. 2018), but recognize and rank Neonemertea as the sister group of Palaeonemertea.

CLASSIFICATION OF NEMERTEA (= RHYNCHOCOELA)

CLASS PALAEONEMERTEA Unarmed nemerteans (Figure 14.1B). Proboscis not armed with stylets and not morphologically specialized into 3 regions. Mouth separate from proboscis pore and located directly below or somewhat posterior to cerebral ganglion. Two or 3 layers of body wall muscles, from external to internal either circular-longitudinal or circular-longitudinal-circular; dermis thin and gelatinous, or absent; longitudinal nerve cords epidermal, dermal, or intramuscular within the longitudinal layer; cerebral organs and ocelli frequently lacking. Palaeonemerteans are marine, primarily littoral forms. There are no designated orders in this class. (e.g., *Carinina*, *Carinoma*, *Cephalothrix*, *Tubulanus*)

CLASS NEONEMERTEA Unarmed or armed nemerteans with separate or fused mouth and proboscis pores. Because Hubrechtiidae was formerly placed in Palaeonemertea, most characters within Neonemertea are variable.

SUBCLASS PILIDIOPHORA Unarmed nemerteans with separate mouth and proboscis pores and with a pilidium larva (when present) and the proboscis musculature bilaterally arranged.

ORDER HETERONEMERTEA With different types of body wall structure and nervous system in Hubrechtiidae and the remaining heteronemerteans, as historically hubrechtiids were regarded as a "transitional stage" between palaeonemerteans and basal heteronemerteans. Except for hubrechtiids, with characters as those of palaeonemerteans, heteronemerteans have 3 layers of body wall muscles, from external to internal longitudinal-circular-longitudinal; dermis usually thick, partly fibrous; longitudinal nerve cords intramuscular, between outer longitudinal and middle circular layers; cerebral organs and ocelli usually present; development indirect (Figure 14.1A,D–F). Primarily marine littoral forms, but a few freshwater species are known. (e.g., *Baseodiscus*, *Cerebratulus*, *Hubrechtia*, *Hubrechtella*, *Lineus*, *Micrura*, *Nemertoscolex*, *Paralineus*)

SUBCLASS HOPLONEMERTEA Typically armed nemerteans (Figure 14.1C,G). Proboscis usually armed with distinct stylets and morphologically specialized into 3 regions (except in *Malacobdella*); mouth and proboscis pore usually united into a common aperture; mouth located anterior to cerebral ganglion; longitudinal nerve cords within mesenchyme, internal to body wall muscles. With marine, freshwater, and terrestrial species; many marine species symbiotic with or parasitic upon other invertebrates.

ORDER MONOSTILIFERA Stylet apparatus consists of a single main stylet and 2 or more sacs housing accessory (replacement) stylets; proboscis apparatus is unarmed and opens into foregut in *Malacobdella*, which has a trunk with a large posterior sucker and a convoluted gut that lacks lateral diverticula. Most species are marine and benthic, but freshwater, terrestrial, and parasitic forms are known; *Malacobdella* species are commensal in the mantle cavities of marine bivalves and, in one species, a freshwater gastropod. (e.g., *Amphiporus*, *Annulonemertes*, *Carcinonemertes*, *Emplectonema*, *Geonemertes*, *Malacobdella*, *Ovicides*, *Paranemertes*)

ORDER POLYSTILIFERA Stylet apparatus consists of many small stylets borne on a basal shield. All species are marine, either benthic or pelagic. (e.g., *Drepanophorus*, *Nectonemertes*, *Pelagonemertes*, *Phallonemertes*, *Punnettia*)

The Nemertean Body Plan

The nemertean body plan is especially interesting, since it presents characteristics of both coelomates (e.g., the closed circulatory system and rhynchocoel) and acoelomates (e.g., the parenchyma and protonephridial system). In Chapter 3 we discussed some of the limitations of the acoelomate body plan, and we will see the results of these constraints in our examination of the flatworms (Chapter 17). Even though it is now clear that nemerteans have true coelomic cavities, these worms have relatively solid bodies. Thus, they are at least functionally acoelomate. Recall that many of the problems inherent in acoelomate architecture are related to restricted internal transport capabilities. The presence of a circulatory system in nemerteans has largely eased this problem; and the functional anatomy of many other systems is related directly or indirectly to the presence of this circulatory system. For example, nemertean protonephridia are usually intimately associated with the blood, from which wastes are drawn, rather than with the mesenchymal tissues as are flatworm protonephridia.

The increased capabilities for internal circulation and transport have allowed a number of developments that would otherwise be impossible. First, the circulatory system provides a solution to the surface-to-volume dilemma, and as a result nemerteans tend to be much larger and more robust than flatworms, having been largely relieved of the constraints of relying on diffusion for internal transport and exchange. Second, the digestive tract is complete and somewhat regionally specialized. With a one-way movement of food materials through the gut, and a circulatory system to absorb and distribute digested products, the anterior region of the gut has been freed to specialize for feeding and ingestion. Third, since the animal does not have to rely on

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diffusion for transport through a loosely organized mesenchyme, that general body area is available for the development of other structures, notably the well-developed layers of muscles. In summary, the presence of a circulatory system in concert with these other changes has resulted in relatively large, active animals, capable of more complex activities than seen in the acoelomate metazoans.

This general body plan is enhanced by the presence of the unique proboscis apparatus (which usually functions in prey capture), the distinctly anterior location of the mouth, and well-developed cephalic sensory organs for prey location. Thus, while variation exists, the "typical" nemertean may be viewed as an active benthic hunter/tracker that moves among nooks and crannies preying on other invertebrates or even on some vertebrate prey and vertebrate remains.

Body Wall

The body wall of nemerteans comprises an epidermis, a dermis, relatively thick muscle layers surrounding the gut and other internal organs, and a mesenchyme of varying thickness (Figure 14.2). The epidermis is a ciliated columnar epithelium (Figure 14.2C). Mixed among the columnar cells are sensory cells (probably tactile), mucous gland cells, and basal replacement cells that may extend beneath the epidermis. Below the epidermis is the dermis, which varies greatly in thickness and composition. In some ribbon worms (e.g., the palaeonemerteans) the dermis is extremely thin or composed of only a homogeneous gel-like layer; in others (e.g., the heteronemerteans), it is typically quite thick and densely fibrous and usually includes a variety of gland cells. Beneath the dermis are well-developed layers of circular and longitudinal muscles. The organization of these muscles varies among taxa and may occur in either a two- or three-layered plan (Figure 14.3). The layering arrangement may also vary to some degree along the body length of individual animals. Internal to the muscle layers is a dense mesenchyme, although in some nemerteans the muscle layers are so thick that they nearly obliterate this inner mass. The mesenchyme

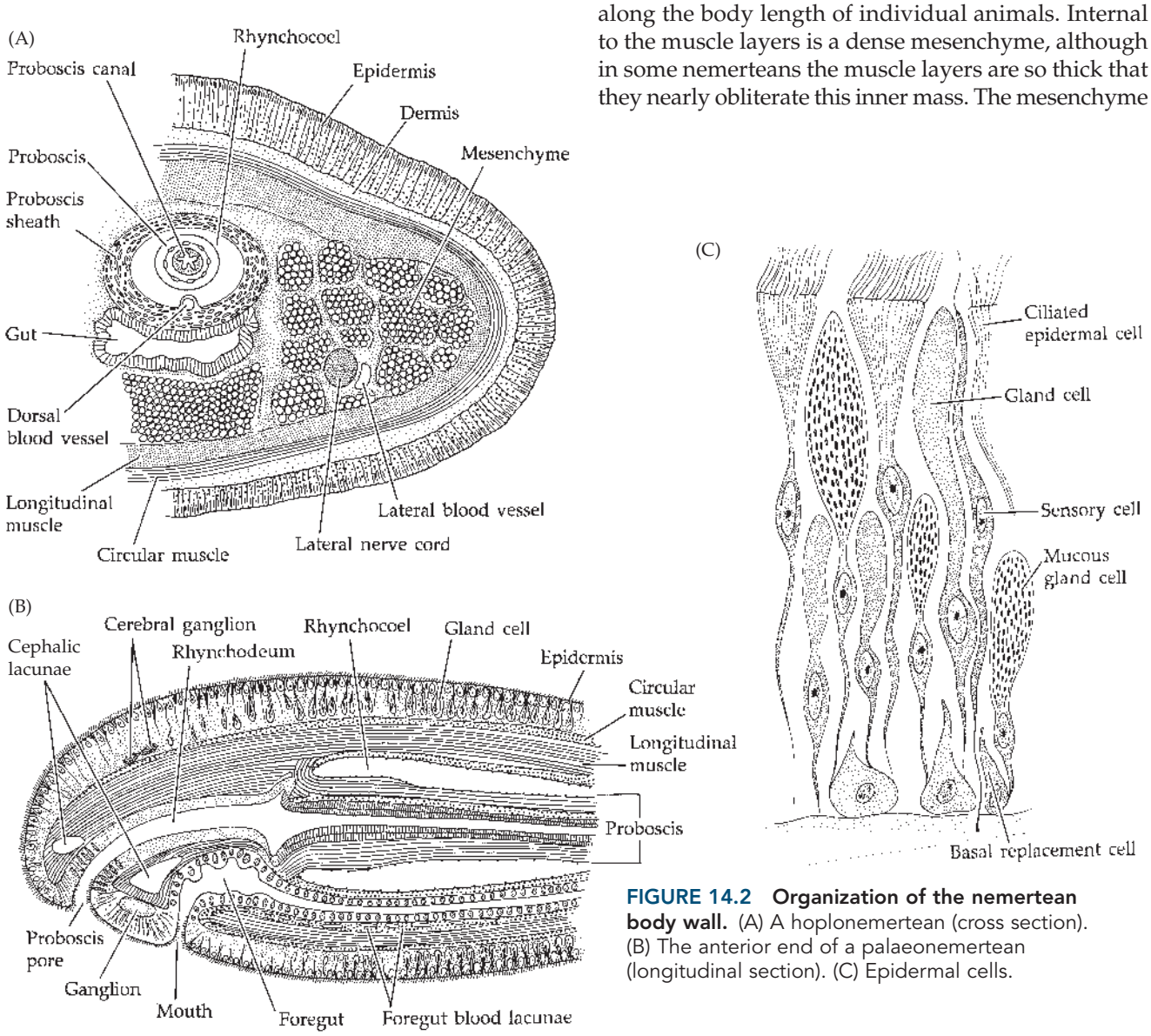

FIGURE 14.2 Organization of the nemertean body wall. (A) A hoplonemertean (cross section). (B) The anterior end of a palaeonemertean (longitudinal section). (C) Epidermal cells.

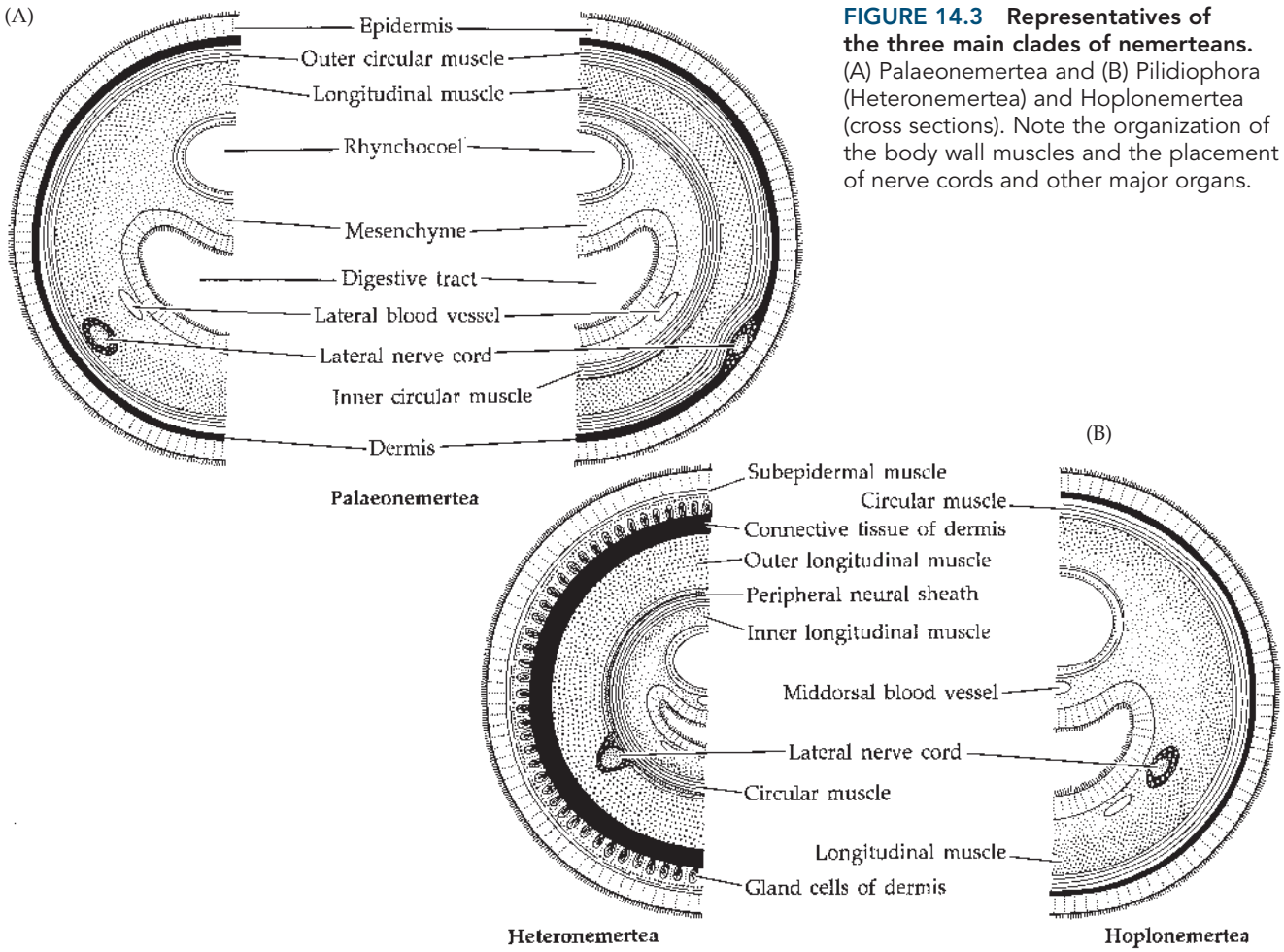

FIGURE 14.3 Representatives of the three main clades of nemerteans. (A) Palaeonemertea and (B) Pilidiophora (Heteronemertea) and Hoplonemertea (cross sections). Note the organization of the body wall muscles and the placement of nerve cords and other major organs.

includes a gel matrix and often a variety of loose cells, fibers, and dorsoventrally oriented muscles. Figure 14.3 depicts cross-sectional views of representatives of the three main clades, showing mesenchyme thickness, muscles, placement of longitudinal nerve cords, major longitudinal blood vessels, and other features.

Support and Locomotion

In the absence of any rigid skeletal elements, the support system of nemerteans is provided by the muscles and other tissues of the body wall and by the hydrostatic qualities of the mesenchyme. These features permit dramatic changes in both length and cross-sectional shape and diameter, characteristics that are closely associated with locomotion and accommodation to cramped quarters. Most very small benthic ribbon worms are propelled by the action of their epidermal cilia. A slime trail is produced by the body wall mucous glands and provides a lubricated surface over which the worm slowly glides. Small nemerteans commonly live among the interstices of filamentous algae, under tidepool rocks, or in the spaces of other irregular surfaces such as those found in mussel beds, sand, mud, or pebble bottoms. Larger epibenthic ribbon worms and most of the burrowing forms employ peristaltic waves of the body wall muscles to propel them over moist surfaces or through soft substrata. Some of the larger forms (e.g., *Cerebratulus*) use undulatory swimming as a secondary means of locomotion, and perhaps as an escape reaction to benthic predators. Fully pelagic nemerteans (certain polystiliferan hoplonemerteans) generally drift or swim slowly. Some of the terrestrial forms produce a slime sheath through which they glide by ciliary action, and some use their proboscis for rapid escape responses.

Feeding and Digestion

Most ribbon worms are active predators on small invertebrates, but some are able to capture live fish, or even active invertebrates like small cephalopods. Some are scavengers, feeding on all sorts of decaying animal matter, including large vertebrates, and still others feed on plant material (at least under laboratory conditions). There is evidence to suggest that species of the commensal genus *Malacobdella*, which inhabit the mantle cavity of bivalve molluscs, feed largely on phytoplankton captured from their host's feeding and gas exchange currents. Field observations indicate that

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the diets of predatory forms may be either extremely varied or quite restricted, depending on the species. Some species are capable of tracking prey over long distances, whereas others must locate food by direct contact. Distance prey location and assessment of food acceptability are almost certainly chemotactic responses. Ribbon worms that actually hunt and track can recognize the trails left by potential prey, and they fire their proboscis along the trail ahead of them to capture food (Figure 14.4). Similar reactions are elicited when infaunal nemerteans encounter burrows in which potential prey might be located. Surface hunters that live in intertidal areas generally forage during high tides or at night and thus avoid the threats of desiccation and visual predators. However, members of some marine genera (e.g., *Tubulanus, Paranemertes, Amphiporus*) may frequently be seen during low tides on foggy mornings, gliding over the substratum in search of prey. The rapid expulsion of their proboscis and successful prey capture can be a memorable moment of high drama for tide pool enthusiasts.

The behavior involved in the capture and ingestion of live prey is significantly different from that associated with scavenging on dead material. In predation, the proboscis is employed both in capturing prey and in moving it to the mouth for ingestion. The proboscis is everted and wrapped around the victim (Figure 14.4). The prey is not only physically held by the proboscis, but may also be subdued or killed by its toxic secretions. In the Pacific species *Paranemertes peregrina*, which feeds primarily on nereid polychaetes, the glandular epithelium of the everted proboscis secretes a potent neurotoxin. Nemerteans with an armed proboscis (Hoplonemertea) actually use the stylets to pierce the prey's body (often numerous times) to introduce the toxin. Once captured, the prey is drawn to the mouth by retraction and manipulation of the proboscis; it is usually swallowed whole. The mouth is expanded and pressed against the food, and swallowing is accomplished by peristaltic action of the body wall muscles aided by ciliary currents in the anterior region of the gut. Scavenging, in contrast, usually does not involve the proboscis. The worm simply ingests the food directly by muscular action of body wall and foregut. In some predatory hoplonemerteans (those in which the lumen of the proboscis is connected with the anterior gut lumen), the foregut itself may be everted for feeding on animals too large to be swallowed whole. In such cases, fluids and soft tissues are generally sucked out of the prey's body. Annelids and amphipod crustaceans seem to be favorite food items for many predatory nemerteans.

Courtesy of S. Stricker

FIGURE 14.4 ***Paranemertes peregrina*** **(Hoplonemertea: Monostilifera) capturing a nereid polychaete.** The proboscis is coiled around the polychaete.

Species of the hoplonemertean genus *Carcinonemertes* are ectoparasites (egg predators) on brachyuran crabs. Different species inhabit different regions of the host's body, but all migrate to the egg masses on gravid female crabs and feed on the yolky eggs. In high numbers, these egg predators can kill all of the embryos in the host's clutch. Some studies have reported up to 99% infestation rates of *Carcinonemertes errans* on the commercially important Pacific Dungeness crab (*Metacarcinus magister*), with up to 100,000 worms per host. This parasite has been implicated in past collapses of the central California Dungeness crab fishery. Several species of *Ovicides* (Carcinonemertidae) live on the abdomens of hydrothermal vent crabs in the Pacific, and *Nemertoscolex parasiticus* (Heteronemertea) lives in the coelomic fluid of the thalassematid annelid *Echiurus echiurus.*

The proboscis apparatus The proboscis apparatus is a complex arrangement of tubes, muscles, and hydraulic systems and contains a glandular epithelium with a role in prey capture (Figure 14.5). The glandular proboscis epithelium of most Palaeonemertea and Pilidiophora also contains specialized gland cells, which produce unique secretory granules with an internal hollow threadlike tubule (core) capable of extrusion, that are termed pseudocnidae. The term *pseudocnidae* refers to the superficial similarity of these structures with cnidae of Cnidaria and historically have been referred to as nematocysts, rhabdites, or barbs. The proboscis itself is an elongate, eversible, blind tube and either is associated with the foregut or opens through a separate proboscis pore. The proboscis, which can be branching in some species, may be regionally specialized and may bear stylets in various arrangements in the so-called "enoplan" nemerteans (today's Hoplonemertea) (Figure 14.5E–H). Nemertean stylets are nail-shaped structures that typically reach lengths of 50–200 μm. Each calcified stylet is composed of a central organic matrix surrounded by an inorganic cortex composed of calcium phosphate. The stylets are formed within large epithelial cells called styletocytes. Because growing ribbon worms must replace

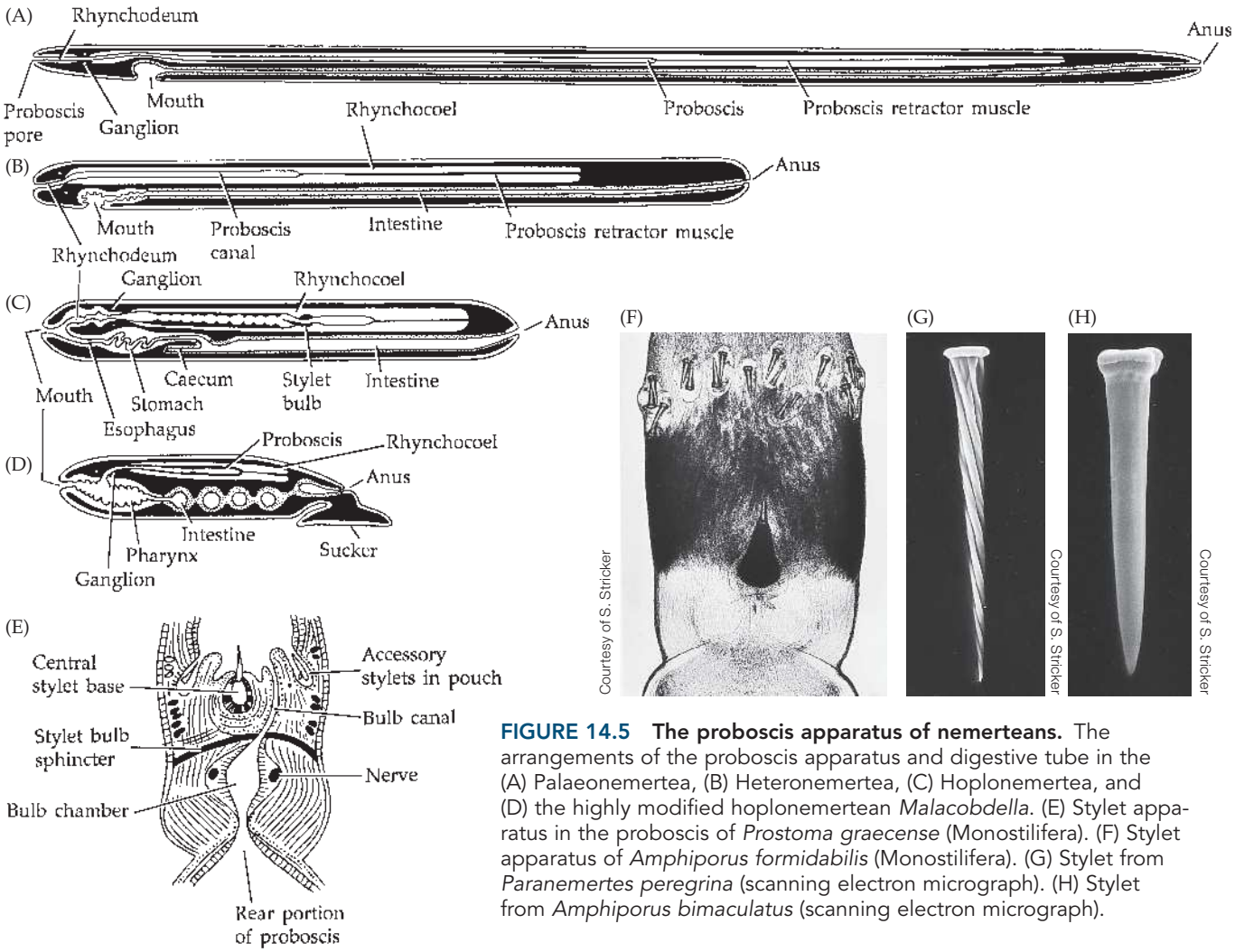

FIGURE 14.5 The proboscis apparatus of nemerteans. The arrangements of the proboscis apparatus and digestive tube in the (A) Palaeonemertea, (B) Heteronemertea, (C) Hoplonemertea, and (D) the highly modified hoplonemertean *Malacobdella*. (E) Stylet apparatus in the proboscis of *Prostoma graecense* (Monostilifera). (F) Stylet apparatus of *Amphiporus formidabilis* (Monostilifera). (G) Stylet from *Paranemertes peregrina* (scanning electron micrograph). (H) Stylet from *Amphiporus bimaculatus* (scanning electron micrograph).

their stylets with new larger ones, and because they often lose the stylet during prey capture, new stylets are continuously produced in reserve stylet sacs and stored until needed, whereupon they are transported and affixed in their proper final position.

The basic structure and action of the proboscis are most easily described where the apparatus is entirely separate from the gut. As shown in Figure 14.5A,B, the proboscis pore leads from the outside directly into the anterior proboscis lumen, called the rhynchodeum, the lining of which is continuous with the epidermis. Posterior to the rhynchodeum, the lumen continues as the proboscis canal that is surrounded by the muscular wall of the proboscis itself; these muscles are derived from the muscles of the body wall. The proboscis is surrounded by a closed, fluid-filled, coelomic space called the rhynchocoel, which in turn is surrounded by additional muscle layers. The inner blind end of the proboscis is connected to the posterior wall of the rhynchocoel by a proboscis retractor muscle. In a few taxa (e.g., *Gorgonorhynchus*), there is no retractor muscle, and eversion and retraction are accomplished hydrostatically. In hoplonemerteans the proboscis shares the opening with the digestive system (Figure 14.5C,D).

Eversion of the proboscis (Figure 14.6) is accomplished by contraction of the muscles around the rhynchocoel; this increases the hydrostatic pressure within the rhynchocoel itself, squeezing on the proboscis and causing its eversion. The everted proboscis moves with the muscles in its wall; the proboscis is retracted back inside the body by the coincidental relaxation of the muscles around the rhynchocoel and contraction of the proboscis retractor muscle. The retracted proboscis may extend nearly to the posterior end of the worm, and usually only a portion of it is extended during eversion.

Digestive system Nemerteans have a complete through gut with an anus (Figures 14.6 and 14.7). Associated with the one-way movement of food from mouth to anus we find various degrees of regional specialization (both structural and functional) in the guts of ribbon worms. The mouth leads inward to an ectodermally derived foregut (stomodeum) consisting of a bulbous buccal cavity, sometimes a short esophagus,

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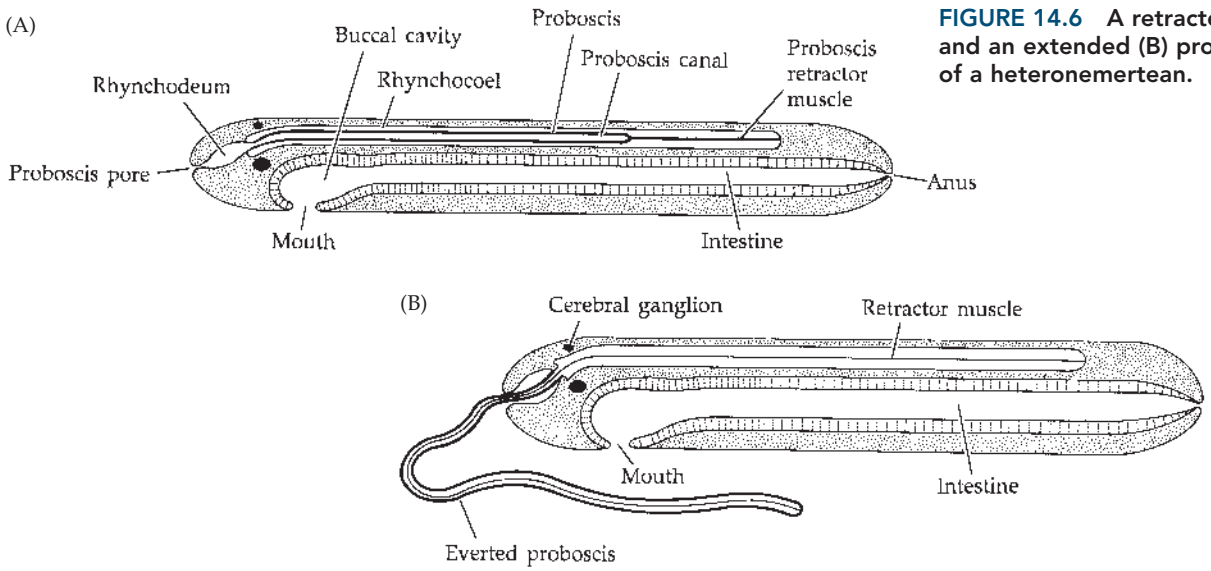

FIGURE 14.6 **A retracted (A) and an extended (B) proboscis of a heteronemertean.**

and a stomach. The stomach leads to an elongate intestine or midgut, which is more or less straight but usually bears numerous lateral diverticula. In *Malacobdella*, the intestine is loosely coiled and lacks diverticula; diverticula are also lacking in the strange "segmented" *Annulonemertes*. At the posterior end of the intestine is a short ectodermally derived hindgut (proctodeum) or rectum, which terminates in the anus. Elaborations on this basic plan are common in certain taxa and may include various ceca arising from the stomach or from the intestine at its junction with the foregut.

The entire digestive tube is ciliated, the foregut more densely than the midgut. The gut epithelium is basically columnar, mixed with gland cells. The foregut contains a variety of mucus-producing cells, sometimes multicellular mucous glands, and occasionally enzymatic gland cells in the stomach region. The midgut is lined with vacuolated ciliated columnar cells; these are phagocytic and bear microvilli, greatly increasing their surface area. Enzymatic gland cells are abundantly mixed with the ciliated cells of the midgut. The hindgut typically lacks gland cells. Food is moved through the digestive tract by cilia and by the action of the body wall muscles; there are usually no muscles in the gut wall itself, except in the foregut of some heteronemerteans.

The process of digestion in nemerteans is a two-phase sequence of protein breakdown. The first step involves the action of endopeptidases released from gland cells into the gut lumen. This extracellular digestion is quite rapid and is followed by phagocytosis (and probably pinocytosis) of the partially digested material by the ciliated columnar cells of the midgut. Protein digestion is completed intracellularly by exopeptidases within the food vacuoles of the midgut epithelium. Lipases have been discovered in at least one species (*Lineus ruber*), and carbohydrases are known in the omnivorous commensal *Malacobdella*. Food is stored primarily in the form

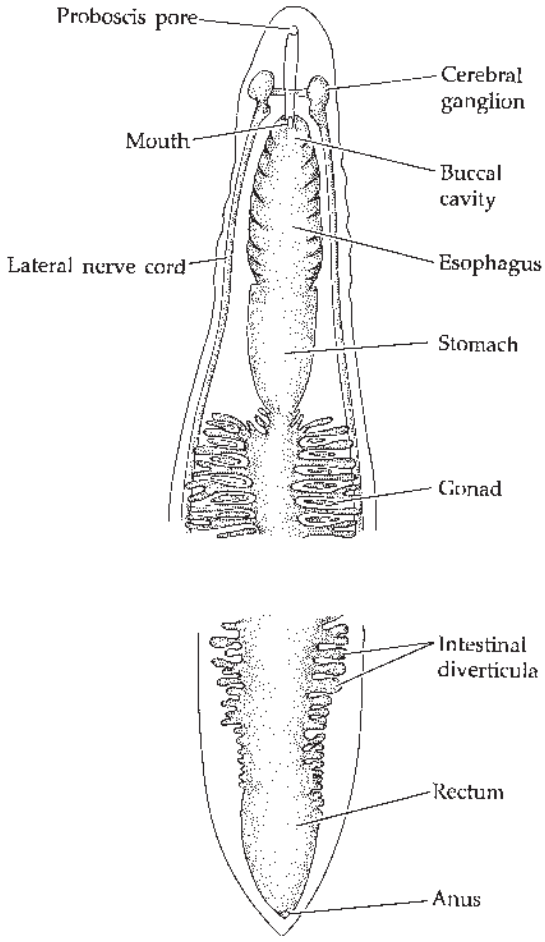

FIGURE 14.7 **A nemertean digestive system.** Anterior and posterior regions of the gut of *Carinoma* (Palaeonemertea) (ventral view).

of fats, and to a much lesser extent as glycogen, in the wall of the midgut. Transportation of digested materials throughout the body is accomplished by the circulatory system, which absorbs these products from the cells lining the intestine. Indigestible materials are moved through the gut and out the anus.

Circulation and Gas Exchange

We have mentioned briefly the evolutionary and adaptive significance of the circulatory system in nemerteans and its general relationship to other systems and functions. This closed system consists of vessels and thin-walled spaces called lacunae (Figure 14.2B). There is a good deal of variation in the architecture of nemertean circulatory systems (Figure 14.8). The simplest arrangement occurs in certain palaeonemerteans in which a single pair of longitudinal vessels extends the length of the body, connecting anteriorly by a cephalic lacuna and posteriorly by an anal lacuna. Elaboration on this basic scheme may include transverse vessels between the longitudinal vessels, enlargement and compartmentalization of the lacunar spaces, and the addition of a middorsal vessel. The walls of the blood vessels are only slightly contractile, and general body movements generate most of the blood flow. There is no consistent pattern to the movement of blood through the system; it may flow either anteriorly or posteriorly in the longitudinal vessels, and currents often reverse directions.

The blood consists of a colorless fluid in which various cells are suspended. These cells can include pigmented corpuscles (yellow, orange, green, red), at least some of which contain hemoglobin, and a variety of so-called lymphocytes and leukocytes of uncertain function. The anatomical association of the circulatory system with other structures, as well as the composition of the blood, suggest several circulatory functions. Although conclusive evidence is lacking, the circulatory system appears to be involved with the transport of nutrients, gases, neurosecretions, and excretory products. Some intermediary metabolism probably occurs in the blood, as several appropriate enzymes have been identified in solution. The blood may also serve as an aid to body support through changes in hydrostatic pressure within the vessels and lacunar spaces. There is some evidence to support the idea that the blood may also function in osmoregulation.

Gas exchange in nemerteans is epidermal and does not involve any special structures. Oxygen and carbon dioxide diffuse readily across the moist body surface, which is usually covered with mucous secretions. Some robust forms (e.g., *Cerebratulus*) augment this passive exchange of gases across the skin with regular irrigation of the foregut, where there is an extensive system of blood vessels. In those species in which hemoglobin occurs, this pigment probably aids in oxygen transport or storage within the blood.

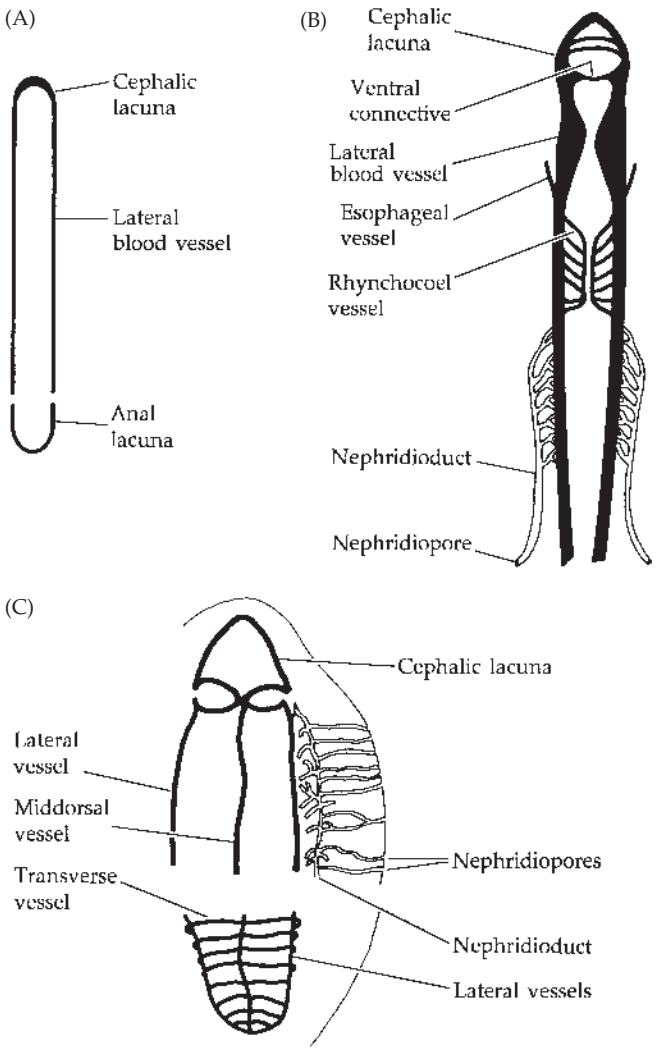

FIGURE 14.8 Nemertean circulatory systems. (A) The simple circulatory loop of *Cephalothrix* (Palaeonemertea) consists of a pair of lateral blood vessels connected by cephalic and anal lacunae. (B) The complex circulatory system of *Tubulanus* (Palaeonemertea). Note the intimate association of the nephridial system with the lateral blood vessels. (C) The circulatory system of *Amphiporus* (Hoplonemertea: Monostilifera) includes a middorsal vessel and numerous transverse vessels.

Excretion and Osmoregulation

The excretory system of most nemerteans consists of two to thousands of flame bulb protonephridia (Figures 14.8 and 14.9) similar to those found in free-living flatworms. However, apparently the deep-sea pelagic hoplonemerteans lack protonephridia altogether. The flame bulbs are usually intimately associated with the lateral blood vessels or less commonly with other parts of the circulatory system. The nephridial units are often pressed into the blood vessel walls, and in some instances the walls are actually broken down such that the nephridia are bathed directly in blood. In the simplest case, a single pair of flame bulbs leads to two nephridioducts, each with its own laterally placed

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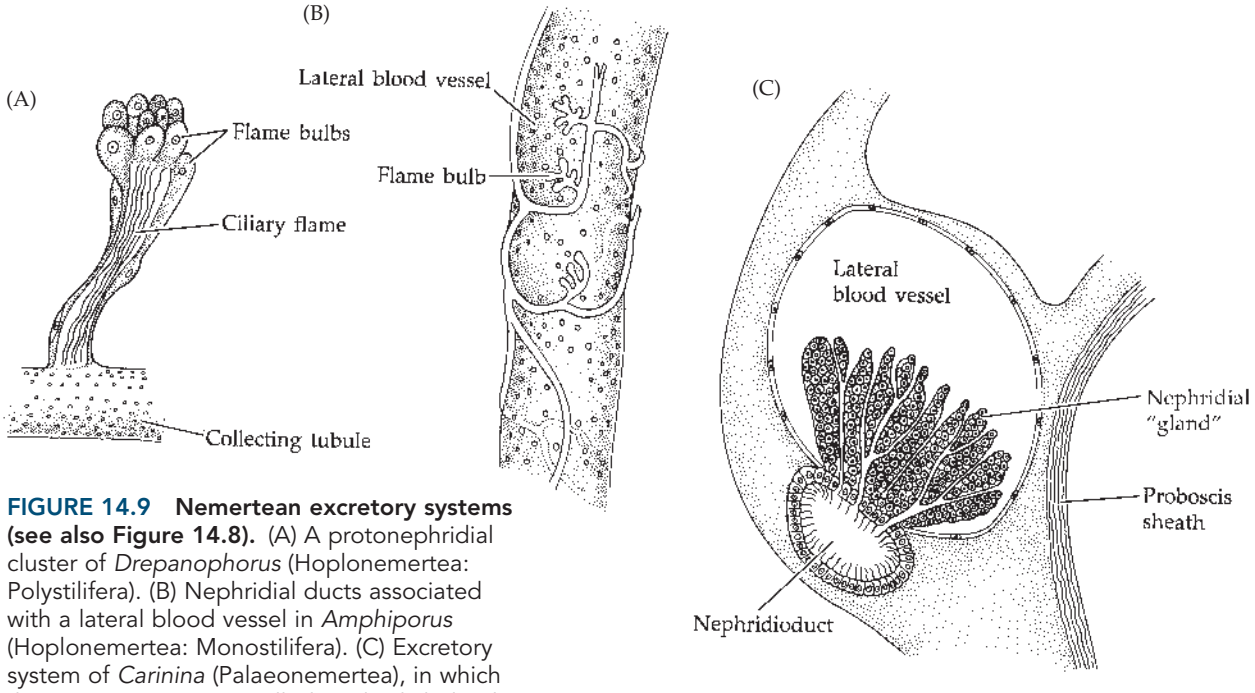

FIGURE 14.9 Nemertean excretory systems (see also Figure 14.8). (A) A protonephridial cluster of *Drepanophorus* (Hoplonemertea: Polystilifera). (B) Nephridial ducts associated with a lateral blood vessel in *Amphiporus* (Hoplonemertea: Monostilifera). (C) Excretory system of *Carinina* (Palaeonemertea), in which the secretory units (so-called nephridial gland) project into the lumen of the lateral blood vessel.

nephridiopore. More complex conditions include rows of single flame bulbs or clusters of flame bulbs with multiple ducts. In some species, the walls of the nephridioducts are syncytial and lead to hundreds or even thousands of pores on the epidermis. The most elaborate conditions occur in certain terrestrial nemerteans where approximately 70,000 clusters of flame bulbs (six to eight in each cluster) lead to as many surface pores. In some heteronemerteans (e.g., *Baseodiscus*), the excretory system discharges into the foregut.

The functioning of nemertean protonephridia in the excretion of metabolic wastes has not been well studied. The close association of the flame bulbs with the circulatory system suggests that nitrogenous wastes (probably ammonia), excess salts, and other metabolic products are removed from the blood as well as from the surrounding mesenchyme by the nephridia. If such is the case, it explains again the significance of the circulatory system in overcoming surface-to-volume problems and the constraints of simple diffusion on body size. Relatively active animals produce large amounts of metabolic wastes. Dependence on diffusion alone would seriously limit any increase in body bulk, but the transport of these wastes from the tissues to the protonephridial system by circulatory vessels greatly eases this limitation. One of the most remarkable evolutionary achievements of the nemerteans has been their ability to grow to great size, particularly in length, without segmentation or the development of a large body cavity.

There is some morphological and experimental evidence that the protonephridia also play an important role in osmoregulation, especially in freshwater and terrestrial ribbon worms. It is in some of these forms, which are subjected to extreme osmotic stress, that the most elaborate excretory systems are found, and these systems are probably associated with water balance. Furthermore, it appears that there may be a very complex interaction between the nervous system (neurosecretions), the circulatory system, and the nephridia to facilitate osmoregulatory mechanisms, but the details remain to be studied. Some members of Heteronemertea and Hoplonemertea have invaded fresh water and must combat water influx from their strongly hypotonic surroundings. Members of some genera (e.g., *Geonemertes, Microplana*) are terrestrial, although restricted to moist shady habitats where they avoid serious problems of desiccation. In addition, they tend to cover their bodies with a mucous coat that reduces water loss. Those forms that inhabit marine subtidal or deep-water environments, or are endosymbiotic (one genus of Heteronemertea and several genera of Hoplonemertea), face little or no osmotic stress. But the many species found intertidally do face periods of exposure to air and to lowered (or elevated) salinities. Their soft bodies are largely unprotected, and they are relatively intolerant of fluctuations in environmental conditions. Intertidal nemerteans rely strongly on behavioral attributes to survive periods of potential osmotic stress and remain in moist areas during low tide periods. Burrowing in soft, water-soaked substrata or living among algae or mussel beds, in cracks and crevices, or in other areas that retain seawater at low tide are lifestyles illustrating how habitat preference and behavior prevent exposure to stress.

In addition, most intertidal nemerteans are somewhat negatively phototactic, and many restrict their activities to night hours or to foggy or overcast mornings and evenings. A marine meiofaunal species from North Carolina lives in sediments at about 1 m depth above high tide level, probably relying on the water that fills the interstices of sand by capillarity.

Nervous System and Sense Organs

The basic organization of the nemertean nervous system reflects a relatively active lifestyle. Nemerteans are cephalized, especially in the anterior placement of the mouth and feeding structures, and we find related concentrations of sensory and other nervous elements in the head. The central nervous system of ribbon worms consists of a complex cerebral ganglion from which arises a pair of ganglionated, longitudinal (lateral) nerve cords (Figure 14.10A). The cerebral ganglion is formed of four attached lobes that encircle the proboscis apparatus (not the gut, as in many other invertebrates). Each side of the cerebral ganglion includes a dorsal and a ventral lobe; the two sides are attached to one another by dorsal and ventral connectives. Several pairs of sensory nerves provide input directly to the cerebral ganglion from various cephalic sense organs. The main longitudinal nerve cords arise from the ventral lobes of the cerebral ganglion and pass posteriorly; they attach to each other at various points by branched transverse connectives and terminally by an anal commissure. The longitudinal nerves also give rise to peripheral sensory and motor nerves along the length of the body. Elaboration on this basic plan includes additional longitudinal nerve cords, frequently a middorsal one arising from the dorsal commissure of the cerebral ganglion, and a variety of connectives, nerve tracts, and plexus.

As noted in the classification scheme, the positions of the major longitudinal nerve cords vary among the nemertean orders (Figure 14.3). These changes in the position of the nerve cords from epidermal to mesenchymal correspond to general increases in body complexity and tendencies toward specialization. Most workers agree that these differences reflect a plesiomorphic (epidermal) to apomorphic (subepidermal) trend among these taxa.

Ribbon worms possess a variety of sensory receptors, many of which are concentrated at the anterior end and associated with an active, typically hunting lifestyle and with other aspects of their natural history. Nemerteans are very sensitive to touch. This tactile sensitivity plays a role in food handling, avoidance responses, locomotion over irregular surfaces, and mating behavior. Several types of modified ciliated epidermal cells are scattered over the body surface (especially abundant at the anterior and posterior ends) and are presumed to have a tactile function. The cells occur either singly or in clusters; some of the latter types are located in small depressions and can be thrust out from the body surface.

The eyes of ribbon worms are located anteriorly and number from two to several hundred; they can be arranged in various patterns (Figure 14.10B). Most of these ocelli are of the inverted pigment-cup type, similar to those seen in flatworms, although a few species possess lensed eyes. As discussed in Chapter 3, these types of eyes typically are sensitive to light intensity and light direction. They help the nemerteans avoid bright light and potential exposure to predators or environmental stresses.

Much of the sensory input important to nemerteans is chemosensory. These worms are very sensitive to dissolved chemicals in their environment and employ this sensitivity in food location, probably mate location, substratum testing, and general water analysis. Probably all nemerteans respond to contact with chemical stimuli, and many are capable of distance chemoreception of materials in solution. At least three different nemertean structures have been implicated (some through speculation) in the initiation of chemotactic responses: cephalic slits or grooves, cerebral organs, and frontal glands (= cephalic glands) (Figures 14.10B–D). **Cephalic slits** are furrows of variable depth that occur laterally on the heads of many ribbon worms (see also Figure 14.1E). These furrows are lined with a ciliated sensory epithelium supplied with nerves from the cerebral ganglion. Water is circulated through the cephalic slits and over this presumably chemosensory epithelial lining.

Most nemerteans possess a pair of the remarkably complex **cerebral organs** (Figure 14.10C). The core of each cerebral organ is a ciliated epidermal invagination (the cerebral canal), which is expanded at its inner end. These canals lead laterally to pores within the cephalic slits (when present) or else directly to the outside via separate pores on the head. The inner ends of the canals are surrounded by nervous tissue of the cerebral ganglion, and by glandular tissue, and they are often intimately associated with lacunar blood spaces. Cilia in the cerebral canal circulate water through the open portion of the organ; this activity intensifies in the presence of food. Nemerteans presumably use this mechanism when hunting and tracking prey or in other chemotactic responses. The association of the cerebral canals with glandular, nervous, and circulatory structures has led some workers to suggest an endocrine and/or neurosecretory function for the cerebral organs. Other suggestions have included auditory, gas exchange, excretory, and tactile activities. Cerebral organs are absent in several genera, including the symbiotic *Carcinonemertes* and *Malacobdella,* and in the pelagic hoplonemerteans.

In the region anterior to the cerebral ganglion, large **frontal glands** open to the outside through a pitlike frontal sense organ (Figure 14.10D). These structures receive nerves from the cerebral ganglion and appear

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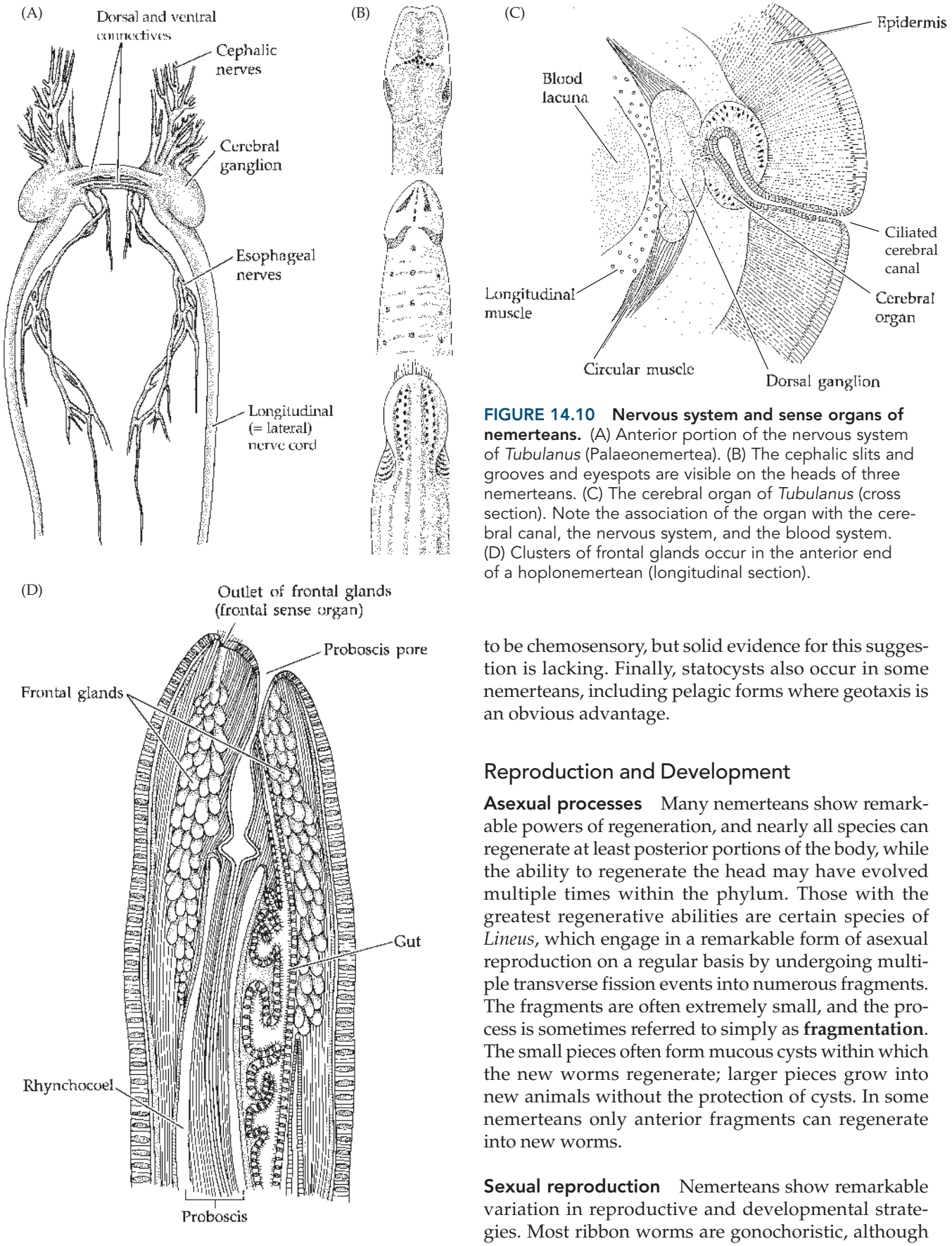

FIGURE 14.10 Nervous system and sense organs of nemerteans. (A) Anterior portion of the nervous system of *Tubulanus* (Palaeonemertea). (B) The cephalic slits and grooves and eyespots are visible on the heads of three nemerteans. (C) The cerebral organ of *Tubulanus* (cross section). Note the association of the organ with the cerebral canal, the nervous system, and the blood system. (D) Clusters of frontal glands occur in the anterior end of a hoplonemertean (longitudinal section).

to be chemosensory, but solid evidence for this suggestion is lacking. Finally, statocysts also occur in some nemerteans, including pelagic forms where geotaxis is an obvious advantage.

Reproduction and Development

Asexual processes Many nemerteans show remarkable powers of regeneration, and nearly all species can regenerate at least posterior portions of the body, while the ability to regenerate the head may have evolved multiple times within the phylum. Those with the greatest regenerative abilities are certain species of *Lineus*, which engage in a remarkable form of asexual reproduction on a regular basis by undergoing multiple transverse fission events into numerous fragments. The fragments are often extremely small, and the process is sometimes referred to simply as **fragmentation**. The small pieces often form mucous cysts within which the new worms regenerate; larger pieces grow into new animals without the protection of cysts. In some nemerteans only anterior fragments can regenerate into new worms.

Sexual reproduction Nemerteans show remarkable variation in reproductive and developmental strategies. Most ribbon worms are gonochoristic, although protandric and even simultaneous hermaphrodites are known. The reproductive system of nemerteans

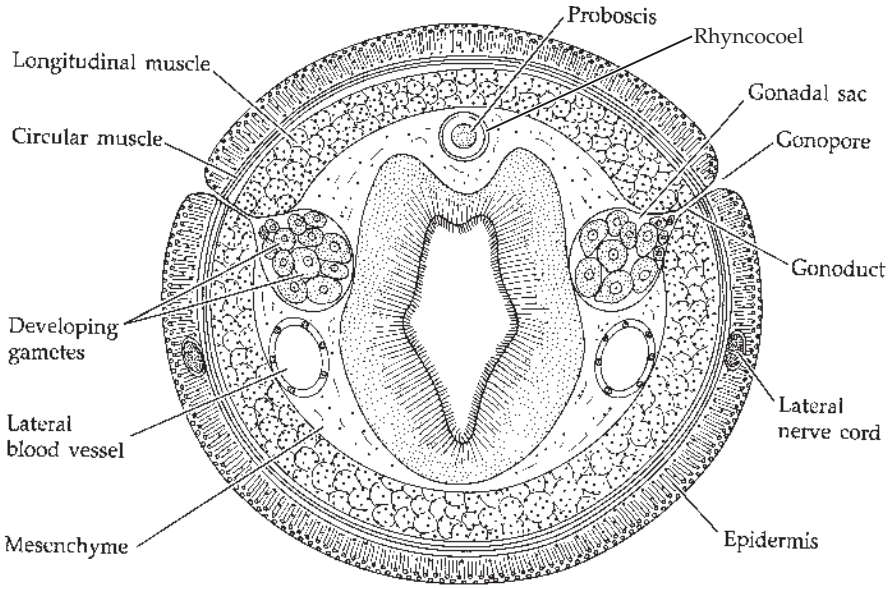

FIGURE 14.11 Arrangement of gonads in the palaeonemertean *Carinina* (cross section). Note the position of a pair of gonads in the mesenchyme. See also Figure 14.7.

has gonads that are simply specialized patches of mesenchymal tissue arranged serially along each side of the intestine, alternating with the midgut diverticula (Figure 14.11). In *Malacobdella* and a few others, the gonads are more or less packed within the mesenchyme (Figure 14.1H). In most nemerteans the development of gonads occurs along nearly the entire length of the body, but in a few species they are restricted to certain regions, usually toward the anterior end. The gonads begin to enlarge and hollow just prior to the onset of breeding activities. Specialized cells in the walls of the rudimentary ovaries and testes proliferate eggs and sperm into the lumina of the enlarging gonadal sacs. In females additional special cells are responsible for yolk production. There is evidence that maturation is under neurosecretory hormonal control, at least in some species. The secretions are probably from the cerebral organ complex.

With the proliferation of gametes, the gonadal sacs expand to almost fill the area between the gut and the body wall. When the animals are nearly ready to spawn, mating behavior is initiated and the worms become increasingly active. As mentioned earlier, mate location probably depends on chemotactic responses. The same is apparently true of spawning itself, at least for some species, because the presence of a ripe conspecific stimulates the release of gametes from other mature individuals. Experimental evidence indicates that physical contact is not necessary for such a spawning response; thus, some sort of pheromone is probably involved. In nature, however, spawning usually occurs in concert with actual physical contact; tactile responses evidently follow chemotactic mate location. During such mating activities, veritable knots of scores of worms may writhe in a mucus-covered mating mass. The coordinated release of ripe gametes under such conditions ensures successful fertilization. The gametes are extruded through temporary pores or through ruptures in the body wall. Rupture occurs by contraction of the body wall muscles or of special mesenchymal muscles surrounding the gonads.

Fertilization is often external, either free in the seawater or in a gelatinous mass of mucus produced by the mating worms. In the latter situation, actual egg cases are frequently formed, and part or all of the embryonic development occurs within them (Figure 14.12). Internal fertilization occurs in certain nemerteans. In some cases the sperm are released into the mucus surrounding the mating worms, and then they move into the ovaries of the females; once fertilized, the eggs are usually deposited in egg capsules, where they develop, although some Antarctic species brood with cocoons. Some terrestrial species are ovoviviparous; the embryos are retained within the body of the female and development is fully direct—an obvious advantage for surviving on land. Ovoviviparity is also known in a few other nemerteans, including deep-sea pelagic forms. Since the population densities of these pelagic worms are extremely low, they must presumably capitalize

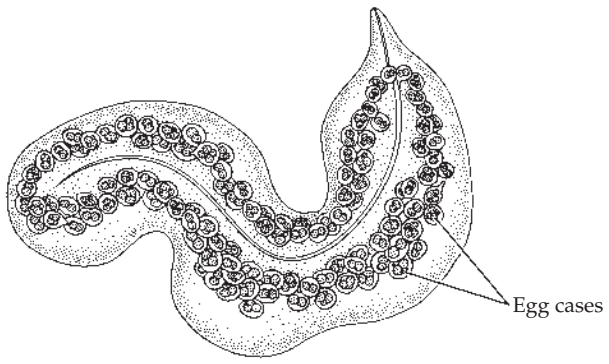

FIGURE 14.12 Egg cases in the heteronemertean *Lineus ruber*.

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on the relatively infrequent encounters of males and females and ensure successful fertilization. In a few cases the males are equipped with suckers, which are used to clasp the female, or, rarely, with a protrusible penis, which is used to transfer sperm.

Regardless of the method of fertilization, development through the gastrula is similar among most of the nemerteans studied to date. Cleavage is holoblastic and spiral, producing either three (*Tubulanus*) or, more typically, four quartets of micromeres. A coeloblastula forms, and this often shows the rudiments of an apical ciliary tuft associated with a slight thickening of the blastula wall at or near the animal pole. Gastrulation is usually by invagination of the macromeres and the fourth micromere quartet to produce a coelogastrula. In at least one genus (*Prostoma*, a hermaphroditic freshwater form), gastrulation is by unipolar ingression of the vegetal macromeres; this movement produces a stereogastrula, which later hollows. Mesoderm may originate in several ways, and in some cases the processes are poorly understood. In *Cerebratulus lacteus*, one of the best-studied nemerteans developmentally, ectomesoderm is derived from two blastomeres (3a and 3b), which give rise to the extensive array of the larval muscle cells. *Cerebratulus lacteus* also possesses a true mesentoblast (4d), which gives rise to a pair of small mesodermal bands, and scattered mesenchymal cells. This dual origin of the mesoderm, as both ectomesoderm and endomesoderm, appears to be a condition present in all spiralians. The gut is formed by all the fourth quartet micromeres as well as the vegetal macromeres (4A, 4B, 4C, 4D). Unraveling the embryogenesis of nemerteans has led to the discovery that the rhynchocoel is formed by schizocoely, and it therefore represents a true coelomic cavity.

Developmental strategies are also varied among nemerteans. Members of Palaeonemertea and Hoplonemertea undergo direct development within egg cases. The embryos in these groups develop gradually to juvenile worms without any abrupt metamorphosis (Figure 14.13) but may have multiple invaginations and shedding of a transitory larval epidermis. These embryos are nourished by yolk until they hatch, whereupon they commence feeding. This is especially true of the palaeonemerteans, in which the proboscis apparatus is not fully formed at hatching (the proboscis of heteronemerteans and *Malacobdella* is functional at the time of hatching).

A recent study of embryogenesis of the palaeonemertean *Carinoma tremaphoros* has shown large squamous cells covering the entire larval surface except for the apical and posterior regions. Although apical and posterior cells continue to divide, in the large surface cells cleavage is arrested and they form a contorted preoral belt. Based on the position, cell lineage, and fate, it has been suggested that this belt corresponds to the prototroch of other trochozoans.

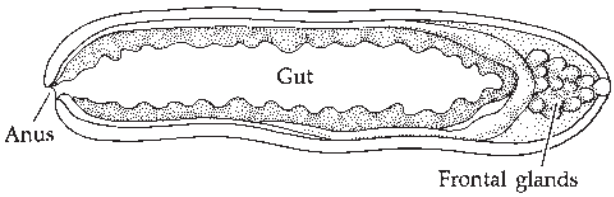

FIGURE 14.13 Hatching form produced by direct development in *Prosorhochmus*, a monostiliferan hoplonemertean.

Members of the subclass Pilidiophora undergo a bizarre and fascinating pattern of indirect development. Most species in this clade produce a free-swimming, planktotrophic larva called the **pilidium** (Figure 14.14). At this stage the gut is incomplete, consisting of a mouth located between a pair of flaplike ciliated lobes, a stomodeal foregut, and a blind intestine; the anus forms later as a proctodeal invagination. Interestingly, the intestinal diverticula of nemerteans do not form as evaginations of the gut wall but are produced by medial encroachments of mesenchyme, which press in the gut wall, thus creating the diverticula. As the pilidium swims and feeds, a series of invaginations in the larval ectoderm (Figure 14.14B) eventually pinch off internally to produce the presumptive adult ectoderm. Perhaps the most striking characteristic of the pilidium is the way the juvenile worm develops inside the larva from a series of isolated rudiments, called the imaginal discs. The paired cephalic discs, cerebral organ discs, and trunk discs originate as invaginations of larval epidermis and subsequently grow and fuse around the larval gut to form the juvenile (Figure 14.14C). The fully formed juvenile ruptures the larval body and, more often than not, devours the larva during catastrophic metamorphosis. In this way, the animal prepares for benthic life before it faces the rigors of settlement. When development is completed, the larval skin is shed and the juvenile assumes its life on the sea floor. Pilidia from different species vary in shape, size, and color. Modifications of pilidial development include **Desor's larva** in *Lineus viridis*, **Schmidt's larva** in *Lineus ruber*, and **Iwata's larva** in several *Micrura* species. Development of Desor's and Schmidt's larva is encapsulated, while the others have planktonic lecithotrophic development. In all of these cases, the pilidial lobes are lacking, the blastocoel is reduced, the larva does not feed, but similar to the canonical pilidium, the juvenile develops via imaginal discs.

Nemertean Phylogeny

The fossil record is, unfortunately, of little use in establishing the origin of nemerteans in geological time, and only one species of crown-group Nemertea, *Archisymplectes rhothon*, has been suggested based on multiple fossils from the Pennsylvanian of Illinois and

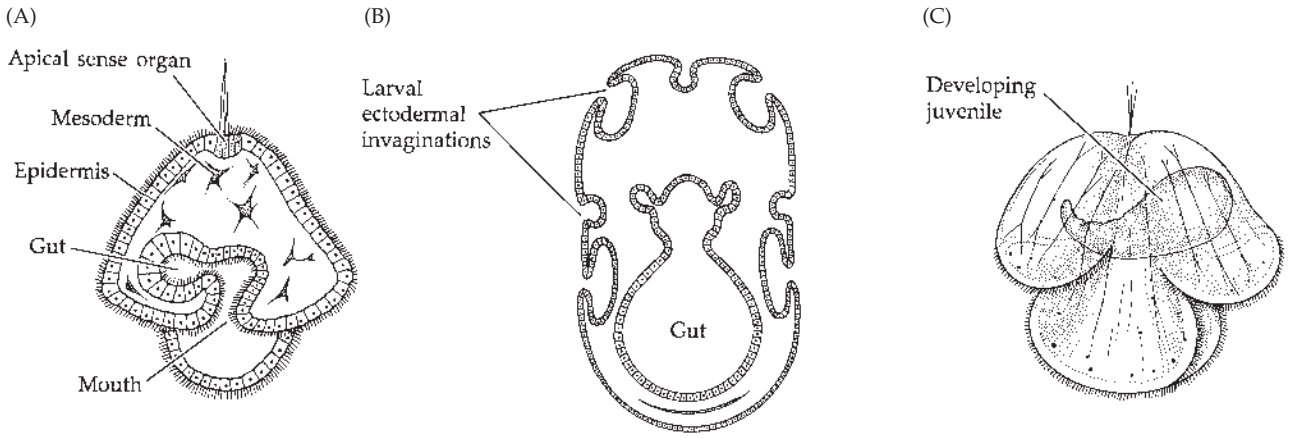

FIGURE 14.14 Development of a pilidium larva. (A) Pilidium larva (sagittal section). (B) A pilidium larva (transverse section) during invagination of larval ectoderm to form adult skin. (C) Late pilidium larva with juvenile formed within.

the Mississippian of Montana (Carboniferous). But, nemerteans obviously diverged sometime after the origin of the spiralian bilateral condition. Although now viewed to be part of the spiralian clade, related to other phyla with trochophore larvae, nemerteans had long been considered to be related to flatworms (Chapter 17). However, this idea is refuted by the discovery of the coelomic nature of the nemertean rhynchocoel and blood vessels, which place them closer to other phyla of coelomate spiralians. An older view is that nemerteans arose from an early archoöphoran "turbellarian" stock, perhaps sharing common ancestry with the macrostomid flatworms. The nemerteans and free-living platyhelminths display a number of similarities including protonephridia, types of ocelli, certain histological characteristics (especially of the epidermis), and the general organization of the nervous system. Furthermore, various ciliated slits and depressions among free-living flatworms resemble the cephalic slits and similar structures of the nemerteans. Some flatworms possess frontal (cephalic) glands long thought to be homologous to those of ribbon worms, but these could be symplesiomorphic for Spiralia or they could be convergences.

Their mode of early egg cleavage also places nemerteans as clear members of the clade Spiralia, and interpretations of the arrested cells of some embryos suggest a relationship to phyla with trochophore larvae—a relationship otherwise unsupported by any other anatomical characters. This is why their phylogenetic placement had been in flux for quite some time. However, molecular data strongly suggest a relationship to Mollusca, Annelida, and the lophophorate phyla (and probably also the Entoprocta).

The phylogenetic relationships among the various taxa of Nemertea have been examined in detail in the past few years and now include a phylogenomic analysis using hundreds of genes (Figure 14.15). These new studies are largely congruent with some of the traditional classifications, but they have found paraphyly of the former class Anopla, and they include some important rearrangements, such as the placement of the monospecific family Hubrechtiidae (*Hubrechtia desiderata*) as the sister group of the remaining Heteronemertea and not as a member of Palaeonemertea, as well as the placement of the former monogeneric order Bdellonemertea (*Malacobdella*) within the order Monostilifera. The former result is not really that surprising, as species of Hubrechtiidae have a mosaic of palaeonemertean and heteronemertean characters and some authors have considered them a "transitional stage" between palaeonemerteans and basal heteronemerteans. Furthermore, the new evolutionary tree implies that certain characters found in the former Anopla are actually symplesiomorphies for Nemertea, including the unarmed proboscis and the separate openings of the mouth and proboscis. Within Hoplonemertea, Monostilifera appear divided into two clades, Cratenemertea and Distromatonemertea, whereas Polystilifera splits into the clades Pelagica and Reptantia.

One of the principal structural trends among the nemerteans is the internalization of the major longitudinal nerve cords. We assume that the earliest ribbon worms possessed epidermal nerve cords, as do some modern palaeonemerteans. Palaeonemerteans and pilidiophorans retain the plesiomorphic feature of the placement of the mouth posterior to the cerebral ganglion. The relatively simple and unarmed proboscis and the placement of the nerve cords external to the mesenchyme suggest further that these clades retain the plesiomorphic character states among the ribbon worms. Pilidiophorans acquired indirect development, the unique formation of the double larval and adult

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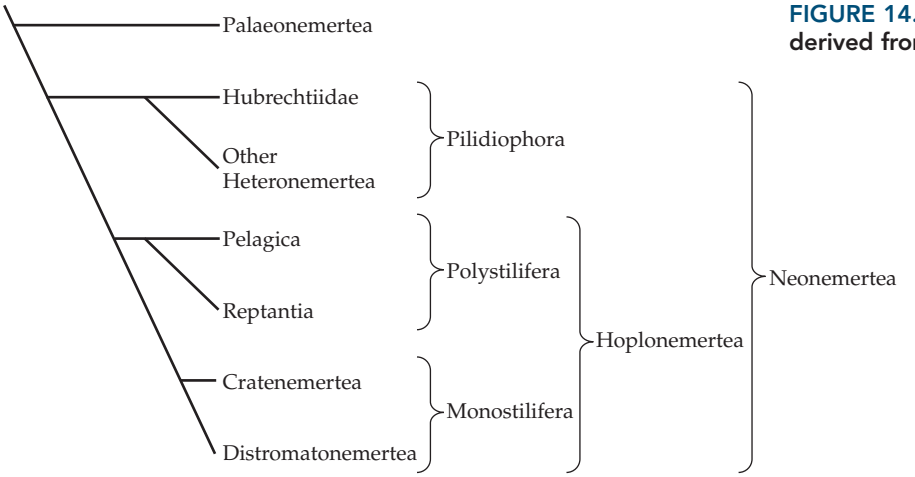

FIGURE 14.15 **Phylogeny of Nemertea derived from recent analyses of molecular data.**

ectoderm during metamorphosis, and the evolution of their unique arrangement of body wall muscles. The encapsulation, and thus functionally direct development, of those heteronemerteans with a Desor larva is almost certainly a secondary abandonment of free pilidial larval life.

The hoplonemerteans show some distinct changes from the groups mentioned so far. Most notable are the regional specialization and armature of the proboscis, the mesenchymal position of the nerve cords, and the placement of the mouth in a more anterior position. *Malacobdella*, formerly constituting the Bdellonemertea, is a specialized offshoot of Monostilifera that displays significant modification for an endosymbiotic lifestyle, including simplification of the proboscis, coiling and increased relative length of the gut (probably associated with their herbivorous habits), a posterior body sucker, and decreased body length.

Chapter Summary

This chapter introduced you to the lophotrochozoan phylum Nemertea, a group of invertebrates often overlooked or ignored in studies of marine diversity. However, ribbon worms are a major group of marine predators and scavengers, with 1,300 described species, and are one of the few animal phyla to have colonized freshwater and terrestrial environments. Nemerteans include what is considered by most the longest animal ever recorded (30 meters), although many species are small or even microscopic. Of all the animal phyla, nemerteans are unique in presenting a compact body and protonephridial excretory system, similar to that of flatworms, while possessing coeloms, as evidenced by their rhynchocoel and their closed circulatory system. The rhynchodeal apparatus is a unique characteristic of nemerteans, used for capturing prey. They can also be beautifully colored, can maintain commensal relationships with many other invertebrates, and can even display parental care. While clearly possessing spiral cleavage, their late developmental modes are varied, as are the ecological niches they inhabit.

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Courtesy of G. Rouse

CHAPTER 15

Phylum Annelida

The Segmented (and Some Unsegmented) Worms

This chapter treats of the segmented worms, or Annelida (Greek, *anellus*, "ringed"), which comprise about 20,000 described species. Annelids include the familiar earthworms and leeches, as well as various marine "sand worms," "tube worms," and an array of worms with other descriptors (Figures 15.1, 15.2, and 15.3). Some are tiny animals of the meiofauna; others, such as certain Southern Hemisphere earthworms and some marine species, can exceed 3 m in length.

Annelids have successfully occupied virtually all habitats where sufficient water is available. They are particularly ubiquitous in the sea but also abound in fresh water, and many occupy damp terrestrial environments. There are also parasitic, mutualistic, and commensal species. Their success is no doubt due in part to the evolutionary plasticity of their segmented bodies and use of a wide variety of life histories and feeding strategies. Most annelids are characterized by having a head followed by a segmented body in which most internal and external parts are repeated with each segment, a condition referred to as **serial homology**. This term refers to body structures with the same genetic and developmental origins that arise repeatedly during the ontogeny of an organism. In annelids this repetition of homologous body structures results in **metamerism**—body segmentation that arises by way of **teloblastic development** (the proliferation of paired, segmental mesodermal bands from teloblast cells at a posterior growth zone in the embryo). There are some dramatic exceptions to this for several annelid groups that have lost their metameric tendencies or transformed from having an obviously segmented body (e.g., Thalassematidae and Sipuncula). Annelids are triploblastic coelomate

This chapter, except for the Sipuncula, was revised by Greg Rouse.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

BOX 15A Characteristics of the Phylum Annelida

1. Bilaterally symmetrical, vermiform, protostomes; terrestrial, freshwater, and marine
2. Segmented (segmentation absent in some groups, e.g., Sipuncula, Thalassematidae); segments arising by teloblastic growth
3. Development typically protostomous, with holoblastic, spiral, schizocoelous embryogeny
4. Digestive tract complete, usually with regional specialization (secondarily lost in some groups)
5. With a closed circulatory system (secondarily lost in some groups) and respiratory pigments that may include hemoglobin, chlorocruorin, and hemerythrin
6. Most adults possessing metanephridia or, less commonly, protonephridia
7. Nervous system well developed, with a dorsal cerebral ganglion, circumenteric connectives, and ventral ganglionated nerve cord(s)
8. Typically with lateral, segmentally arranged epidermal chaetae (absent in some, e.g., Sipuncula)
9. In most, head composed of presegmental prostomium and peristomium (often with body segments fused to it; peristomium may be reduced), not observed in nonsegmented groups
10. Gonochoristic or hermaphroditic; development indirect or direct; often with trochophore larva

worms with a complete gut (with few exceptions), a closed circulatory system (again with some exceptions), a well-developed nervous system, and excretory structures in the form of protonephridia or, more commonly, metanephridia (Box 15A). Marine annelids typically produce trochophore larvae, a feature shared with several other protostome taxa (e.g., Mollusca, Nemertea, Entoprocta). The story of annelid diversity and success is one of variation on this basic theme.

Taxonomic History and Classification

As mentioned in earlier chapters, the roots of modern animal classification can be traced to Linnaeus (1758), who placed all invertebrates except insects in the taxon Vermes. In 1802, Lamarck established the taxon Annelida; he had a reasonably good idea of their unity and of their differences from other groups of worms. He and many other workers recognized the affinity among most annelids, but Hirudinea (leeches and allies) were often erroneously allied with trematode platyhelminths.

Recent phylogenetic studies have shown that several groups previously regarded as separate phyla are actually annelids. These include Echiura (now the family Thalassematidae), Sipuncula, Orthonectida, and a group comprising the former phyla Pogonophora and Vestimentifera (now together comprising the family Siboglinidae). Although now known to be highly modified annelids, these groups are so distinct that they are given detailed treatment at the end of this chapter. The overall classification within Annelida is also currently undergoing significant revision and has yet to stabilize. Phylogenomic and other molecular phylogenetic analyses have shown that taxonomic groupings based on morphology are often invalid. Annelida was traditionally divided into three classes. Polychaeta was the largest and most diverse group, the other two being Oligochaeta (earthworms and their kin) and Hirudinea (leeches and their relatives). It is now clear that the closest relative of Hirudinea is the freshwater group Lumbriculidae, a taxon that was inside the Oligochaeta, and these two former classes (Hirudinoidea and Oligochaeta) are now referred to as Clitellata, a taxon that dates back to 1919. Furthermore, Clitellata has been shown to have arisen deep within the older formulation of Polychaeta, making the former "Polychaeta" synonymous with "Annelida." As a result of these recent studies, many annelid researchers have redefined "Polychaeta" as a clade of annelids that includes only the two major groups Errantia and Sedentaria (Figure 15.43A). Clitellata, Siboglinidae, and Thalassematidae are all part of Sedentaria and thus well within the newly designated clade Polychaeta.

SYNOPSES OF MAJOR GROUPS

As noted above, the taxonomy for Annelida has yet to fully stabilize, but our understanding of relationships within this phylum has undergone momentous changes in the last two decades. For a current assessment of the overall relationships among the major annelid groups, see Figure 15.43A, which is based on a synthesis of the phylogenomic studies of Weigert et al. (2014), Andrade et al. (2015), and Martín-Durán et al. (2021). No Linnaean ranks are used in the following classification, although those names ending with *-idae* have traditionally carried the rank of family.

OWENIIDA This clade is the sister group to all other Annelida. It has been given the misleading name of Paleoannelida, but the name Oweniida has priority and is less misleading.

> OWENIIDAE Fewer than 50 species (Figures 15.1A and 15.12B). Generally small-bodied (some reaching 10 cm), tube-dwelling annelids with numerous fine parapodial hooks. The prostomium may be lobed or folded into a ciliated crown (e.g., *Owenia*). The group is best known for its unusual and beautiful "mitraria" larvae (Figure 15.20H,I).
>
> MAGELONIDAE Around 70 species, all in the genus *Magelona* (Figure 15.2A). Relatively similar in appearance, with shovel-shaped anterior ends and a pair of papillated palps. Thin, cylindrical worms, less than 1 mm wide, but reaching 15 cm in length. Live as burrowers in sands and muds; do not seem to form permanent tubes, though they do line their burrows with mucus.

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FIGURE 15.1 Representative annelids spanning the phylogenetic breadth of the group. (A) *Owenia* sp. (Oweniidae). (B) *Spiochaetopterus* sp. (Chaetopteridae). (C) *Protobonellia* sp. (Thalassematidae). (D) *Phascolion* sp. (Sipuncula). (E) *Arcovestia ivanovi* (Siboglinidae). (F) *Lumbricus terrestris* (Clitellata, Crassiclitellata). (G) *Boccardia proboscidea* (Spionidae). (H) *Harmothoe* sp. (Aphroditiformia, Polynoidae). (I) *Dorvillea* sp. (Eunicida, Dorvilleidae).

CHAETOPTERIDAE Around 70 species, placed mostly in the genera *Chaetopterus*, *Mesochaetopterus*, *Phyllochaetopterus*, or *Spiochaetopterus* (Figures 15.1B and 15.10C–E). Adults range in size from less than 1 cm to more than 40 cm, though there are fewer than 60 segments in most taxa. Body distinctly heteronomous, divided into 2 or 3 functional regions with varying parapodia. Chaetopterids live in straight or U-shaped tubes, and most are mucous-net filter feeders, eating plankton and detritus pumped through the tube in water currents they generate. The group is best known for the extraordinary filter-feeding mechanism employed by *Chaetopterus*, which is also renowned for the blue luminescence that it produces.

AMPHINOMIDA Includes Amphinomidae and Euphrosinidae; over 200 species (Figure 15.2B). The more motile forms, amphinomids, are often quite large (e.g., *Chloeia, Eurythoe, Hermodice*) and commonly referred to as fire worms. This name comes from a feature unique to Amphinomida, namely brittle calcareous chaetae that break off when touched and can be intensely irritating in the skin. Amphinomids are more common in shallow warm seas, whereas the more sessile Euphrosinidae (e.g., *Euphrosine*) are found in deeper, colder waters.

A–L courtesy of G. Rouse

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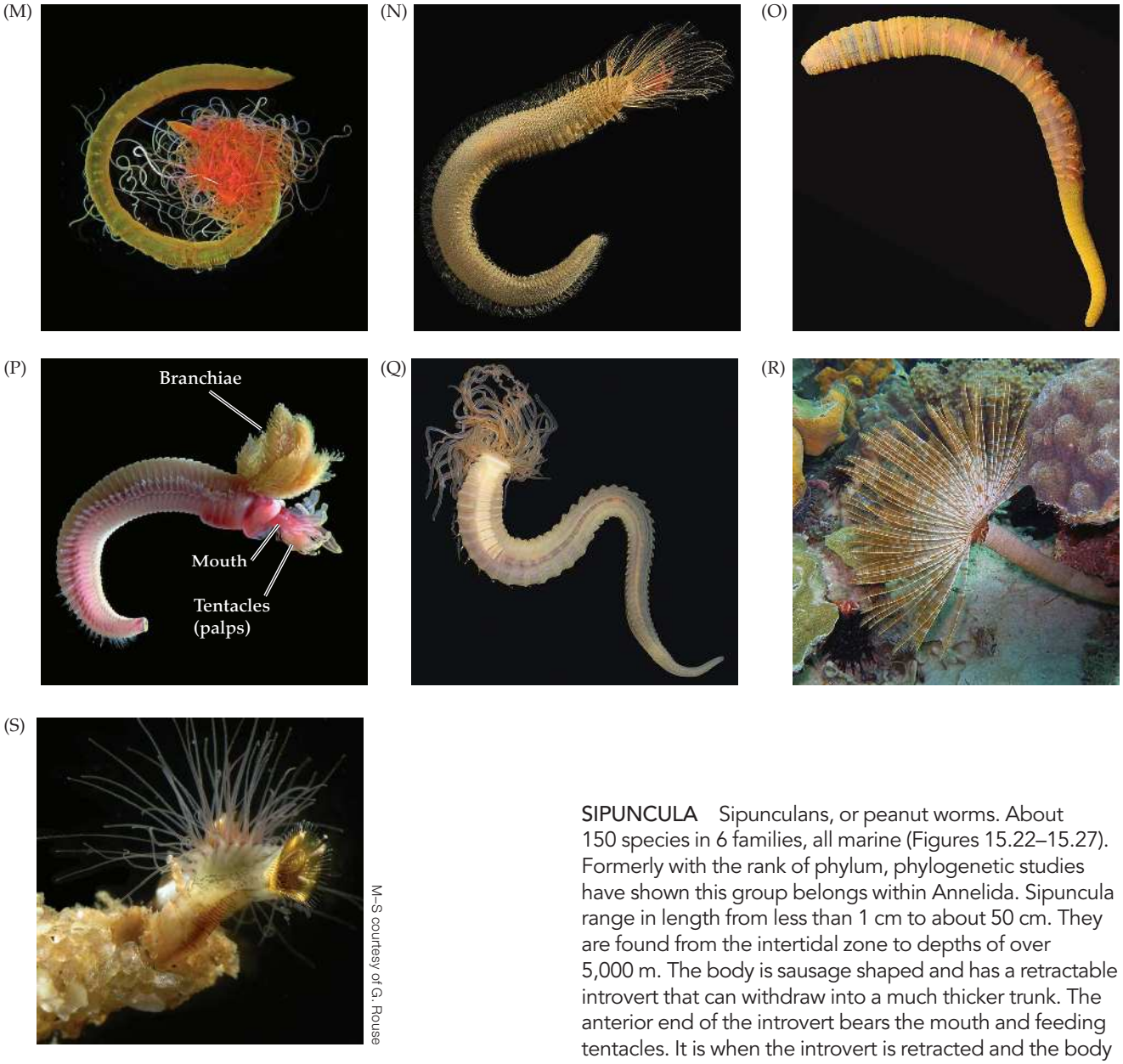

FIGURE 15.2 Further examples of annelid diversity. (A) *Magelona pitelkai* (Magelonidae). (B) *Hermodice carunculata* (Amphinomida). (C) *Saccocirrus* sp. (Protodrilida, Saccocirridae). (D) *Chrysopetalum* sp. (Chrysopetalidae). (E) *Platynereis dumerilii* (Nereididae). (F) The pelagic *Lopadorrhynchus* sp. (Lopadorrhynchidae). (G) *Trypanosyllis californiensis* (Syllidae). (H) *Lumbrineris* sp. (Lumbrineridae). (I) *Diopatra cuprea* (Onuphidae). (J) *Scoloplos armiger* (Orbiniidae). (K) *Thoracophelia mucronata* (Opheliidae). (L) *Capitella* sp. (Capitellidae). (M) *Cirriformia* sp. (Cirratulidae). (N) *Pherusa* sp. (Flabelligeridae). (O) *Abarenicola pacifica* (Arenicolidae). (P) *Paralvinella fijiensis* (Alvinellidae). (Q) *Amphitrite kerguelensis* (Terebellidae). (R) *Sabellastarte magnifica* (Sabellidae). (S) *Neosabellaria cementarium* (Sabellariidae).

SIPUNCULA Sipunculans, or peanut worms. About 150 species in 6 families, all marine (Figures 15.22–15.27). Formerly with the rank of phylum, phylogenetic studies have shown this group belongs within Annelida. Sipuncula range in length from less than 1 cm to about 50 cm. They are found from the intertidal zone to depths of over 5,000 m. The body is sausage shaped and has a retractable introvert that can withdraw into a much thicker trunk. The anterior end of the introvert bears the mouth and feeding tentacles. It is when the introvert is retracted and the body is turgid that some species resemble a peanut (e.g., *Phascolosoma*). Sipuncula lack a closed circulatory system and segmentation but have a spacious coelom. The gut is U-shaped and coiled, with the anus located dorsally on the body near the introvert-trunk junction. The body surface is usually beset with minute bumps, warts, tubercles, or spines. For a detailed classification of this taxon, see the Sipuncula section of this chapter.

ERRANTIA This is an old taxonomic grouping that has again found favor. It contains more than a quarter of all described annelid species diversity, in three major groups: Protodriliformia, Eunicida, Phyllodocida (the latter two comprising a sister group called Aciculata).

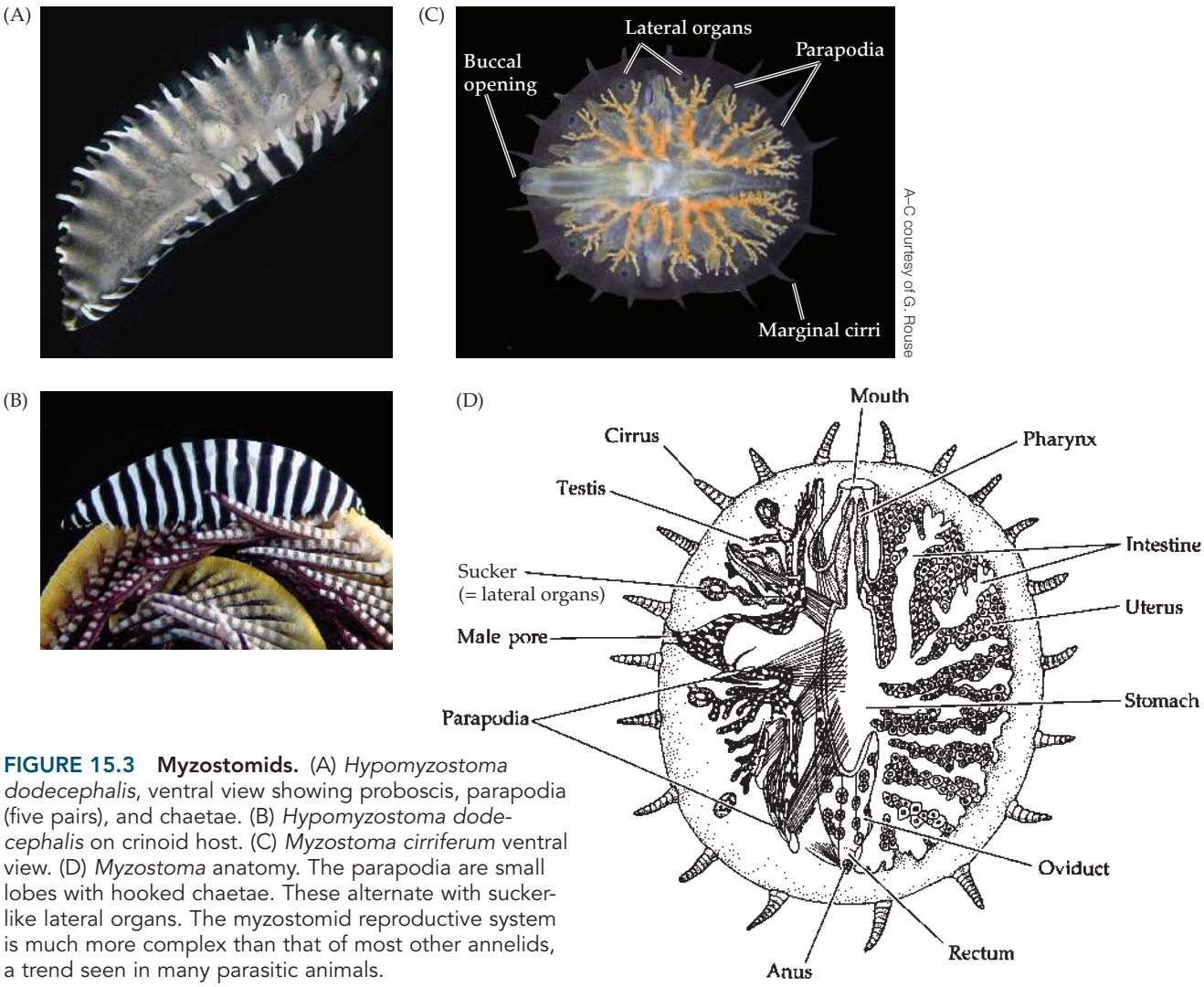

FIGURE 15.3 Myzostomids. (A) *Hypomyzostoma dodecephalis*, ventral view showing proboscis, parapodia (five pairs), and chaetae. (B) *Hypomyzostoma dodecephalis* on crinoid host. (C) *Myzostoma cirriferum* ventral view. (D) *Myzostoma* anatomy. The parapodia are small lobes with hooked chaetae. These alternate with sucker-like lateral organs. The myzostomid reproductive system is much more complex than that of most other annelids, a trend seen in many parasitic animals.

PROTODRILIFORMIA

PROTODRILIDA Over 60 species, mainly living interstitially in sediments (Figure 15.2C). Includes Protodrilidae, Protodriloididae, and Saccocirridae, best known for being members of the now defunct taxon Archiannelida. Taxa such as *Protodrilus* and *Saccocirrus* are found in medium to coarse sediments in shallow waters. Adult Protodrilida range in length from 2 to 30 mm and can have up to 200 segments. Protodrilidae lack chaetae, though these are found in Protodriloididae and Saccocirridae. All have a pair of palps emerging from the prostomium that form highly mobile sensory structures.

POLYGORDIIDAE Nicknamed "knot worms," they are generally found in coarse, well-sorted sediments and resemble very large nematodes as they writhe around. Lacking chaetae and obvious external segmentation, they were once thought to represent the ancestral annelid state. One accepted genus, *Polygordius*.

EUNICIDA Over 1,000 species that have a ventral muscularized pharynx with complex jaws that include elements such as ventral mandibles and dorsal maxillae. Their parapodia are supported by rodlike chaetae called aciculae and often bear compound chaetae. They generally have 3 antennae and a pair of sensory palps on the head. Eunicida include some of the smallest and largest known annelids. Currently with 7 family-ranked taxa (4 of which are described here).

DORVILLEIDAE Over 200 species (Figures 15.1I and 15.8F). Includes some of the smallest annelids (*Neotenotrocha*), while others may reach several centimeters and have many segments (e.g., *Dorvillea*). The head often has 3 antennae, and there can be a pair of palps that may either resemble or differ from the shape of the antennae. *Ophryotrocha* is a well-known "model annelid" as it is easily kept in culture on spinach or similar foods. Dorvilleids are also very commonly found in extreme habitats such as hydrothermal vents, methane seeps, and whale falls, where they are bacteriovores.

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EUNICIDAE Over 450 species (Figure 15.17H). A group that contains arguably the largest of annelids, some exceeding 3 m in length, with only a megascolecid earthworm species coming near this size. Usually with 3 antennae and a pair of palps that resemble antennae. Motile, though also living in burrows or temporary tubes in mucous or parchmentlike tubes. Carnivores, omnivores, or herbivores. Famous examples include palolo worms and the Bobbitt worms. (e.g., *Eunice*, *Marphysa*, *Palola*).

LUMBRINERIDAE Over 300 species (Figure 15.2H). Thin and elongate and, except for *Lysarete* and *Kuwaita*, lacking head appendages. Most crawl about in algal mats and holdfasts, and small cracks in hard substrata; some burrow in sand or mud. Carnivores, scavengers, detritivores, and deposit feeders. Other genera include *Lumbrineris*, *Lumbrinerides*, and *Ninoe*.

OENONIDAE Over 100 species. Elongate, with small parapodia; lacking head appendages, or with 3 small antennae. Resembling Lumbrineridae, though their jaws and chaetae differ. Often found in soft substrata where they burrow aided by secretion of copious amounts of mucus. Predatory carnivores: many have an endoparasitic juvenile stage living inside other annelids. (e.g., *Arabella*, *Drilonereis*).

ONUPHIDAE Over 330 species (Figure 15.2I). Closest relatives are Eunicidae, though onuphids generally have prominent gills on anterior segments. Most live in tubes, but others roam through sediments. Most tube dwellers are sessile (e.g. *Diopatra*), while others carry their tubes with them. Generally, scavengers or predators. Interesting forms include quill worms (*Hyalinoecia*) and the Australian beach worms (*Australonuphis*, etc.).

HISTRIOBDELLIDAE The "Charlie Chaplin worm" are tiny members of Eunicida that live as commensals on a variety of Crustacea. There are currently 13 nominal species placed in this family, including *Histriobdella, Steineridrilus*, and *Stratiodrilus*, with most of them known from rivers of South America. They lack chaetae but share other features with Eunicida.

PHYLLODOCIDA With more than 4,500 species, is distinguished by its members having an axial muscular proboscis (often armed with 2 or more jaws). They tend to show fusion of some anterior segments with the head, often only identifiable by the retention of anterior enlarged cirri, and the head usually has 2 or 3 antennae and a pair of sensory palps. Like Eunicida, their parapodia are also often supported by aciculae and bear compound chaetae. Currently with around 20 family-ranked taxa; the more species-rich ones are introduced here.

APHRODITIFORMIA Scale worms comprise a diverse group of over 1,500 species in 7 family-ranked taxa (Figures 15.1H, 15.5E, and 15.11A,B): Acoetidae, Aphroditidae, Eulepethidae, Polynoidae (contains most species), Iphionidae, and Sigalionidae. Aphroditiformia also includes the scaleless scale worms of the former family Pisionidae. Most are relatively short and somewhat flattened dorsoventrally; one highly unusual Antarctic species, *Eulagisca gigantea*, reaches a length of nearly 30 cm and a width of about 15 cm. Most also have relatively few segments at adulthood, some sigalionids being exceptions. Most of the dorsal surface is normally covered by transformed flattened cirri (called elytra, or scales), hence the common name. The eversible pharynx has one pair of jaws that close dorsoventrally somewhat like a parrot's beak. Most scale worms are motile but usually cryptic (under stones, etc.). Many are predators while others are bacteriovores. Many scale worms are commensals, living on the bodies or in the dwellings of other animals. Other genera include *Arctonoe*, *Gorgoniapolynoe*, *Halosydna*, *Harmothoe*, *Hesperonoe*, *Macellicephala*, and *Polynoa*.

CHRYSOPETALIDAE Over 100 species (Figure 15.2D). The name (Latin for "golden petals") refers to the shape and color of the golden, flattened notochaetae (called paleae) that cover the dorsal surface in many species (e.g., *Chrysopetalum*). These worms are of small to moderate size, with adults varying in length from 1 to 50 mm, and with as few as 10 to over 300 segments. Those with the dorsum covered by flattened paleae tend to be yellowish-brown to golden, sometimes with transverse stripes. One clade, Calamyzinae, contains parasitic forms that live in bivalve molluscs (these were formerly in their own family, Nautiliniellidae, as they show little resemblance to other chrysopetalids, e.g., *Shinkai*). Other genera include *Ichthyotomus* (Figure 15.11C).

GLYCERIDAE Over 90 species (Figures 15.5B, 15.8D, and 15.12C). Cylindrical, tapered, homonomous segmentation, usually red or pink, reaching 30 cm in length. Enormous eversible pharynx that can be retracted into one-third of the body length, armed with 4 hooklike jaws used in prey capture; each jaw has a venom gland. The pharynx is also used in burrowing. Most are infaunal burrowers in soft substrata. (e.g., *Glycera*, *Glycerella*, *Hemipodus*)

HESIONIDAE Over 175 species (Figure 15.11D). Generally beautiful worms, adults measuring from a few millimeters in length to more than 10 cm. Subtidal, especially on rocky and mixed bottoms, and increasingly known from hydrothermal vents and methane seeps. A famous hesionid is the ice worm, *Sirsoe methanicola,* which lives on methane hydrates in the Gulf of Mexico. Many Hesionidae have striking pigmentation patterns, and some are commensals, particularly with echinoderms. The number of segments in adults may be fixed at 21 (e.g., *Hesione*, *Leocrates*) or varying up to about 50–60. Other genera include *Hesiolyra*.

NEPHTYIDAE Over 150 species (Figure 15.5C). Usually long and slender, with well-developed

parapodia but simple heads. They can be very abundant in shallow-water sediments, and there are often several different taxa in a single sediment sample. While they are easily identified to this family level, species identification is difficult. Adults range from a few millimeters to 30–40 cm and up to 150 segments. Eversible jawed pharynx used in prey capture and burrowing. (e.g., *Aglaophamus*, *Micronephthys*, *Nephtys*)

NEREIDIDAE Over 700 species (Figures 15.2E, 15.8A–C, and 15.13A). Among the best-known marine annelids and widely used in teaching, in laboratories, and as fishing bait. Most nereidids are found in shallow waters, though some are found at hydrothermal vents. Small to very large (over 100 cm) with homonomous segments. Mostly errant predators or scavengers with well-developed eyes and parapodia. Immediately recognized by their pair of large, curved pharyngeal jaws (e.g., *Cheilonereis*, *Dendronereis*, *Neanthes*, *Nereis*, *Platynereis*). One group, Namanereidinae, is semiterrestrial or lives in fresh water. (e.g., *Lycastella*, *Namanereis*).

PHYLLODOCIDAE Over 500 species (Figures 15.5F, 15.8E, and 15.16D). Thin, often elongate (over 50 cm) bodies of up to 700 homonomous segments; commonly active epibenthic predators on solid substrata; a few burrow in mud (e.g., *Eteone*, *Eulalia*, *Notophyllum*, *Phyllodoce*). One clade, Alciopini, comprise holopelagic forms, in which the body is transparent except for pigment spots and a large pair of lensed eyes. Other genera include *Alciopa*, *Alciopina*, *Torrea*, *Vanadis*.

SPHAERODORIDAE Over 140 species. Easily recognized by conspicuous tubercles and/or papillae all over the body, generally arranged in transverse rows. Adults range from a few millimeters to several centimeters. Bodies can be short and grublike with up to about 30 segments (e.g., *Sphaerodoridium, Sphaerodoropsis*) or elongate and slender with a larger number of segments. Other genera include *Ephesiella*.

SYLLIDAE Over 1,000 species (Figures 15.2G, and 15.17C,D,G). Mostly small, homonomous worms found on various substrata. Best known for their diversity in reproductive biology, including various forms of epitoky. Adult sizes from 1 to 150 mm; with only a few segments or with many segments. Syllids show some of the most striking coloration patterns among annelids. Mainly predators on small invertebrates. The pharynx has a distinct barrel-shaped region that may be armed with a single tooth or a ring of small teeth for grasping prey. (e.g., *Autolytus*, *Brania*, *Myrianida*, *Odontosyllis*, *Ramisyllis*, *Syllis*, *Typosyllis*, *Trypanosyllis*)

PELAGIC PHYLLODOCIDA A polyphyletic grouping of about 150 pelagic species. In addition to Alciopini, several other groups of Phyllodocida have independently evolved into holopelagic forms, though the number of evolutionary events has yet to be fully resolved. Holopelagic forms are included in the families Lopadorrhynchidae (Figure 15.2F), Pontodoridae, Tomopteridae, Typhloscolecidae. Most are likely to be predators. Tomopterids are spectacular forms with transparent flattened bodies, finlike parapodia, and only a few chaetae.

MYZOSTOMIDA 156 species (Figure 15.3). During the twentieth century, these animals were treated as annelids with a rank of family or order, or even as a separate class. Some workers suggested that Myzostomida are more closely related to Platyhelminthes than to any annelids. However, the pendulum swung back in favor of myzostomids being annelids, starting with a molecular analysis by Bleidorn et al. (2007). Recent phylogenomic analyses have not been able to stabilize the phylogenetic position of the group, and while they clearly appear to be annelids, their closest relative is still not known, though there are morphological similarities with the Errantia. Myzostomids include several groups of flattened, oval, or elongate forms, always with 5 chaetae-bearing segments. They are mainly ectosymbionts, endosymbionts, or parasites of crinoid echinoderms, though a few are parasitic on Anthozoa. (e.g., *Hypomyzostoma* and *Myzostoma*).

SEDENTARIA Another previously defunct taxonomic group resurrected in the 2010s and containing over 13,000 species. It comprises a series of major groups, though the relationships among them are not fully resolved. The former phyla Echiura and Pogonophora (and Vestimentifera) are placed here, as well as a variety of tube-dwelling and burrowing forms. Clitellata are also nested in Sedentaria.

ORBINIIDAE Over 230 species (Figures 15.2J and 15.16G). Prostomium can be rounded or pointed, without appendages. Adults from 3 to 300 mm long and large forms can have several hundred segments: usually with an anterior "muscular" thoracic region and a more fragile abdomen. Usually with complex parapodia and a wide range of chaetae. Generally burrowing forms, they are usually found in the sediments of shallow bays and estuaries (e.g., *Orbinia*, *Scoloplos*) but also have been recorded from hydrothermal vents and methane seeps. (e.g., *Methanoaricia, Proscoloplos*)

CIRRATULIDA

ACROCIRRIDAE Around 50 species. Often found intertidally, under rocks or in shallow sediments and muds. The head is simple with a rounded prostomium and a pair of grooved peristomial palps used for feeding. Each of the first 4 segments bears a pair of simple unbranched branchiae, which are easily lost. Adults reach 5 to 150 mm and have from as few as 10 segments to more than 200. Live acrocirrids tend to be yellowish to greenish-brown in color (e.g., *Acrocirrus*, *Macrochaeta*). An extraordinary new group of holopelagic Acrocirridae was recently described in which the anterior branchiae have transformed into bioluminescent structures that glow when shed, presumably to distract predators. (e.g., *Swima*)

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CIRRATULIDAE Over 350 species (Figures 15.2M and 15.17B). Elongate, with relatively homonomous segmentation, with up to 350 segments, often each with a pair of threadlike branchial filaments (e.g., *Cirratulus*, *Cirriformia*). In others there may be only 4 pairs of branchiae anteriorly (e.g., *Dodecaceria*), or none in smaller forms (e.g., *Ctenodrilus*). Cirratulids are mostly shallow-water burrowers lying just beneath the surface of the sediment, from where they extend their branchiae into the overlying water. Most are selective deposit feeders, extracting organic detritus from surface sediments, using grooved palps that may be a simple pair (e.g., *Chaetozone*, *Dodecaceria*) or transformed into 2 clusters. Other genera include *Timarete*.

FLABELLIGERIDAE Over 200 species (Figure 15.2N). Sometimes called bristle-cage worms. With papillae covering the body, papillae often sticky, hence some have a sediment coating. Others have a thick, transparent gelatinous sheath, allowing the body contents and green circulatory system to be seen. The head, which has a pair of grooved palps and presumably some achaetous anterior segments bearing branchiae, is often retractable into the following anterior segments that bear a "cage" of protective chaetae. Mostly benthic, from the intertidal under stones to deep-sea muds, though there are two holopelagic groups, *Poeobius* and *Flota*, that were in their own families until recently. Adults are 5 mm to more than 10 cm in length. Other genera include *Brada*, *Pherusa*.

SPIONIDA

SPIONIDAE Over 600 species (Figures 15.1G and 15.9F). Body thin, elongate, homonomously segmented. The head is simple with a pair of grooved peristomial palps. Most burrow or form delicate sand or mud tubes. A few bore into calcareous substrata, including rocks and mollusc shells; most use the grooved peristomial palps to selectively extract food from the sediment surface. (e.g., *Boccardia*, *Polydora*, *Scolelepis*, *Spio*, *Spiophanes*)

SABELLARIIDAE Over 130 species (Figures 15.2S and 15.7H,I). Sabellariidae are easily distinguished from most other annelids by having an operculum that is developed from anterior segments and a robust tube built from coarse sand grains. The operculum comprises two fleshy lobes that are fused (e.g., *Sabellaria*), or free (e.g., *Lygdamis*), and it includes 1–3 rows of large golden or black stout chaetae (paleae). Generally found in intertidal to slightly subtidal areas, though deep-water forms are known. Sabellariids can form extensive biogenic reefs and can reach densities of up to 6,000 individuals/m^2 (e.g., *Phragmatopoma*, *Sabellaria*), while others are solitary.

SABELLIDA

SABELLIDAE Over 550 species (Figures 15.2R, 15.7A, and 15.16E). Commonly called fan worms or feather-duster worms. Sabellids live in sediment and mucous tubes and are common at all depths. The body is heteronomous, divided into a thorax and an abdomen, and can be 3 to 300 mm long. The thorax bears long dorsal "capillary" or hooded chaetae and ventral hooks, while the abdomen shows the inverse (chaetal inversion). The prostomium is a crown of branched, feathery palps (radioles) that projects from the tube and functions in gas exchange and ciliary suspension feeding (e.g., *Bispira*, *Eudistylia*, *Myxicola*, *Sabella*, *Schizobranchia*) and may bear simple eyes (e.g., *Demonax*) or compound eyes (e.g., *Megalomma*). Some species bore into calcareous substrates (e.g., *Pseudopotamilla*). Sabellidae also once included Fabriciidae, all small-bodied feather-duster worms, but these have been shown to be more closely related to Serpulidae and were placed in their own family. Other genera include *Acromegalomma*, *Amphiglena, Neosabellaria, Sabellastarte*.

SERPULIDAE Over 560 species (Figures 15.7E,F,J and 15.20A–C). Like sabellids, except the secreted tube is calcareous and usually attached to rocks. The body is heteronomous, divided into thorax and abdomen, ranging in size from 3 to 200 mm. Anterior end bears radiolar crown as in sabellids; many species have one radiole transformed into an operculum that plugs the end of the tube when the worm withdraws (e.g., *Hydroides*, *Serpula*, *Spirobranchus*), though many lack this (e.g., *Filograna, Protula*). The most well-known serpulid group is *Spirobranchus*, the Christmas tree worms, which bore into coral substrates and have colorful spiral radiolar crowns (Figure 15.7J). One speciose clade, Spirorbinae, contains small-bodied forms that secrete coiled calcareous tubes. Other genera include *Circeis*, *Ditrupa*, *Paralaeospira*, *Spirorbis*.

FABRICIIDAE Over 80 species. Fabriciidae were for many years considered part of Sabellidae, and they share similarities such as the radiolar crown and dwelling in a mucus/sediment tube. These characters alone are taxonomically misleading, and the closest relative of Sabellidae is Serpulidae. Unlike Sabellidae, Fabriciidae are consistently small bodied as adults, the smallest of which is *Fabriciola minuta*, which has an adult length of only 0.85 mm. When alive, fabriciids are usually translucent but can have patches of pigment on the crown and body. They often abandon their tubes when disturbed, and they may have eyes behind the crown and in the pygidium. All are intratubular brooders with crawl-away larvae and so can reach very high population densities.

SIBOGLINIDAE Over 200 species (Figures 15.1E, 15.32, and 15.33). Previously classified as the phyla Pogonophora and Vestimentifera. Morphological and molecular analyses now recognize this group as a clade within Annelida; the original family name, Siboglinidae, has since been generally adopted. Siboglinidae all appear to live via symbiotic bacteria in their bodies

and are generally found at greater than 1,000 m depth, even down to nearly 10,000 m, though exceptionally they are found in depths of less than 100 m. Though most are known from deep-sea muds (e.g., *Siboglinum*), mud volcanoes, or sunken plant material (e.g., *Sclerolinum*), vestimentiferan siboglinids (e.g., *Riftia*) are spectacular members of hydrothermal vent communities or methane seeps (e.g., *Lamellibrachia*). Siboglinidae vary greatly in size, with adults of some *Siboglinum* reaching 5 cm in length (and only 0.1 mm in width), while *Riftia pachyptila* are more than 150 cm in length and live in tubes more 2.5 m long. The most recently discovered group of Siboglinidae is the genus *Osedax*, a group that devours the bones of marine vertebrates by dissolving through them with tissue that resembles plant roots. Other genera include *Arcovestia, Lamellisabella, Polybrachia*.

MALDANOMORPHA

ARENICOLIDAE Over 25 species (Figures 15.2O and 15.5H). Arenicolids or lugworms have simple heads and a thick, fleshy, heteronomous body divided into two or three distinguishable regions; the pharynx is unarmed but eversible and aids burrowing and feeding. Most arenicolids live in J-shaped burrows in intertidal and subtidal sands and muds, where they are direct deposit feeders. (e.g., *Abarenicola*, *Arenicola*)

MALDANIDAE Over 250 species (Figure 15.7C,D). Known as bamboo worms because of the long cylindrical segments with ridgelike parapodia that resemble stalks of bamboo. Like arenicolids, the head has no appendages; maldanids are 0.3 cm to more than 20 cm in length. They usually have 20–30 segments and the body does not taper posteriorly as in most other annelids. (e.g., *Axiothella*, *Clymenella*)

TEREBELLIFORMIA

ALVINELLIDAE An unusual hydrothermal vent group from the Pacific and Indian Oceans, the Pompeii worms (2 genera and 11 species: *Alvinella*, *Paralvinella*). Adult alvinellids can be up to 15 cm long (Figures 15.2P and 15.11D).

AMPHARETIDAE Over 260 species. Ampharetids are tubicolous and easily distinguished from the similar Terebellidae in that their multiple grooved palps, usually called tentacles, can be retracted into the mouth. Generally, 4 pairs of branchiae. Relatively uncommon in intertidal and shallow waters; in recent years, most new taxa have been described from deeper sediments. The body consists of 2 distinct regions in addition to the head, a thoracic region that generally has biramous parapodia and an abdomen that has neuropodia only. (e.g., *Ampharete, Amphicteis*). Used to include Melinnidae, which is now a separate family. Adult Ampharetidae are 0.5–6 cm long.

PECTINARIIDAE Over 70 species (Figures 15.7G and 15.9G). The ice-cream-cone worms. Body short and conical with stout golden chaetae projecting from the head. Also, easily recognizable from their elegant cone-shaped tubes, constructed from sand, small shells, or other small particles, open at both ends. Body length 1 to 10 cm, with no more than 20 segments bearing chaetae. Multiple grooved palps ("tentacles") used to feed on detritus extracted from sediment. (e.g., *Pectinaria, Petta*)

TEREBELLIDAE Over 620 species (Figures 15.2Q and 15.9B–E). Tube dwelling, though many are burrowers or "creepers" and some are even capable of swimming. The grooved palps are often seen extending out over the sediment in shallow marine waters. When disturbed, the tentacles, often brightly colored, are retracted back toward the worm, though they are not retracted into the mouth. Usually, three pairs of branchiae. The body usually consists of 2 distinct regions in addition to the head: a thoracic region that generally has biramous parapodia, and a long tapering abdomen that has neuropodia only. (e.g., *Amphitrite*, *Pista*, *Polycirrus*, *Terebella*, *Thelepus*)

CAPITELLIFORMIA

OPHELIIDAE Over 170 species (Figure 15.2K). With homonomous segmentation, usually less than 3 cm long, with up to 60 segments. Body shape varies from short and thick to elongate and somewhat tapered. Most opheliids burrow in soft substrata, but some can swim by undulatory body movements. The eversible pharynx is unarmed. Most are direct deposit feeders. (e.g., *Armandia*, *Euzonus*, *Ophelia*, *Polyophthalmus, Thoracophelia*)

CAPITELLIDAE Over 200 species (Figure 15.2L). Easily recognized by the division of the body into an anterior region with capillary chaetae only and a posterior region with long-handled hooks. The body is a simple cylindrical shape, resembling Clitellata. The head has no appendages and is a simple conical structure in most. Body less than 1 cm to more than 20 cm in length; usually bright red. Extensions of the body wall, often erroneously called "branchiae" (erroneous, since capitellids lack a circulatory system), are present in abdominal segments of some taxa. Some, such as *Capitella,* are well known as pollution indicators since their numbers explode in nutrient-rich conditions that exclude many other annelid species. Other genera include *Dasybranchus*, *Notomastus*.

THALASSEMATIDAE (FORMERLY ECHIURA) Around 160 species (Figures 15.1C and 15.28–15.30). Spoon worms, anchor worms. Unusual annelids in that they have a muscular extensible preoral proboscis at the anterior end of an apparently unsegmented trunk. The proboscis cannot be withdrawn into the mouth, but it can be extended for several meters in some species. The trunk ranges from 1 to 40 cm in length and bears a single pair of chaetae anteriorly, or both anteriorly and with rings of chaetae posteriorly. Thalassematidae were generally considered annelids, but W. W. Newby proposed a separate phylum, Echiura, based on a detailed embryological study of

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Urechis caupo. His proposal was generally accepted until molecular evidence showed that they are, in fact, annelids. Subsequent morphological studies supported that conclusion, and recent molecular analyses have shown the group to be closely related to Capitellidae. Thalassematids appear to be unsegmented, but their nervous system proceeds from anterior to posterior during embryogenesis, suggesting the occurrence of a posterior growth zone (teloblasty). Genera include *Bonellia, Echiurus, Ikeda, Listriolobus, Metabonellia, Onchnesoma, Protobonellia, Prometor, Thalassema, Urechis*.

CLITELLATA Over 8,500 species. Earthworms, leeches, and related forms. Without parapodia; chaetae usually greatly reduced or absent. Hermaphroditic, with complex reproductive systems. A distinct ring, the clitellum, functions in cocoon formation; development is direct. Cephalic sensory structures reduced; body externally homonomous except for clitellum. Mostly terrestrial or freshwater annelids, although there are also many marine species.

CAPILLOVENTRIDAE 5 species. The morphology and arrangement of their chaetae resemble those of some errantiate annelids, but the presence of a clitellum and other features reveals they are clitellates. Interestingly, both morphological and molecular evidence suggests they are the sister group to all other clitellates and lends support to the hypothesis that Clitellata has an aquatic origin. Two of the species are marine, 2 live in fresh water, and 1 in brackish water. A single genus, *Capilloventer*.

NAIDIDAE (FORMERLY KNOWN AS TUBIFICIDAE) Around 700 species. Range in length from a few millimeters to several centimeters. The best known of the freshwater clitellates, though some live in marine or brackish water. Some build tubes, others are burrowers. Usually, the body is homonomous throughout with a simple head, though several species bear an elongate prostomial proboscis; some have branchiae. Many reproduce asexually, but most have gonads at some stage of development. Some species are very common in areas of high pollution. Some small, gutless species that rely on symbiotic bacteria for nutrition are known from tropical regions (e.g., *Inanidrilus*, *Olavius*). Other genera include *Branchiodrilus*, *Branchiura*, *Clitellio*, *Dero*, *Limnodrilus*, *Ripistes*, *Slavina*, *Stylaria*, and *Tubifex*.

CRASSICLITELLATA Earthworms and their allies (Figures 15.1F, 15.12F, 15.15F, and 15.18). Over 5,500 valid species that are mainly terrestrial, but some taxa (e.g., Biwadrilidae and Almidae) live in aquatic or semiaquatic environments. The most species-rich families are Megascolecidae (e.g., *Amynthas*, *Pheretima*), Lumbricidae (e.g., *Eisenia*, *Lumbricus*), and Glossoscolecidae. Crassiclitellata include the common terrestrial earthworms, including *Lumbricus terrestris*, which has been spread to soils across the world from its native Europe. Crassiclitellates are relatively large, with well-developed and complex reproductive systems. They are deposit feeders, living in soil, feeding on live and dead organic matter. The largest of all clitellates belong to Megascolecidae, for example the giant Gippsland earthworm, *Megascolides australis* (an endangered species native to Australia), can stretch to about 3 m in length, though their normal length is said to be around 1 m long and 2 cm in diameter. Invasion of nonnative earthworms can profoundly alter native soil ecosystems. Such invasions are particularly problematic in regions of North America that were historically devoid of native earthworms prior to European settlement. Earthworm invasions can accelerate litter loss and reduce soil horizon thickness, alter nutrient pools, increase soil microbial biomass and activities, shift understory plant community composition and diversity, and decrease native soil microbes, fungi, and invertebrates. Among the many invasive earthworms in North America are the Asian jumping earthworms (*Amynthas agrestis* and *A. tokioensis*), notable for their rapid snakelike movements and jumping behavior when disturbed. Reaching 15 cm in length, these worms can reduce soil surface litter by up to 95%.

ENCHYTRAEDIDAE 700 species. Found mainly in soil but also in a wide range of freshwater and marine/brackish water habitats. Marine enchytraeids are common in intertidal sands, but they are also known from deep-sea sediments. Those of the genus *Mesenchytraeus* are known as ice worms, as they thrive in glacial ice.

LUMBRICULIDAE Over 150 species (Figure 15.18H). Worms of moderate size, found in marshes, streams, and lakes. The group shows a great deal of endemism, mainly in Siberia (notably Lake Baikal) and the western parts of North America. This is the sister group of Hirudinea. (e.g., *Alma*, *Lamprodilus*, *Phagodrilus*, *Rhynchelmis*, *Stylodrilus*, *Styloscolex*, *Trichodrilus*)

HIRUDINEA Leeches and their relatives (Figures 15.34–15.40). Body with fixed number of segments, each with superficial annuli; chaetae generally absent; heteronomous, with clitellum and a posterior and usually an anterior sucker; most live in freshwater or marine habitats, a few are semiterrestrial; ectoparasitic, predaceous, or scavenging. There are 3 major clades within Hirudinea.

ACANTHOBDELLIDA Two species, *Acanthobdella peledina* and *A. livanowi*, both from Northern Hemisphere freshwater lakes (Figure 15.34A). Part of the animal's life is spent as an ectoparasite on freshwater fishes, especially salmonids and thymallids, and presumably the rest of the time is spent in vegetation. Body with 30 segments, reaching 3 cm in length; with posterior sucker only in *A. peledina*; chaetae on anterior segments; coelom partially reduced but obvious and with intersegmental septa.

BRANCHIOBDELLIDA Around 150 species (Figure 15.34B). Usually less than 1 cm long; ectocommensal or ectoparasitic on freshwater crayfish;

body with 15 segments; with anterior and posterior suckers; chaetae absent; coelom partially reduced but spacious throughout most of the body. A single family, Branchiobdellidae. (e.g., *Branchiobdella*, *Cambarincola*, *Stephanodrilus*)

HIRUDINIDA Over 700 species (Figures 15.34C, 15.37, and 15.38). The "true" leeches. Around 100 species are marine, 90 are terrestrial, and the remainder freshwater. Many are ectoparasitic bloodsuckers, others are free-living predators or scavengers; some parasitic forms serve as vectors for pathogenic protozoa, nematodes, and cestodes. Body always with 34 segments; with anterior and posterior suckers; no chaetae; coelom reduced to a complex series of channels (lacunae). About 12 families, in 2 main groups. Rhynchobdellida (proboscis leeches) is a paraphyletic group of several families that contains the marine species as well as many freshwater forms (e.g., *Glossiphonia*, *Johanssonia*, *Piscicola*). Arhynchobdellida is a clade that lacks a proboscis, although many have jaws; all are either freshwater or terrestrial. (e.g., *Erpobdella*, *Haemopsis*, *Hirudo*, *Macrobdella*).

DIURODRILIDAE These tiny animals reach only 500 µm in length as adults in the case of *Diurodrilus* and about 1 mm for *Apharyngtus*. They are exclusively marine, tidal to subtidal meiofaunal sand dwellers. They lack chaetae and obvious segmentation. Their position as part of Annelida was debated, but they now appear to be part of this group, though with an uncertain position in Sedentaria.

DINOPHILIFORMIA This name applies to the clade composed of Dinophilidae and *Lobatocerebrum*, two groups of tiny annelids that also lack chaetae. *Lobatocerebrum* has only recently been accepted as an annelid group. Dinophilidae can be strikingly colorful, and *Dimorphodrilus* shows remarkable sexual size dimorphism, with minute males that mate with their sisters after emerging from their brood cocoon.

The Annelid Body Plan

The typical annelid body is composed of four regions: a presegmental region derived from the larval episphere, the prototroch region around the mouth, the serially repeated body segments, and the posterior pygidium. The episphere (see the section on Reproduction and Development) becomes the presegmental **prostomium** in the adult, and the prototroch and buccal region give rise to the **peristomium**, the region surrounding the mouth (Figures 15.1F, 15.2L, and 15.8). The body segmentation of annelids is referred to as metamerism. The extreme posterior end of the body is the **pygidium,** and it bears the anus and often some cirri. As with the prostomium, the pygidium is nonsegmental and may well contain remnants of the larval body. From this basic scheme, the tremendous diversity of body forms seen in annelids is built. Externally visible metamerism and a greatly elongated cylindrical body typify most annelids. They are triploblastic, have a through (complete) gut, and have a spacious coelom. Exceptions concerning obvious metamerism include Sipuncula, Thalassematidae (formerly Echiura), Dinophiliformia, and Diurodrilidae, where this has been lost. In other groups, like Hirudinea and Myzostomida, the coelom is reduced. The gut (lost in some clitellates and in all Siboglinidae) is separated from the body wall by the coelom, except in those where the body cavity has been secondarily reduced.

The simplest annelid head is composed of a prostomium and a peristomium. The segmentation of the main body is typically visible externally as rings, or annuli, and is reflected internally by the serial arrangement of coelomic compartments separated from one another by intersegmental septa (Figure 15.4). This basic arrangement has been modified to various degrees among annelids, particularly by reduction in the size of the coelom or by loss of septa; the latter modification leads to fewer but larger internal compartments. The bodies of many annelids are **homonomous**, bearing segments that are very much alike. Many others, particularly tubicolous forms, have groups of segments specialized for different functions and are thus **heteronomous** (as in many Chaetopteridae). Specialization of segment groups (i.e., **heteronomy**) has contributed greatly to morphological diversification among annelids.

Our current view of annelid phylogeny (Figure 15.43) hypothesizes Oweniida, Chaetopteridae, and Amphinomida + Sipuncula forming a grade of three basal groups leading to the Polychaeta. These basal groups encompass a wide variety of body forms, and so inferring the structure of the ancestral annelid is challenging. A relatively homonomous body may be plesiomorphic since it is seen in Oweniida, some Chaetopteridae, and Amphinomida, though taxa such as Sipuncula and most Chaetopteridae may have dramatically different body forms.

Body Forms

Most annelids are marine, living in habitats ranging from the intertidal zone to extreme depths, although about a third of all annelid species live on land or in fresh water. But a good number inhabit brackish or fresh water, and the majority of Clitellata (thousands of species) live on land. Annelids range in length from less than 0.5 mm as adults for some interstitial species, to over 3 m for some giant eunicids and megascolecid clitellates (earthworms). The myriad variations in body form among annelids can best be described relative to the basic annelid regions of a head, segmented trunk, and pygidium. Note, though, that some groups such as Thalassematidae, Hirudinea, Siboglinidae, and

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Sipuncula are so transformed from this condition, each in its own interesting way, that they are treated as special sections near the end of this chapter. However, in general, the annelid head is composed of the prostomium and peristomium, which take various forms, and may also have one or more body segments fused with it, in which cases cirri and lateral chaetae may be present (Figures 15.8, 15.12A, and 15.15). The prostomium and peristomium often bear appendages in the form of antennae and/or palps, or they may be naked, as in many infaunal burrowers such as the clitellates. The nature of these head appendages varies greatly and often reveals clues as to the worms' habits. The trunk may be homonomous or variably heteronomous, and each segment often bears a pair of unjointed appendages, called parapodia, and bundles of chaetae (Figures 15.4C and 15.5).

Chaetae are a distinctive feature of annelids, although they are also found in some Brachiopoda (and perhaps some other phyla). They come in a huge range of shapes and sizes, each is derived from the microvillar border of an invaginated epidermal cell, and they are essentially bundles of parallel longitudinal canals, the walls of which are the sclerotized chitin (Figure 15.5). Chaetae have been lost in several annelid groups, most notably in Sipuncula and Hirudinea.

Parapodia, when present, are generally biramous, with a dorsal **notopodium** and a ventral **neuropodium**, each lobe with its own cluster of chaetae (Figures 15.4C and 15.5). However, annelids have evolved a huge diversity of parapodia that serve a variety of functions (locomotion, gas exchange, protection, anchorage, creation of water currents). In heteronomous annelids, the morphology of the parapodia may vary greatly in different body regions. Often, for example, parapodia in one region are modified as gills, in another region as locomotory structures, and elsewhere to assist in food gathering. In some cases, particularly in burrowing forms, as well as Sipuncula, Thalassematidae,

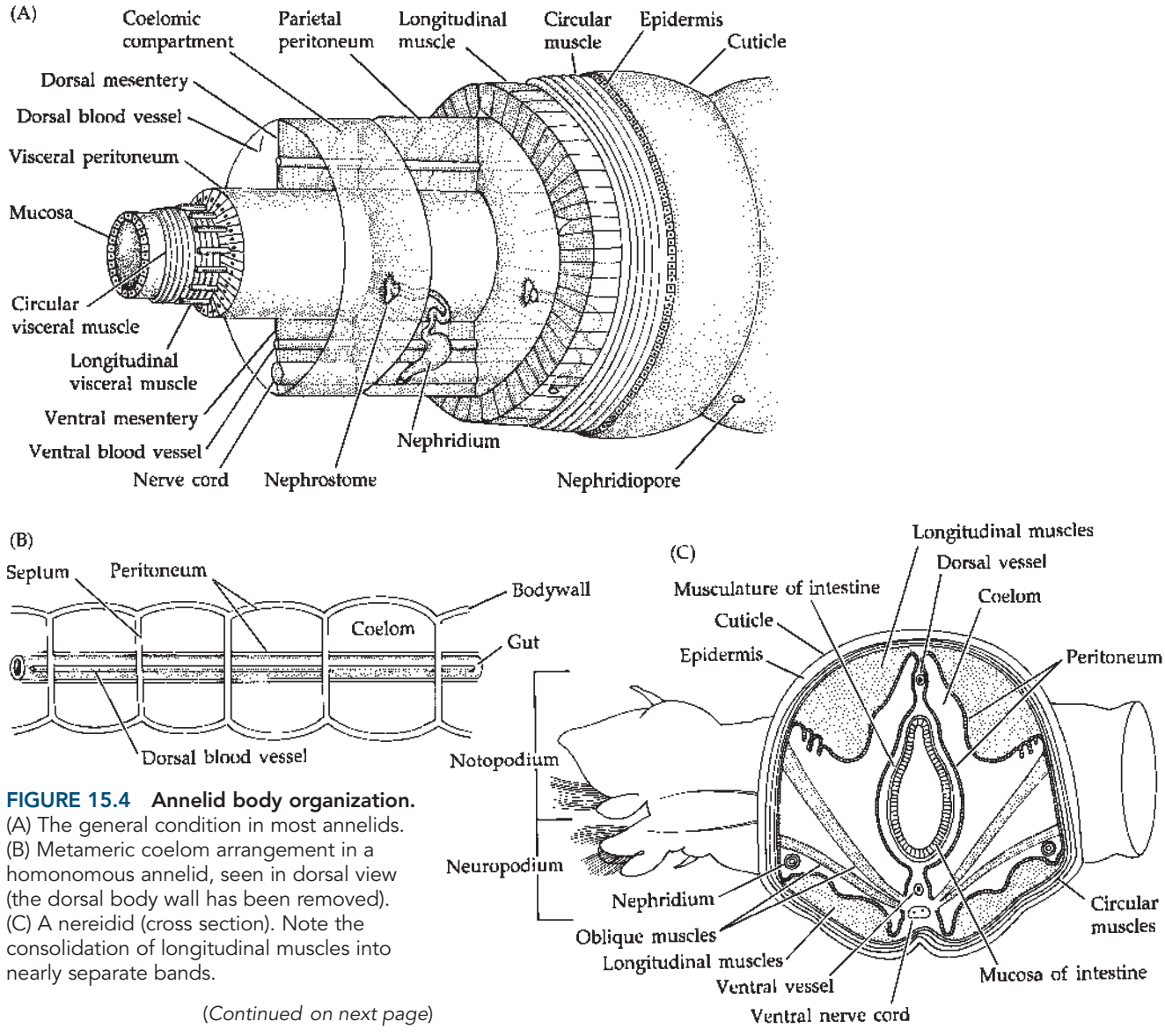

FIGURE 15.4 Annelid body organization. (A) The general condition in most annelids. (B) Metameric coelom arrangement in a homonomous annelid, seen in dorsal view (the dorsal body wall has been removed). (C) A nereidid (cross section). Note the consolidation of longitudinal muscles into nearly separate bands.

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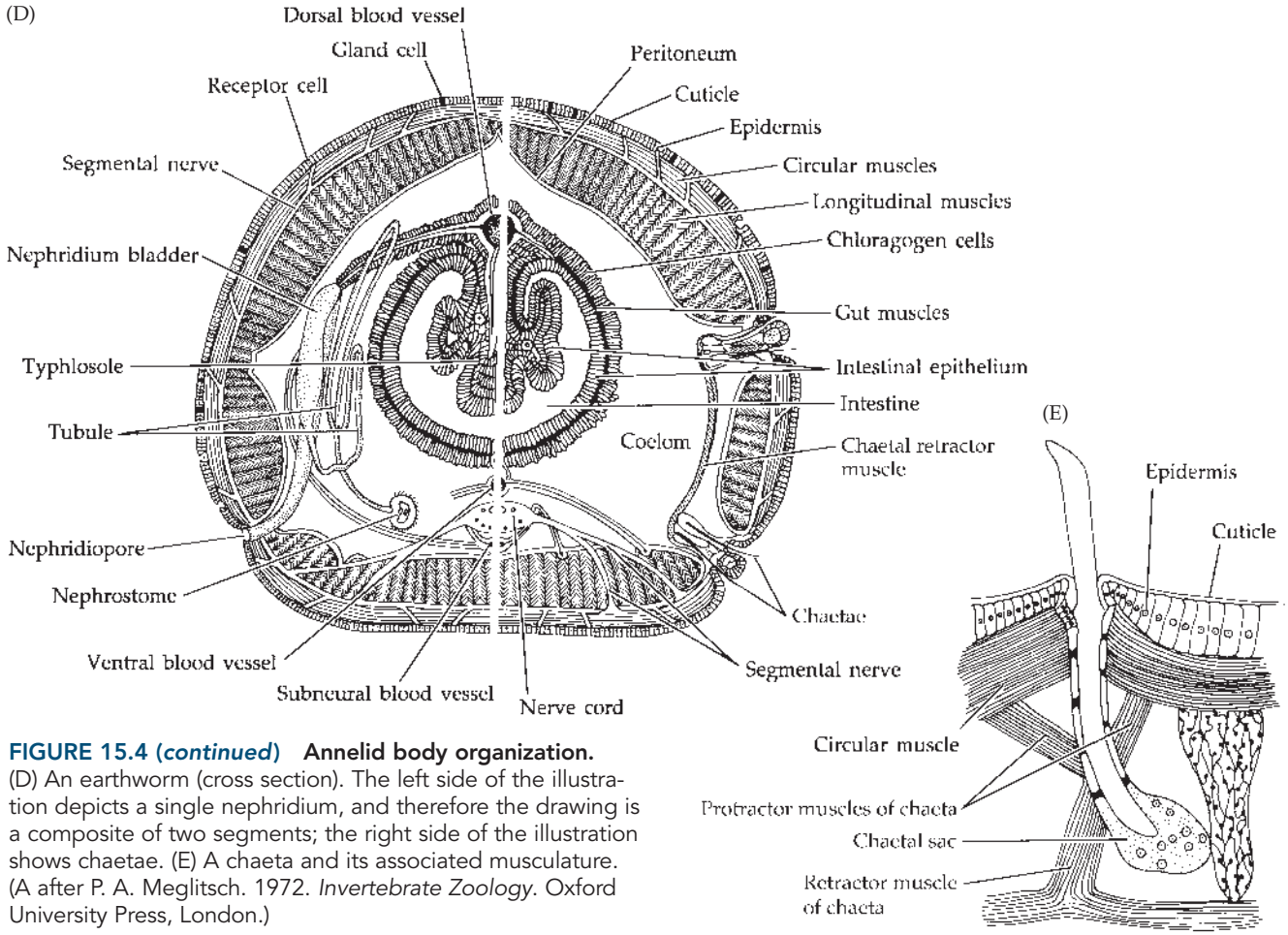

FIGURE 15.4 (*continued*) Annelid body organization. (D) An earthworm (cross section). The left side of the illustration depicts a single nephridium, and therefore the drawing is a composite of two segments; the right side of the illustration shows chaetae. (E) A chaeta and its associated musculature. (A after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

Diurodrilidae, *Polygordius*, and Clitellata, parapodia have been lost altogether.

Most annelids are gonochoristic and proliferate the gametes from the peritoneum into the coelom, where they develop. Many annelids have broadcast spawning and produce free-swimming larvae, but there is a great variety of life history strategies in this phylum, with a wide range of kinds of parental care also present. Notably, many annelids are hermaphrodites, including all members of Clitellata, which typically exchange sperm and produce brooded or encapsulated embryos that develop directly to juveniles.

Body Wall and Coelomic Arrangement

The annelid body is covered by a thin cuticle, which is composed of scleroprotein and mucopolysaccharide fibers deposited by epidermal cellular microvilli. The epidermis is a columnar epithelium that is often ciliated on certain parts of the body. Beneath the epidermis lies a layer of connective tissue, circular muscles (sometimes absent), and thick longitudinal muscles, the latter often arranged as four bands (Figure 15.4C). The circular muscles do not form a continuous sheath but are interrupted at least at the positions of the parapodia. The inner lining of the body wall is the peritoneum, which surrounds the coelomic spaces and lines the surfaces of internal organs. The coelom of annelids with homonomous bodies is generally arranged as laterally paired (i.e., right and left) spaces, serially (segmentally) arranged within the trunk. Dorsal and ventral mesenteries separate the members of each pair of coeloms, and muscular intersegmental septa isolate each pair from the next along the length of the body. In several annelid lineages, the intersegmental septa have been secondarily lost or are perforated, so in these animals the coelomic fluid and its contents, such as gametes, are continuous among segments. This is of course the case for Thalassematidae and Sipuncula, where there are no segments.

In addition to the main body wall and septal muscles, other muscles function to retract protrusible or eversible body parts (e.g., branchiae, pharynx) and to operate the parapodia (Figure 15.4C). Each parapodium is an evagination of the body wall and contains a variety of muscles. Movable parapodia are operated primarily by sets of diagonal (oblique) muscles, which have their origin near the ventral body midline. These muscles branch and insert at various points inside the parapodium. In the clades Aciculata and Amphinomida, and some Orbiniidae, the large parapodia may contain stout internal

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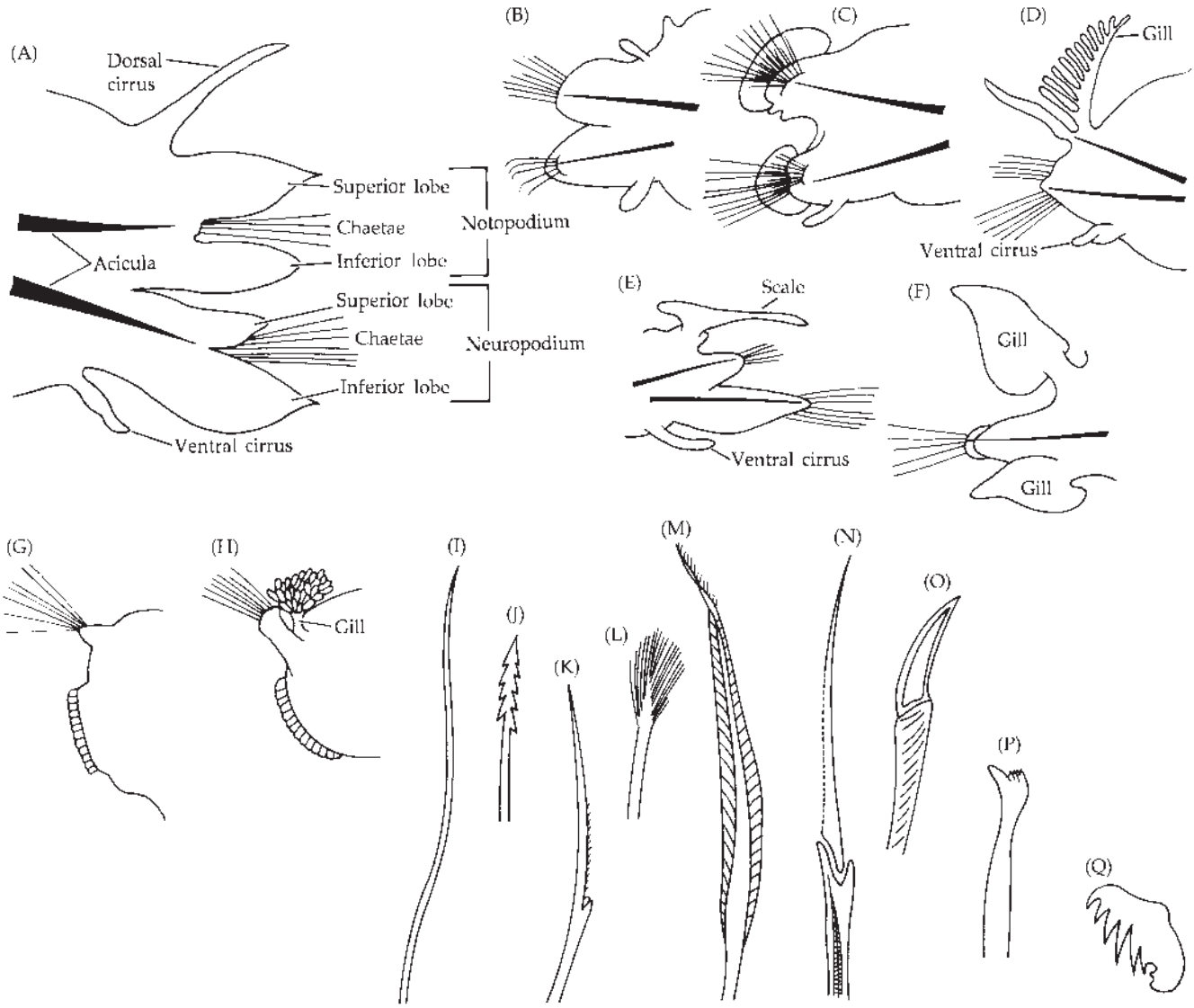


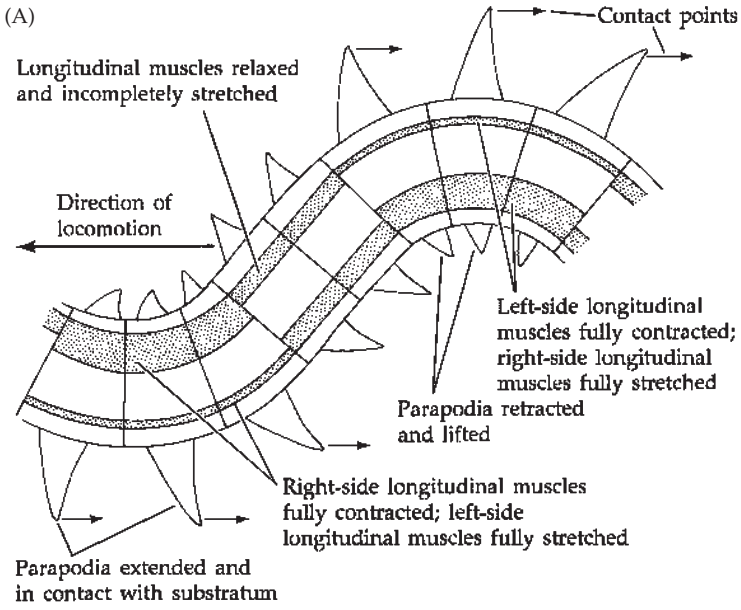
FIGURE 15.5 Parapodial and chaetal types among annelids. (A) A stylized parapodium. (B) The parapodium of a glycerid, with reduced lobes. (C) The parapodium of a nephtyid. (D) The parapodium of a eunicid with its modified notopodium; note the dorsal filamentous gill. (E) The parapodium of a polynoid (a scale worm) has the dorsal cirrus modified as a scale, or elytron. (F) The parapodium of a phyllodocid; the noto- and neuropodia are modified as gill blades. (G) The reduced parapodium of a tube-dwelling sabellid. (H) The parapodium of an arenicolid. (I–Q) Chaetae from various annelids. The classification of chaetal types rivals that of sponge spicules in complexity and terminology. A few general types are distinguished here as simple chaetae (I–M), compound chaetae (N–O), hooks (P), and uncini (Q). (A–H after P. A. Meglitsch, 1972. *Invertebrate Zoology*. Oxford University Press, London.)

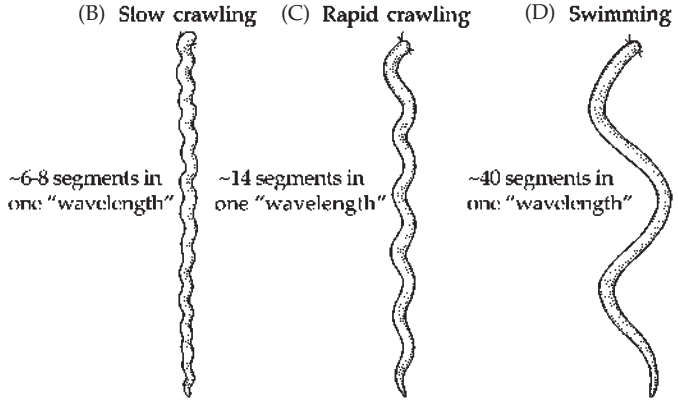
chaetae called **aciculae** (Figure 15.5), on which some muscles insert and operate. In general, chaetae are also maneuvered by muscles and can usually be retracted and extended (quite unlike the setae of arthropods).

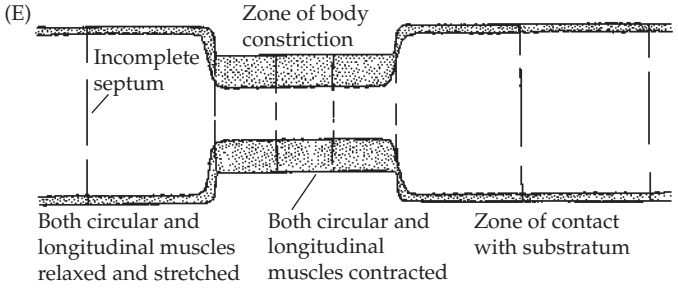
Support and Locomotion

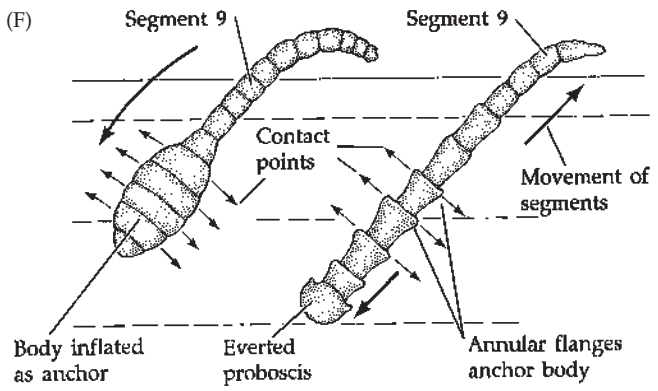
Annelids provide a great example of the employment of coelomic spaces as a hydrostatic skeleton for body support. Coupled with the well-developed musculature, the metameric body, and the parapodia, this hydrostatic quality provides the basis for understanding locomotion in these worms. The genera *Nereis* and *Platynereis* (Phyllodocida, Nereididae) are errant, homonomous annelids that show a variety of locomotory patterns that are worth describing (Figures 15.2E and 15.6A–D). In such annelids the intersegmental septa are functionally complete, and thus the coelomic spaces in each segment can be effectively isolated hydraulically from each other. Modifications on this fundamental arrangement are discussed later.

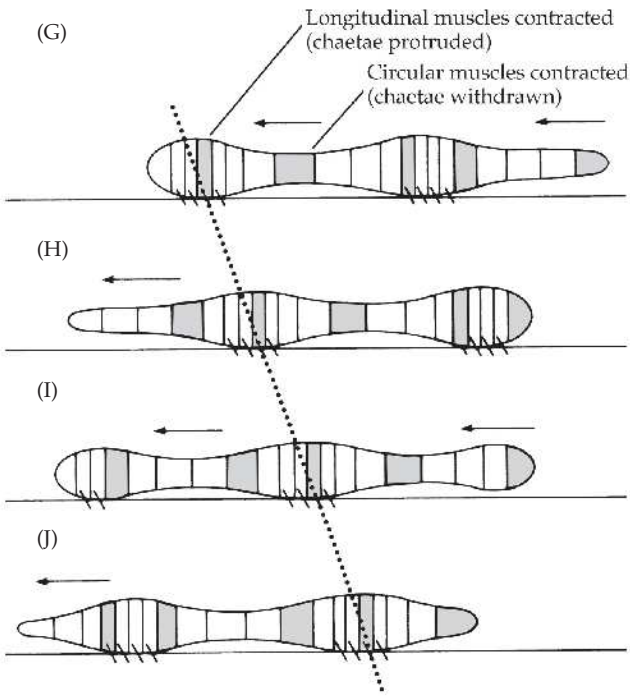
In addition to burrowing *Nereis* can engage in three basic epibenthic locomotory patterns: slow crawling, rapid crawling, and swimming (Figure 15.6A–D). All these methods of movement depend primarily on the bands of longitudinal muscles, especially the larger











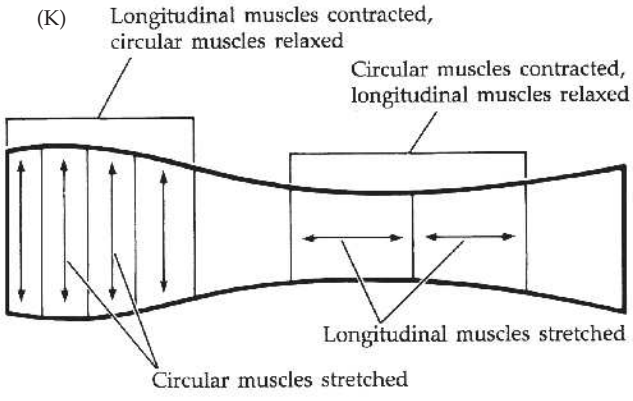


FIGURE 15.6 Patterns of locomotion in annelids. (A) Dorsal view of several segments of *Nereis* during crawling. Note the states of contraction of longitudinal muscles (stippled), the body curvature, and the retraction and extension of parapodia. (B–D) *Nereis* crawling and swimming. Note the changes in metachronal wavelength and amplitude. (E) Midsagittal section through an annelid. The perforated intersegmental septa allow peristaltic body contractions to cause volumetric changes in segments. (F) Burrowing movements in *Arenicola*. (G–J) An earthworm moving to the left. Every fourth segment is darkened for reference. The dotted line passes through a posteriorly moving point of contact with the substratum. (K) Several segments of an earthworm (sagittal section). Since each segment is a functionally isolated compartment, shortening and elongation accompany the contraction of longitudinal and circular muscles, respectively, while each segment essentially maintains a constant volume.

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dorsolateral bands, and on the parapodial muscles. The circular muscles are relatively thin and serve primarily to maintain adequate hydrostatic pressure within the coelomic compartments. Each method of locomotion in *Nereis* (and similar forms) involves the antagonistic action of the longitudinal muscles on opposite sides of the body in each segment.

During movement, the longitudinal muscles on one side of any given segment alternately contract and relax (and are stretched) in opposing synchrony with the action of the muscles on the other side of the segment. Thus, the body is thrown into undulations that move in metachronal waves from posterior to anterior. Variations in the length and amplitude of these waves combine with parapodial movements to produce the different patterns of locomotion. The parapodia and their chaetae are extended maximally in a power stroke as they pass along the crest of each metachronal wave. Conversely, the parapodia and chaetae retract in the wave troughs during the recovery stroke. Thus, the parapodia on opposite sides of any given segment are exactly out of phase with one another.

When *Nereis* is crawling slowly, the body is thrown into a high number of metachronal undulations of short wavelength and low amplitude (Figure 15.6B). The extended parapodial chaetae on the wave crests are pushed against the substratum and serve as pivot points as the parapodia engage in the power stroke. As each parapodium moves past the crest, it is retracted and lifted from the substratum as it is brought forward during its recovery stroke. The main pushing force in this sort of movement is provided by the oblique parapodial muscles (Figure 15.4C). During rapid crawling, much of the driving force is provided by the longitudinal body-wall muscles in association with the longer wavelength and greater amplitude of the body undulations (Figure 15.6C), which accentuate the power strokes of the parapodia.

Nereis can also leave the substratum to swim (Figure 15.6D). In swimming, the metachronal wavelength and amplitude are even greater than they are in rapid crawling. When watching a nereidid swim, however, one gets the impression that the "harder it tries," the less progress it makes, and there is some truth to this. The problem is that, even though the parapodia act as paddles pushing the animal forward on their power strokes, the large metachronal waves continue to move from posterior to anterior and create a water current in that same direction; this current tends to push the animal into reverse. The result is that *Nereis* can lift itself off the substratum, but it then largely thrashes about in the water. This behavior is used primarily as a short-term mechanism to escape benthic predators rather than to get from one place to another. There are, however, some annelid groups, such as Alciopini (Phyllodocidae) and *Tomopteris* (Tomopteridae), whose members live their whole lives as pelagic swimming animals.

With these basic patterns and mechanisms in mind, we consider a few other methods of locomotion in annelids. *Nephtys* (Nephtyidae) superficially resembles *Nereis*, but its methods of movement are significantly different. Although *Nephtys* is less efficient than *Nereis* at slow walking, it is a much better swimmer, and it is also capable of effective burrowing in soft substrata. The large, fleshy parapodia serve as paddles, and when swimming, *Nephtys* does not produce long, deep metachronal waves. Rather, the faster it swims, the shorter and shallower the waves become, thus eliminating much of the counterproductive force described for *Nereis*. When initiating burrowing, *Nephtys* swims head first into the substratum, anchors the body by extending the chaetae laterally from the buried segments, and then extends the proboscis deeper into the sand. A swimming motion is then employed to burrow deeper into the substratum.

In contrast to the above descriptions, scale worms (Polynoidae) have capitalized on the use of their muscular parapodia as efficient walking devices. The body undulates little if at all, and there is a corresponding reduction in the size of the longitudinal muscle bands and their importance in locomotion. These worms depend almost entirely on the action of the parapodia for walking, and most adult polynoids cannot swim, except for very short bursts.

Nereis is also a burrower and studies on *N. virens* showed that they can extend their burrows in muddy sediments by using a mechanically efficient fracturing style of locomotion called "crack propagation." This is an efficient use of energy as the worm forces its way through the mud, and it involves everting the pharynx to apply dorsoventral forces to burrow walls that are amplified at the burrow tip making a crack in a forward direction. The worm then anchors itself by expanding the body laterally and pushing its narrow head into the crack, whereupon it repeats the process. Other annelid groups such as cirratulids, glycerids, and orbiniids are also known to use this form of burrowing. Burrowing in sand presents different challenges than burrowing in mud, since sand doesn't "crack" but instead needs to be fluidized. Sand burrowing has been described for *Arenicola* (Arenicolidae), which, like many burrowers, has lost most of the intersegmental septa. Some burrowers have septa that are perforated. This means that segments are not of constant volume; in other words, a loss of coelomic fluid from one body region causes a corresponding gain in another. *Arenicola* also has reduced parapodia. The chaetae, or simply the surface of the expanded portions of the body, serve as anchor points, while the burrow wall provides an antagonistic force resisting the hydraulic pressure. *Arenicola* burrows in sand by first embedding and anchoring the anterior body region in the substratum. The anchoring is accomplished by contracting the circular muscles of the posterior portion of the body, thus forcing coelomic fluid anteriorly and causing the first

few segments to swell. Then the posterior longitudinal muscles contract, thereby pulling the back of the worm forward. To continue the burrowing, a second phase of activity is undertaken. As the anterior circular muscles contract and the longitudinal bands relax, the posterior edges of each involved segment are protruded as anchor points to prevent backward movement; the proboscis is thrust forward, deepening the burrow. Then the proboscis is retracted, the front end of the body is engorged with fluid, and the entire process is repeated (Figure 15.6F).

Clitellates such as crassiclitellates (earthworms) face the problem of burrowing in soils, which may not crack or fluidize like marine sediments. It is argued that they solve this by eating their way through compacted soils or pushing sediment aside in looser soils. In some cases, they line the burrows with mucus to stop the burrows from collapsing. Movement in most clitellates involves the alternately contracting circular and longitudinal muscles within each segment, and this is seen in many other annelids with complete body septa. The shape of a segment changes from long and thin to short and thick with the respective muscle actions (Figure 15.6G–J). These shape changes move anteriorly along the body in a peristaltic wave generated by a sequence of impulses from the ventral nerve cord and associated motor neurons. So, at any moment during locomotion, the body of the worm appears as alternating thick and thin regions. Without some method of anchoring the body surface, this action would not produce any motion. The chaetae provide this anchorage as they protrude like barbs from the thicker portions of the body. When the longitudinal muscles relax and the circular muscles contract, the body diameter decreases, and the chaetae are turned to point posteriorly and lie close to the body. As shown in Figure 15.6G–K, as the anterior end of the body is extended by circular-muscle contraction, the chaetae prevent backsliding, the head is pressed into the substratum, and the worm advances. The anterior end then swells by contraction of the longitudinal muscles, and the rest of the body is pulled along.

Most tube-dwelling annelids (Figure 15.7) are heteronomous and many, such as Terebelliformia, have rather soft bodies and relatively weak muscles. The parapodia are reduced, so the chaetae are used to position and anchor the animal in its tube. Movement within the tube is usually accomplished by slow peristaltic action of the body or by chaetae movements. When the anterior end is extended for feeding, it may be quickly withdrawn by special retractor muscles while the unexposed portion of the body is anchored in the tube. Annelid tubes provide protection as well as support for these soft-bodied worms and keep the animal oriented properly in relation to the substratum. Some annelids build tubes composed entirely of their own secretions. Most notable among these tube builders are the serpulids, which construct their tubes of calcium carbonate secreted by a pair of large glands near a fold of the peristomium called the collar. The crystals of calcium carbonate are added to an organic matrix; the mixture is molded to the top of the tube by the collar fold and held in place until it hardens.

FIGURE 15.7 Tube-dwelling annelids. (A) *Eudistylia vancouveri* (Sabellidae in and out of its tube). (B) The ventral base of the radiolar crown of a sabellid. Note the addition of a mucus-sand mixture to the lip of the tube. (C) The bamboo worm, *Axiothella rubrocincta* (Maldanidae), oriented head down in its sand tube. (D) Bamboo worm *Clymenella* (Maldanidae) out of tube. (E) A cluster of serpulid tubes formed of calcium carbonate and cemented to the substratum. (F) *Ditrupa arietina* (Serpulidae) in its calcareous tube. (G) The particulate tube of the ice-cream-cone worm, *Pectinaria* (Pectinariidae), and animals out of their tubes. (H) A colony of *Phragmatopoma californica* (Sabellariidae). (I) Specimen of *Phragmatopoma californica* (Sabellariidae) removed from its tube. (J) *Spirobranchus giganteus* (Serpulidae), with algae-encrusted operculum.

Sabellids, close relatives of serpulids, produce parchmentlike or membranous tubes of organic secretions molded by the collar. Some, such as *Sabella*, mix mucous secretions with size-selected particles extracted from feeding currents, then lay down the tube with this material (Figures 15.7A,B and 15.10A,B). Numerous other annelid groups form similar tubes of sediment particles collected in various ways and cemented together with mucus. Some of the most beautiful are made by pectinariids, the ice-cream-cone worms, where the ornate tube is only one particle thick (Figure 15.7G).

A few annelids can excavate burrows by boring into calcareous substrata, such as rocks, coral skeletons, or mollusc shells (e.g., certain members of the families Cirratulidae, Eunicidae, Spionidae, Sabellidae). In extreme situations, the activity of the annelids may have deleterious effects on the "host." For example, a boring sabellid, *Terebrasabella*, which lives in abalone shells, can cause fatalities by making them deform their shells. Species of *Polydora* (Spionidae) often excavate galleries in various calcareous substrata (e.g., shells) and have been responsible for killing oysters in commercially harvested areas of Europe, Australia, and North America (Figure 15.9F).

Feeding and Digestion

Feeding The great diversity of form and function among annelids has allowed them to exploit nearly all marine food resources, in one way or another, and to be critical ecosystem components of most terrestrial soils. For convenience we have categorized annelids as raptorial, deposit, and suspension feeders (see Chapter 3). However, there are several feeding methods and dietary preferences within each of these basic designations. Following a discussion of selected examples of these feeding types, we mention a few of the symbiotic annelids.

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(A)

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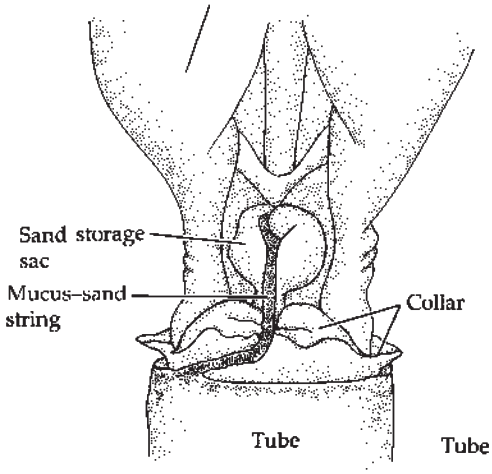
(B)



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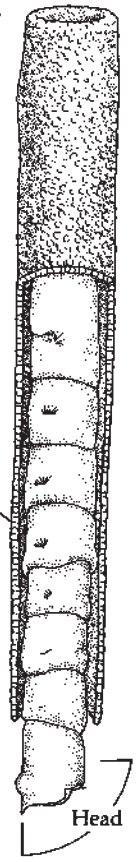

(D)

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The most familiar raptorial annelids are hunting predators belonging to the clade Errantia (e.g., many phyllodocids, syllids, nereidids, and eunicids, all part of Aciculata). These animals tend toward homonomy and are capable of rapid movement across the substratum. For the most part they feed on small invertebrates. When prey is located by chemical or mechanical means, the worm everts its pharynx by quick contractions of the body wall muscles in the anterior segments, increasing the hydrostatic pressure in the coelomic spaces and causing the eversion. As a result of the design of the pharynx, the jaws (if present) gape at the anterior-most end when the pharynx is everted (Figure 15.8). Once the prey is positioned within the jaws, the coelomic pressure is released, the jaws collapse on the prey, and the proboscis and captured victim are pulled into the

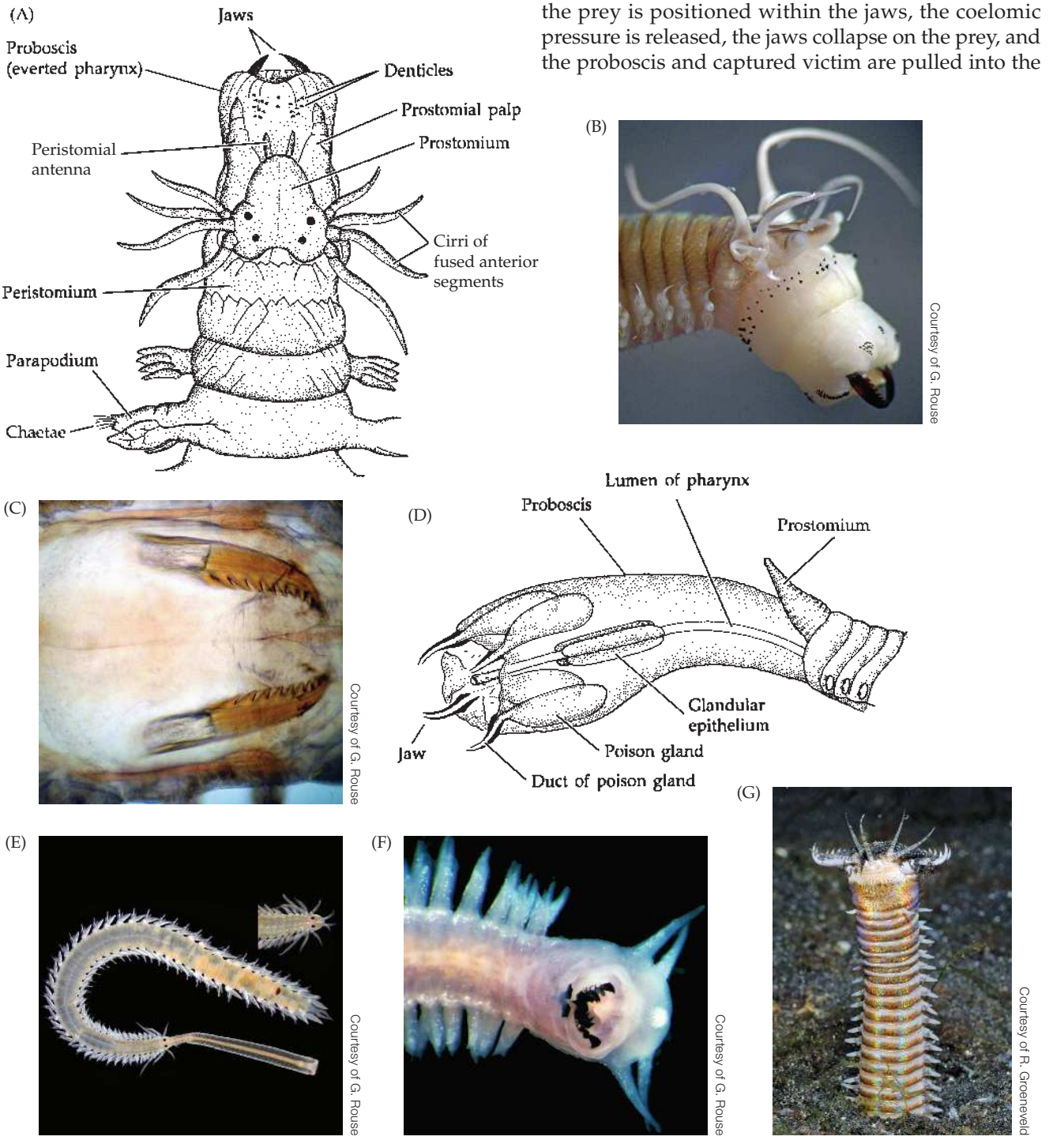

FIGURE 15.8 The eversible pharyngeal jaws of annelids. (A) *Nereis* (Nereididae) with jaws everted. (B) *Perinereis* (Nereididae) with jaws everted. (C) Nereidid with jaws retracted inside body. (D) *Glycera* (Glyceridae) with jaws everted. (E) *Eumida* (Phyllodocidae) with proboscis (lacking jaws but with numerous papillae) withdrawn and everted. (F) *Ophryotrocha* (Dorvilleidae). Complex jaws being everted. (G) The giant (1–3 m) tropical sand striker worm, *Eunice aphroditois*, with its head extended from the sediment at night. The jaws are locked open while it awaits a passing victim, typically a fish. When the antennae or palps detect the prey, the jaws snap shut and it draws the victim into its burrow.

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body by large retractor muscles. Many of these raptorial feeders can also ingest plant material and detritus. Some scavenge, feeding on almost any dead organic material they encounter. Raptorial feeding also occurs in some freshwater clitellates such as Lumbriculidae (e.g., *Phagodrilus*), which capture prey (often other clitellates!) with their muscular pharynx.

Some predatory annelids do not actively hunt. Many scale worms (Polynoidae) sit and wait for passing prey, then ambush it by sucking it into their mouth or grasping it with their pharyngeal jaws. In addition, not all raptorial annelids are surface dwellers. Some live in tubes (*Diopatra*) or in complex branched burrows (*Glycera*). Such annelids detect the presence of potential prey outside their tubes or burrows by sensing chemicals or vibrations and extend their everted proboscis to capture the prey. Some leave their residence to hunt for short periods of time, or they emerge from their burrows and wait for a fish to swim into range (e.g., *Eunice aphroditois* [Figure 15.8G], a famous worm known as the "sand striker"). Poison glands, associated with the jaws, occur in some genera (e.g., *Glycera*; Figure 15.8D).

Several groups of annelids are deposit feeders that are relatively unselective, simply ingesting the substratum and digesting the organic matter contained therein (e.g., members of Arenicolidae, Opheliidae, Maldanidae, and many clitellates). Lugworms, such as *Arenicola*, excavate an L-shaped burrow; the worm irrigates the burrow with water drawn into the open end by peristaltic movements of its body (Figure 15.9A). The water percolates upward through the overlying sediment and tends to liquefy the sand at the blind end of the L, near the worm's mouth. This sand is ingested by the muscular action of a bulbous proboscis. The water brought into the burrow also adds suspended organic material to the sand at the feeding site. The worm periodically moves to the open end of its tunnel and defecates the ingested sand outside the burrow in characteristic surface castings. Some maldanids live in straight vertical burrows, head down, and ingest the sand at the bottom (Figure 15.7C). They periodically move upward (backward) to defecate on the surface. A number of other direct deposit feeders (e.g., some opheliids) do not live in constructed burrows but simply move through the substratum ingesting sediments as they go. In high concentrations, populations of these annelids can pass thousands of tons of sediments through their guts each year—which has a significant impact on the nature of the deposits in which they live. Most terrestrial and many aquatic clitellates are, at least in part, direct deposit feeders. Earthworms burrow through the soil, ingesting the substratum as they move. As the soil is passed along the digestive tract, the organic material is digested and absorbed from the gut. The inorganic, indigestible material passes out the anus. Earthworms are said to "work" the soil in this manner, loosening and aerating it. Many of these terrestrial burrowers, including the common earthworm *Lumbricus*, are more selective and retrieve organic material from the surface. These worms can burrow to the surface of the soil and there use their suckerlike mouth to obtain relatively large pieces of food (e.g., partially decomposed leaves), which they carry back underground for ingestion.

Selective deposit feeders are defined by their ability to effectively sort the organic material from the sediment prior to ingestion (e.g., many species of Terebellidae, Spionidae, and Pectinariidae). However, the methods used to sort food differ among these groups. Most terebellids (e.g., *Amphitrite*, *Pista*, *Terebella*) establish themselves in shallow burrows or permanent tubes (Figure 15.9B–E). The feeding tentacles are grooved prostomial palps that are extended over the substratum. These are extended by ciliary crawling and can be retracted by muscles. Once extended, their epithelium secretes a mucous coat to which organic material, sorted from the sediment, adheres. The tentacle edges curl up to form a longitudinal groove along which food and mucus are carried by cilia to the mouth. Tube-dwelling spionids engage in a similar method of feeding. In these animals, the feeding structures are more muscular and derived from the peristomial palps (Figure 15.9F). They are swept through the water or brushed through the surface sediments, extracting food and moving it to the mouth.

Pectinaria, the ice-cream-cone worms, live in a tube constructed of sand grains and shell fragments. The tube is open at both ends. The animal orients itself head down, with the posterior end of the tube projecting to the sediment surface (Figure 15.9G). Head appendages partially sort the sediment, and a relatively high percentage of organic matter is ingested. Several other annelids employ these and other methods of selective deposit feeding.

Various forms of suspension feeding are accomplished by many tube-dwelling annelids (e.g., members of Serpulidae and Sabellidae) and by some that live in relatively permanent burrows (e.g., Chaetopteridae). The feeding structures of *Sabella* and many related types are a crown of branching prostomial palps called **radioles**. Some of these worms generate their own feeding currents, whereas others "fish" their tentacles in moving water. As food-laden water passes over the tentacles, the water is driven by cilia upward between the pinnules (branches) of the radioles (Figure 15.10A,B). Eddies form on the medial side (inside) of the tentacular crown and between the pinnules, slowing the flow of water, decreasing its carrying capacity, and thus facilitating extraction of suspended particles. The particles are carried, with mucus, along a series of small ciliary tracts on the pinnules to a groove along the main axis of each radiole. This groove is widest at its opening and decreases in width in a stepwise fashion to a narrow slot deep in the groove. By this means, particles are mechanically sorted into three size categories as they are carried into the groove. Typically, the smallest particles are carried to the mouth and ingested, the largest particles are rejected, and the medium-sized ones are stored for use in tube building. In the freshwater naidid clitellate

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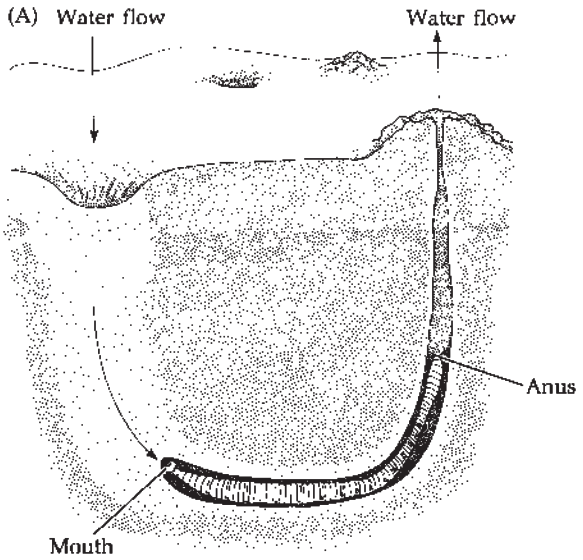
Courtesy of P. Smith



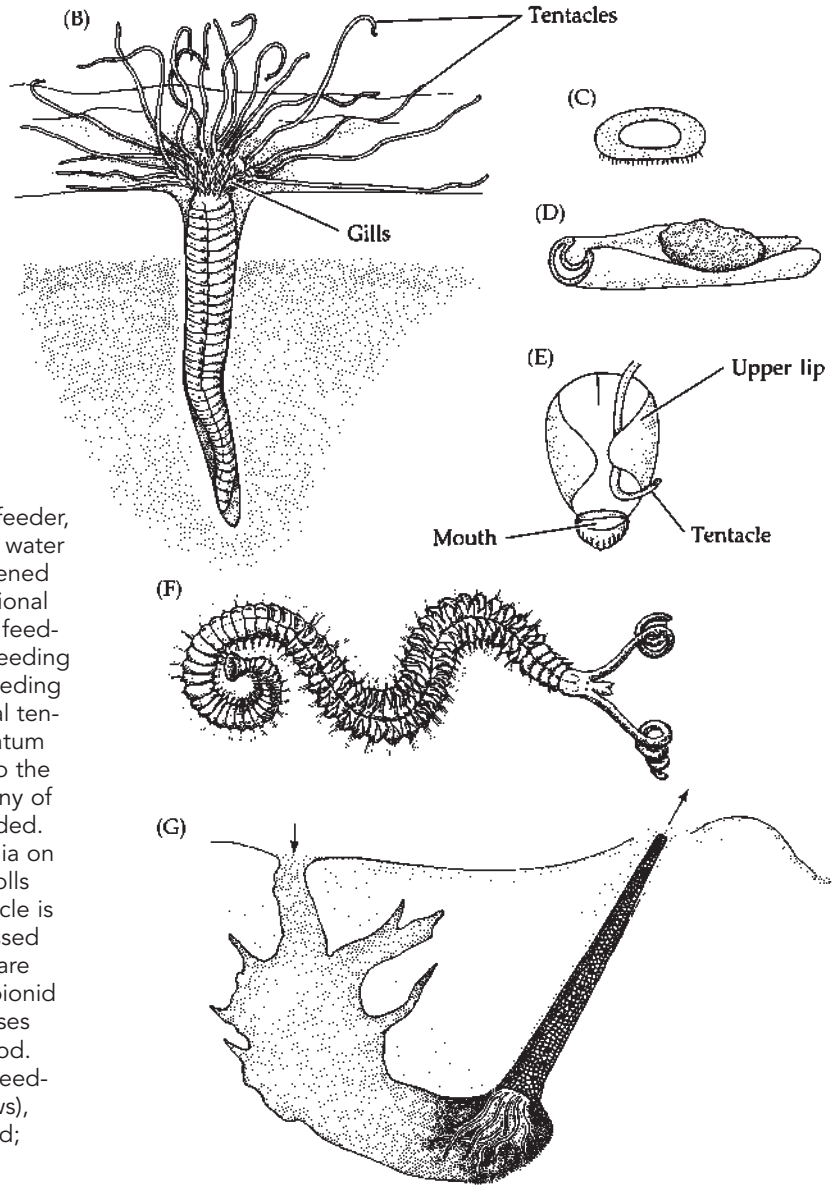


FIGURE 15.9 Deposit-feeding annelids.
(A) *Arenicola* (Arenicolidae), a direct deposit feeder, in its burrow. Arrows indicate direction of the water flow; the substratum around the head is loosened and ingested by the worm (see text for additional explanation). Castings ("cleaned" sand) from feeding have a characteristic appearance. (B–E) Feeding in terebellid annelids. (B) A terebellid in its feeding posture within the substratum. The prostomial tentacles "creep" over the surface of the substratum and accumulate food, which is then passed to the mouth. Color photograph shows a large colony of terebellids with their feeding tentacles extended. (C) A terebellid tentacle (cross section) has cilia on the underside. (D) A section of the tentacle rolls to form a temporary food groove. (E) A tentacle is wiped across the oral area, where food is passed to the mouth and ingested. Such terebellids are indirect (selective) deposit feeders. (F) The spionid *Polydora*, another selective deposit feeder, uses its tentacle-like prostomial palps to obtain food. (G) The ice-cream-cone worm, *Pectinaria*, in feeding position. A water current is created (arrows), liquefying the sand around the tentacled head; organic matter is removed and ingested.

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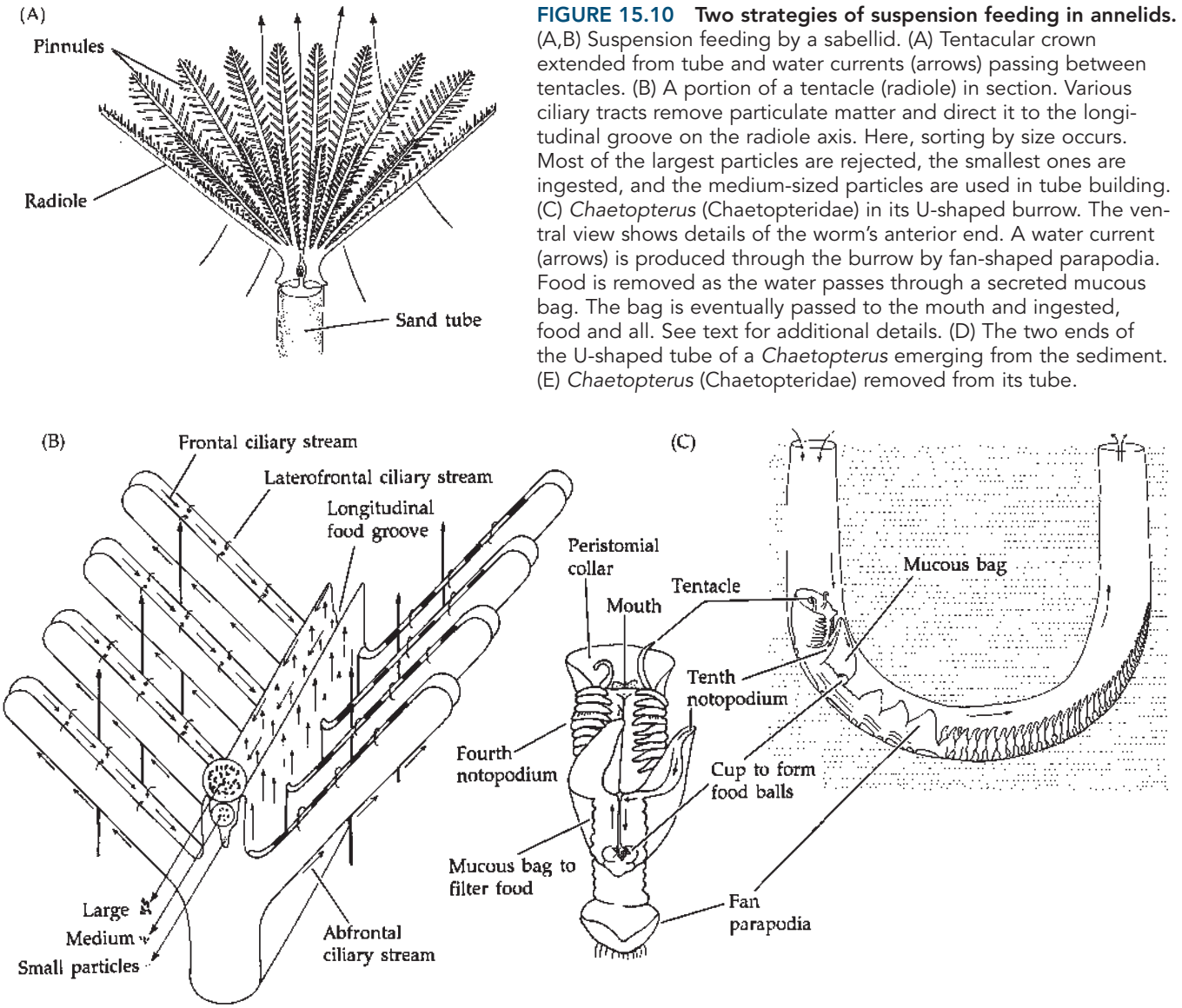

Courtesy of G. Rouse

Courtesy of G. Rouse

FIGURE 15.10 Two strategies of suspension feeding in annelids. (A,B) Suspension feeding by a sabellid. (A) Tentacular crown extended from tube and water currents (arrows) passing between tentacles. (B) A portion of a tentacle (radiole) in section. Various ciliary tracts remove particulate matter and direct it to the longitudinal groove on the radiole axis. Here, sorting by size occurs. Most of the largest particles are rejected, the smallest ones are ingested, and the medium-sized particles are used in tube building. (C) *Chaetopterus* (Chaetopteridae) in its U-shaped burrow. The ventral view shows details of the worm's anterior end. A water current (arrows) is produced through the burrow by fan-shaped parapodia. Food is removed as the water passes through a secreted mucous bag. The bag is eventually passed to the mouth and ingested, food and all. See text for additional details. (D) The two ends of the U-shaped tube of a *Chaetopterus* emerging from the sediment. (E) *Chaetopterus* (Chaetopteridae) removed from its tube.

Ripistes parasita, long chaetae located on the anterior segments are waved about in the water, and small detrital particles adhere to them; food material is then ingested by wiping the chaetae across the mouth.

Some members of Chaetopteridae, such as *Chaetopterus*, are among the most heteronomous of all annelids, and the body is distinctly regionally specialized (Figures 15.1B and 15.10C–E). *Chaetopterus* filters water for food. These animals reside in U-shaped burrows through which they move water, extracting suspended materials. Each body region plays a particular role in this feeding process. Segments 14–16 bear greatly enlarged notopodial fans that serve as paddles to create the water current through the burrow. A mucous bag, produced by secretions from segment 12, is held as shown in Figure 15.10C, so that water flows into the open end of the bag and through its mucous wall. Particles as small as 1 μm in diameter are captured by this structure, and there is some evidence that even protein molecules are held in the mucous net (probably by ionic charge attraction rather than mechanical filtering). During active feeding, the bag is rolled into a ball, passed to the mouth by a ciliary tract, and ingested every 15–30 minutes or so; then a new bag is produced.

Symbiotic relationships with other animals occur among several groups of annelids. There are some interesting cases that reflect, again, the adaptive diversity of these worms. Many symbiotic annelids are hardly modified from their free-living counterparts and do not show the drastic adaptive characteristics often associated with this sort of life. For many, the relationship with their host is a loose one, the annelid often using the host merely as a protective refuge. We have already mentioned annelids, otherwise quite like their free-living relatives, that burrow into the shells of other invertebrates. Among the most commonly found commensal annelids are polynoid scale worms, especially members of the genera *Arctonoe*, *Halosydna,* and *Macellicephala,* which live on the bodies of various molluscs, echinoderms, and cnidarians (Figure 15.11A,B). A polynoid has even been

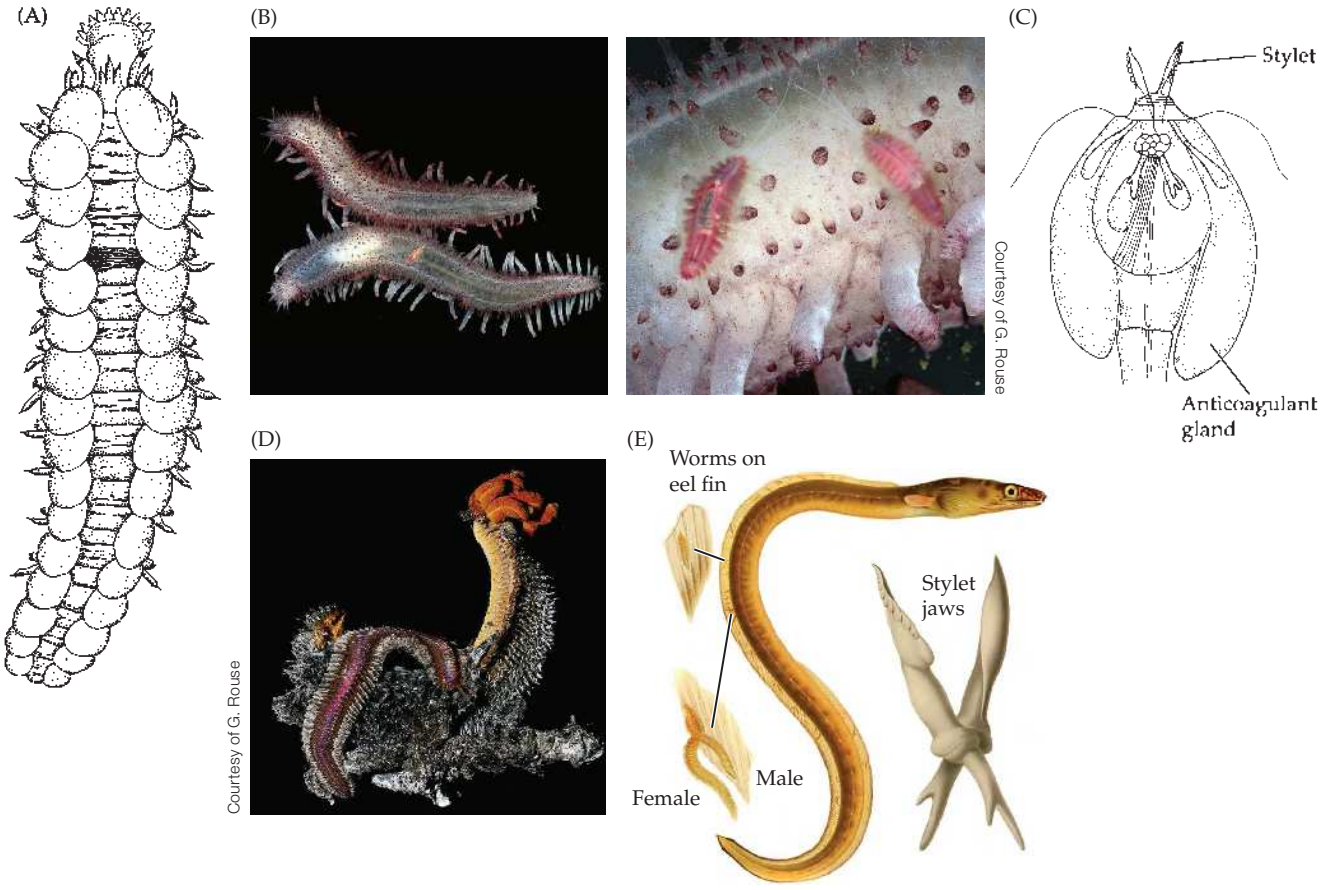

FIGURE 15.11 Symbiosis in annelids. (A) *Arctonoe* (Polynoidae), a scale worm that lives in the ambulacral grooves of starfish and the mantle chambers of certain molluscs (with proboscis extended). (B) Two specimens of *Macellicephala* sp. (Polynoidae) on *Pannychia* sp. (Holothuroidea). (C) The anterior end of *Ichthyotomus sanguinarius*, a parasite on fishes. The stylets anchor the worm to its host, and the large glands secrete an anticoagulant. (D) Photo of *Alvinella pompejana* (Alvinellidae) partly removed from its tube, showing symbiotic bacteria all over its back, and a specimen of the hesionid *Hesiolyra bergi* (Hesionidae) that is often seen in the tubes of *A. pompejana*. (E) *Ichthyotomus sanguinarius* (Chrysopetalidae), a parasite on eels. The worm attaches to the host's dorsal or ventral fins, sometimes in large numbers. The stylet jaws of the pharynx (line drawing) anchor the worm to its host, and the large glands secrete an anticoagulant.

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discovered living as a commensal in the mantle cavity of giant deep-sea mussels residing near thermal vents on the East Pacific Rise. One scale worm, *Hesperonoe adventor*, inhabits the burrows of the Pacific innkeeper worm, *Urechis caupo* (Thalassematidae) (Figure 15.28G). One group of annelids, Myzostomida, is nearly always symbiotic with echinoderms, chiefly crinoids, but also asteroids and ophiuroids. Myzostomids show a variety of adult body shapes and lifestyles, with most described species living freely on the exterior of their hosts as adults, while others live in galls, cysts, or in the host's mouth, digestive system, coelom, or even the gonads. Myzostomid lifestyles range from stealing incoming food from the host's food grooves to consuming the host's tissue directly (Figure 15.3).

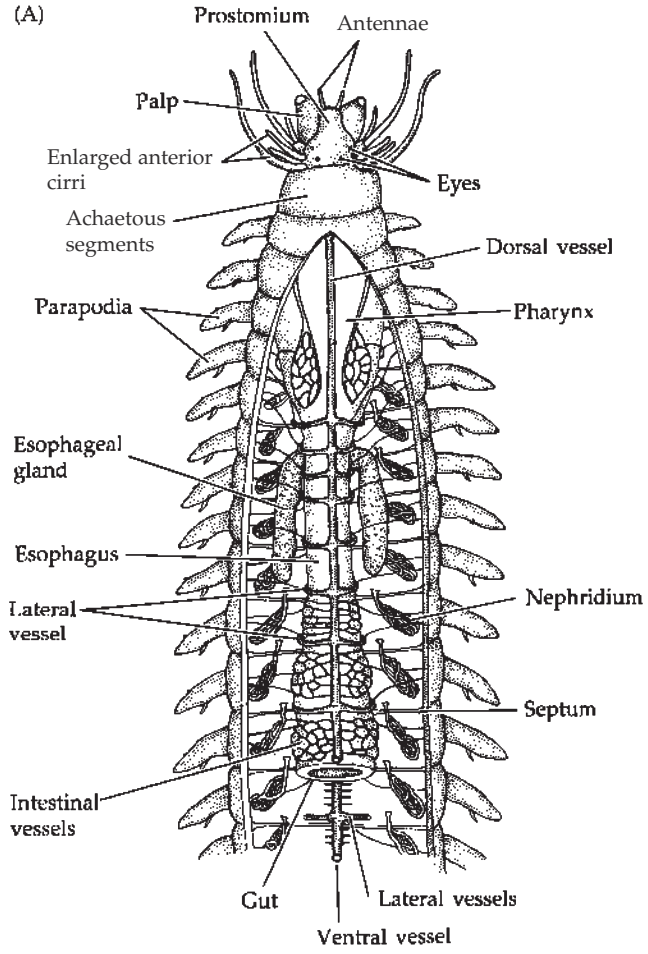
There are many examples of these rather informal associations: certain syllids that live and feed on hydroids, a nereidid (*Nereis fucata*) that resides in the shells of hermit crabs, and so on. Most of these animals do not feed upon their hosts but prey upon tiny organisms that happen into their immediate environment. Others consume detritus or scraps from their host's meals. Several other odd associations are known among the annelids. Most oenonids live part of their lives as parasites in the bodies of thalassematids and other annelids. Again, these endosymbionts show little structural modification associated with their lifestyles, other than a tendency for small body size and reduction in the pharyngeal jaws. An example of a fully parasitic annelid is *Ichthyotomus sanguinarius* (Chrysopetalidae). These small (1 cm long) worms attach to eels by a pair of stylets or jaws. The stylets are arranged so that when their associated muscles contract, the stylets fit together like the closed blades of scissors. The stylets are thrust into the host, and when the muscles relax, they open and anchor the parasite to the fish (Figure 15.11C,E). The Pacific hydrocoral *Stylaster californicus* typically harbors colonies of the spionid *Polydora alloporis*, whose paired burrow openings are often mistaken for the hydrozoan's polyp cups.

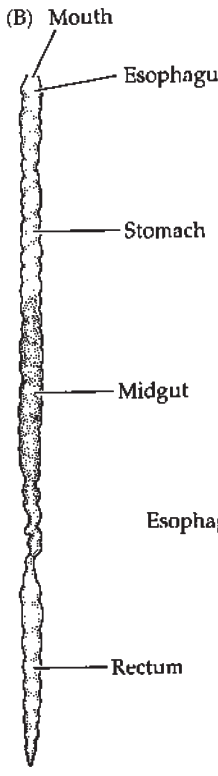
A most unusual symbiotic relationship exists between the strange ampharetid Pompeii worm *Alvinella pompejana* (Figure 15.11D) and a variety of marine chemoautotrophic sulfur bacteria. *Alvinella* (the genus named after the deep-sea submersible *Alvin*) is a notable member of deep hydrothermal vent communities of the East Pacific Rise. It lives closer to the hot water extrusions than any other animal in the vent community, often near perforated structures called "snowballs" or "beehives" formed by the thermal plumes. Temperatures inside the tubes of *Alvinella* can reach an astonishing 80°C. The bodies of Pompeii worms are covered with unique vent bacteria. The worms are somehow protected from the hot temperatures, and they feed on these symbiotic bacteria. A hesionid worm, *Hesiolyra bergi*, is often found living in the tubes of *Alvinella pompejana* and may also be eating the bacteria or possibly preying on the worm itself.

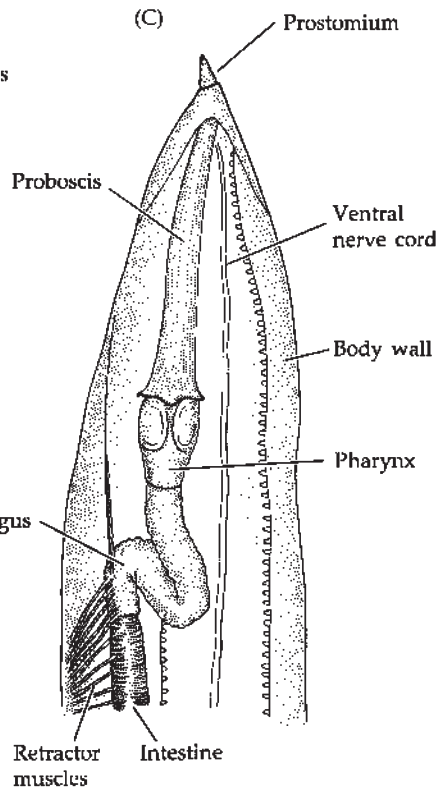
Over 80 species of gutless marine clitellates, all in the family Naididae, have been described in shallow coral-sand habitats and in anaerobic, sulfide-rich subsurface sediments. These worms typically harbor a range of coexisting subcuticular symbiotic bacteria (up to five species), whose precise role in the host's nutritional regimen is not yet fully understood. The endosymbiotic bacteria are clearly important to the worms; they are passed to the fertilized eggs during oviposition from storage areas next to the female's gonopore.

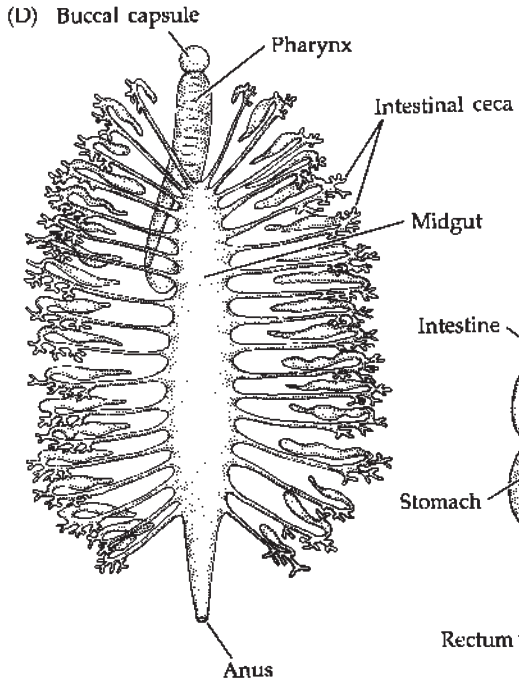
Digestion The gut of annelids is constructed on a basic plan of foregut, midgut, and hindgut; some examples are shown in Figure 15.12. The foregut is a stomodeum and includes the buccal capsule or tube, the pharynx, and at least the anterior portion of the esophagus. It is lined with cuticle, and the teeth or jaws, when present, are derived from scleroproteins produced along this lining. The jaws are often hardened with calcium carbonate or metal compounds. When present, the eversible portion of this foregut (the proboscis) is derived from the buccal tube or the pharynx. Various glands are often associated with the foregut, including poison glands (glycerids), esophageal glands (nereidids and others), and mucus-producing glands in several groups. In earthworms the posterior esophagus often bears enlarged regions forming a crop, where food is stored, and one or more muscular gizzards lined with cuticle and used to mechanically grind ingested material. The esophagus of many clitellates also has thickened portions of the wall in which are located lamellar evaginations lined with glandular tissue (Figure 15.12G). These **calciferous glands** remove calcium from ingested material. The excess calcium is precipitated by the glands as calcite and then released back into the gut lumen. Calcite is not absorbed by the intestinal wall and so passes out of the body via the anus. In addition, the calciferous glands apparently regulate the level of calcium ions and carbonate ions in the blood and coelomic fluids, thereby buffering the pH of those fluids.

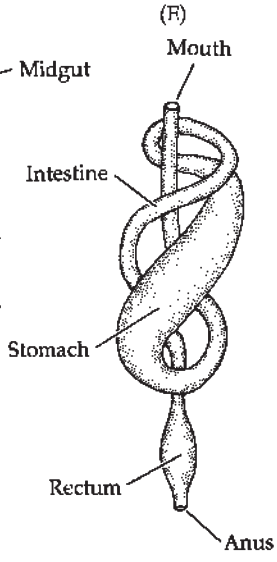
The endodermally derived midgut generally includes the posterior portion of the esophagus and a long, straight intestine, the anterior end of which may be modified as a storage area, or stomach. The midgut may be relatively smooth, or its surface area may be increased by folds, coils, or many large evaginations (or ceca). The midgut is often histologically differentiated along its length. Typically, the anterior midgut (stomach or anterior intestine) contains secretory cells that produce digestive enzymes. The secretory midgut grades to a more posterior absorptive region. In many terrestrial clitellate species, the surface area of the intestine is enlarged by a middorsal groove called the **typhlosole**. Associated with the midgut of many clitellates, and some other annelids as well, are masses of pigmented cells called **chloragogen cells**. These modified peritoneal cells contain greenish, yellowish, or brownish globules

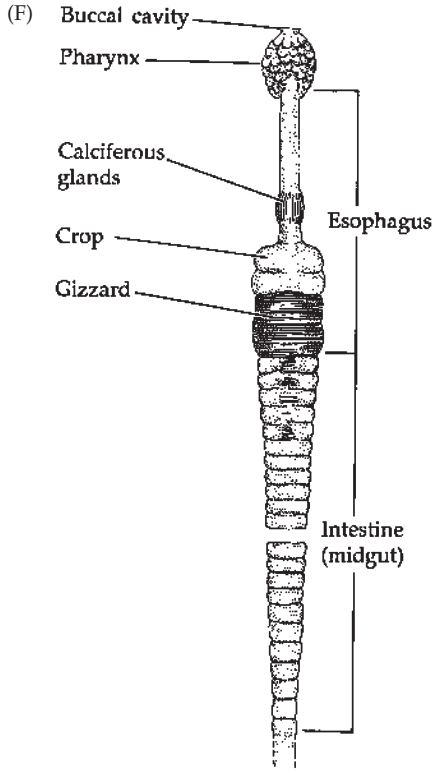

(A)
Prostomium
Antennae
Palp
Enlarged anterior cirri
Eyes
Achaetous segments
Dorsal vessel
Parapodia
Pharynx
Esophageal gland
Esophagus
Lateral vessel
Nephridium
Septum
Intestinal vessels
Gut
Lateral vessels
Ventral vessel


(B) Mouth
Esophagus
Stomach
Midgut
Rectum


(C)
Prostomium
Proboscis
Ventral nerve cord
Body wall
Pharynx
Esophagus
Retractor muscles
Intestine


(D) Buccal capsule
Pharynx
Intestinal ceca
Midgut
Anus


(E)
Mouth
Intestine
Stomach
Rectum
Anus


(F) Buccal cavity
Pharynx
Calciferous glands
Esophagus
Crop
Gizzard
Intestine (midgut)

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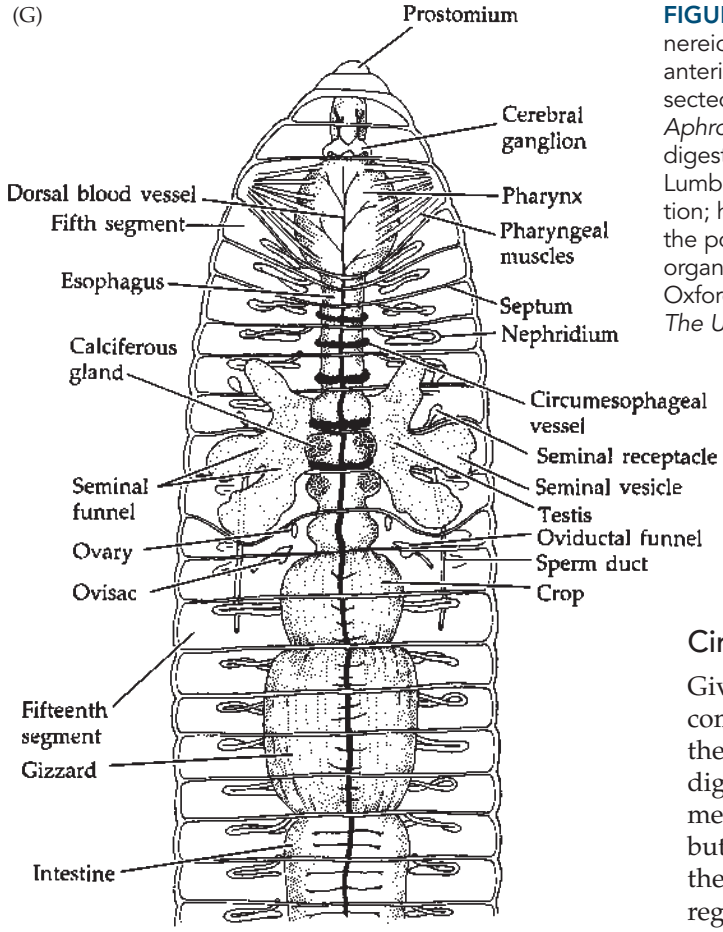

FIGURE 15.12 Annelid digestive system. (A) A dissected nereidid (dorsal view). Note the regional specialization of the anterior gut. (B) The simple tubular gut of *Owenia*. (C) A dissected *Glycera* (dorsal view). (D) The multicecate gut of *Aphrodita*. (E) The coiled digestive tract of *Petta*. (F) The digestive tract of *Eisenia fetida*, the "manure worm" (Clitellata, Lumbricidae), dorsal view (note the marked regional specialization; hindgut not shown). (G) The foregut of *Lumbricus*. Note the positional relationship of the anterior gut regions to other organs. (D,E after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London; F after B. G. Jamieson. 1981. *The Ultrastructure of the Oligochaeta*. Academic Press, London.)

that impart the characteristic coloration to this **chloragogenous tissue**. This tissue lies within the coelom but is pressed tightly against the visceral peritoneum of the intestinal wall and typhlosole. Chloragogenous tissue serves as a site of intermediary metabolism (e.g., synthesis and storage of glycogen and lipids, deamination of proteins). It also plays a major role in excretion.

Toward the posterior end of the gut, there may be additional secretory cells that produce mucus. This mucus is added to the undigested material during the formation of fecal pellets. Food is moved along the midgut by cilia and by peristaltic action of gut muscles, usually comprising both circular and longitudinal layers. A short rectum connects the midgut to the anus, located on the pygidium. A variety of digestive enzymes are known from different species. Predators tend to produce proteases, while herbivores largely produce carbohydrases. Some omnivorous forms (e.g., *Nereis virens*) produce a mixture of proteases, carbohydrases, lipases, and even cellulase. Digestion is predominantly extracellular in the midgut lumen, although intracellular digestion is known in some groups (e.g., *Arenicola*). Some annelids harbor symbiotic bacteria in their guts that aid in the breakdown of cellulose and perhaps other compounds.

Circulation and Gas Exchange

Given the relatively large size of many annelids, the compartmentalization of their coelomic chambers, and the fact that only certain portions of their gut absorb digested food products, it is essential that a circulatory mechanism be present for internal transport and distribution of nutrients. Furthermore, many annelids have their gas exchange structures limited to certain body regions. Hence, they depend on the circulatory system for internal transport of gases.

It is easiest to understand the circulatory system of annelids by considering it in concert with their gas exchange structures, which are remarkably varied. In many annelids that lack appendages, the entire body surface functions in gas exchange (e.g., lumbrinerids, oenonids). Some of the active epibenthic forms utilize highly vascularized portions of the parapodia as gills. Special gas exchange structures, or branchiae, are found in the form of trunk filaments (cirratulids, orbiniids), anterior gills (ampharetids, terebellids), and tentacular, or branchial, crowns on the head (sabellids, serpulids, and siboglinids). Since the blood generally carries respiratory pigments, the anatomy of the circulatory system has evolved along with the structure and location of these gas exchange structures.

We again begin our examination with a homonomous annelid, such as *Nereis*, in which the parapodia are more or less like one another and the notopodia function as gills. The major blood vessels include a middorsal longitudinal vessel, which carries blood anteriorly, and a midventral vessel, which carries blood posteriorly. Exchange of blood between these vessels occurs through posterior and anterior vascular networks and serially arranged segmental vessels (Figure 15.13A). Anterior vessel networks are especially well developed around the muscular pharynx and the region of the cerebral ganglion.

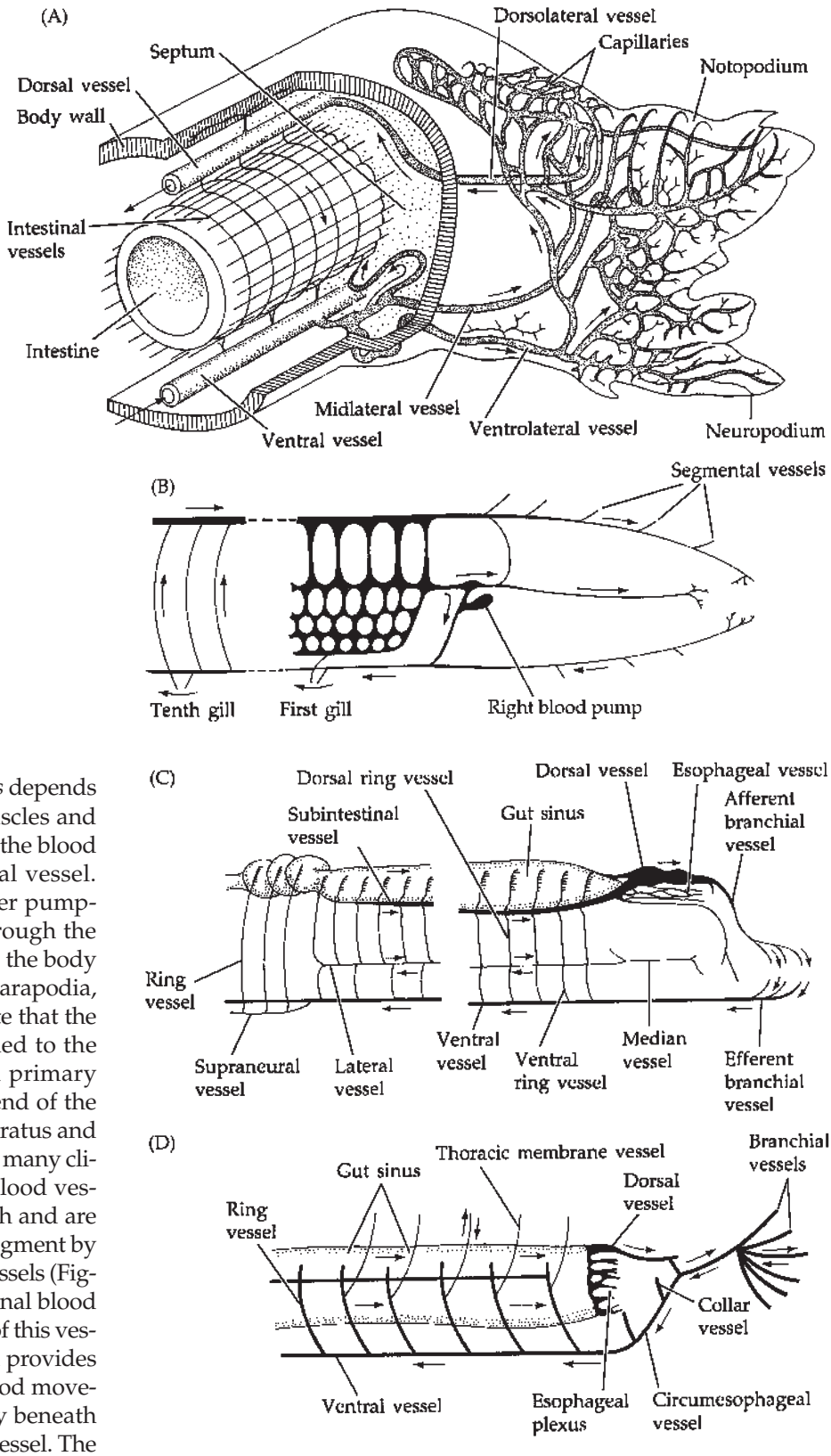

FIGURE 15.13 Annelid circulatory and gas exchange systems. Variations from the basic plan include additional vessels, sinuses associated with the foregut, and branchial vessels serving anterior gills. (A) A segment and parapodium (cutaway view) of a nereid. Note the major blood vessels and blood flow pattern (arrows). Blood flows anteriorly in the dorsal vessel and posteriorly in the ventral vessel. In such annelids the flattened parapodia serve as gills. (B–F) Circulatory patterns in an arenicolid (B), a terebellid (C), a serpulid (D), and *Lumbricus* (Clitellata). (E) Anterior blood vessels (lateral view) and (F) the circulatory pattern in one segment (cross section). (E After C. A. Edwards and J. R. Lofty. 1972. *Biology of Earthworms*. Chapman and Hall, London. https://link.springer.com/chapter/10.1007/978-1-4899-6912-5_1)

The movement of blood in *Nereis* depends on the action of the body wall muscles and on intrinsic muscles in the walls of the blood vessels, especially the large dorsal vessel. There are no special hearts or other pumping organs. The blood passing through the various segmental vessels supplies the body wall muscles, gut, nephridia, and parapodia, as illustrated in Figure 15.13A. Note that the oxygenated blood is being returned to the dorsal vessel, thus maintaining a primary supply of oxygen to the anterior end of the animal, including the feeding apparatus and cerebral ganglion. In *Lumbricus* and many clitellates, three main longitudinal blood vessels extend most of the body length and are connected to one another in each segment by additional segmentally arranged vessels (Figure 15.13E,F). The largest longitudinal blood vessel is the dorsal vessel; the wall of this vessel is quite thick and muscular and provides much of the pumping force for blood movement. Suspended in the mesentery beneath the gut is the longitudinal ventral vessel. The third longitudinal vessel lies ventral to the nerve cord and is called the subneural vessel. Exchanges between the longitudinal vessels occur in each segment through various routes supplying the body wall, gut, and nephridia (Figure 15.13F). Most of the exchanges between the blood and the tissues take place through capillary beds supplied by afferent and efferent vessels. Blood flows posteriorly in ventral and subneural vessels and anteriorly in the dorsal vessel; exchange between the dorsal and ventral vessels occurs in each segment, as shown in Figure 15.13E.

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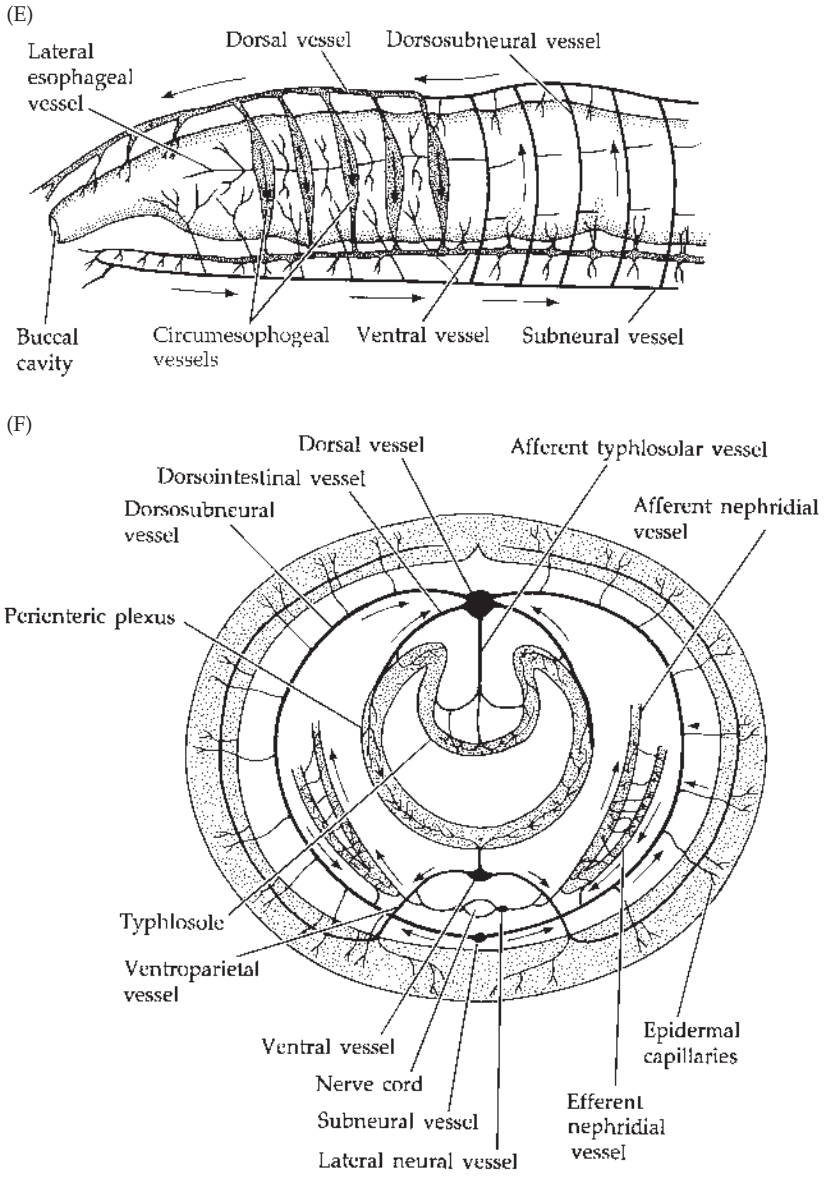

There are many variations on the basic circulatory schemes just outlined, and we mention only a few variations to illustrate the diversity within annelids. Drastic differences are present even among annelids of generally similar body forms. Among the homonomous forms, for example, the circulatory system may be reduced (e.g., Phyllodocidae) or lost (e.g., Capitellidae, Glyceridae, and Sipuncula). In some cases, reduction is probably associated with small size. This hypothesis, however, cannot be applied to capitellids and glycerids, many of which are large and quite active. In these worms and some others, the circulatory system is greatly reduced and has become fused with remnants of the coelom. The coeloms of glycerids and capitellids contain red blood cells (with hemoglobin). Since glycerids have incomplete septa, the coelomic fluid can pass among segments, moved by body activities and ciliary tracts on the peritoneum. In their burrowing lifestyle, enlarged parapodial gills or delicate anterior gills would be disadvantageous, so the general body surface has probably taken over the function of gas exchange, and the coelom the function of circulation. A similar phenomenon may have occurred in Sipuncula.

Compared with *Nereis* or *Lumbricus*, many annelids display additional blood vessels, modification of vessels, differences in blood flow patterns, and formation of large sinuses. As might be predicted, some striking differences are seen among certain heteronomous annelids with reduced parapodia and anteriorly located branchiae (e.g., terebellids, sabellids, and serpulids). In many of these worms, in the region of the stomach and anterior intestine, the dorsal vessel is replaced by a voluminous blood space called the gut sinus (Figure 15.13C,D). Usually, the dorsal vessel continues anteriorly from this sinus, and it often forms a ring connecting with the main ventral vessel. In the sabellids and serpulids, a single, blind-ended vessel extends into each branchial tentacle. Blood flows in and out of these branchial vessels that, in some forms (e.g., serpulids), are equipped with valves that prevent backflow into the dorsal vessel. This two-way flow of blood within single vessels is quite different from the capillary exchange system in most closed vascular systems. A few clitellates possess extensions of the body wall that increase the surface area and function as simple gills (e.g., *Branchiura*, *Dero*), but most exchange gases across the general body surface.

Specialized pumping structures have evolved in several annelid groups. They are especially well developed in certain tube-dwelling forms where they compensate for the reduced effect of general body movements on circulation. These structures, sometimes called hearts, are often little more than an enlarged and muscularized portion of one of the usual vessels; the dorsal muscular vessel of chaetopterids is such a structure. Terebellids possess a "pumping station" at the base of the gills that functions to maintain blood pressure and flow within the branchial vessels (Figure 15.13B). A variety of similar structures are known among other annelids, including the 5 pairs of aortic arches of earthworms.

Most annelids contain respiratory pigments within their circulatory fluid, which is generally acellular. Those without any such pigment include some very small forms and various syllids, phyllodocids, polynoids,

aphroditids, *Chaetopterus*, and a few others. When a pigment is present, it is usually some type of hemoglobin, although chlorocruorin is common in some taxa (e.g., certain flabelligerids, sabellids, and serpulids), and hemerythrin occurs in magelonids. Magelonidae are also interesting in that their blood contains cells (corpuscles). Some annelids have more than one type of pigment; for example, the blood of some serpulids contains both hemoglobin and chlorocruorin.

Annelid respiratory pigments may occur in the blood itself, the coelomic fluid, or both. With a few exceptions, blood pigments occur in solution and coelomic pigments are contained within corpuscles. The latter situation is generally associated with reduction or loss of the circulatory system (as in glycerids). The incorporation of coelomic pigments, usually hemoglobin, into cells is probably a mechanism to prevent the serious osmotic effects that would result from large numbers of free dissolved molecules in the body fluid. Corpuscular coelomic hemoglobins tend to be of much smaller molecular sizes than those dissolved in the blood plasma. The significance of this difference is not clear, but in the case of arenicolids it could be related to oxygen challenges, as these worms often burrow in low-oxygen sediments.

The types of respiratory pigments and their disposition within the body of annelids are related at least in part to lifestyles. As discussed in Chapter 3, different pigments—even different forms of the same pigment—have different oxygen loading and unloading characteristics. The nature of the pigments in a particular worm reflects its ability to store oxygen and then release it during periods of environmental oxygen depletion. Species in several intertidal burrowing annelid groups take up and store oxygen during high tides and dissociate the stored oxygen during low tides. This sort of physiological cycle ameliorates the potential stress of oxygen depletion in the body during low tide periods. In some species, one form of hemoglobin is used for normal conditions, and another form stores oxygen and releases it during periods of stress. Some annelids (e.g., *Euzonus*) can convert to anaerobic metabolic pathways during extended periods of anoxic conditions. Many terrestrial clitellates are capable of sufficient gas exchange only when exposed to air; they will drown if submerged. (Remember, air contains far more oxygen than water.) We have all seen earthworms crawling about the surface following a heavy rain. One species of earthworm (*Alma emini*) has evolved a remarkable adaptation that allows it to survive the rainy season in its East African habitat. When rains cause its burrow to flood, the worm moves to the surface of the soil and forms a temporary opening. The worm then projects its posterior end out through the opening and rolls the sides of the body wall into a pair of folds, forming an open chamber that serves as a kind of "lung." The highly vascularized posterior epithelium enhances the exchange of gases. Several aquatic clitellates can tolerate periods of low availability of oxygen and even anoxic conditions for short periods of time. This includes the sludge worms such as *Tubifex*, members of Naididae that live in very enriched, low-oxygen environments such as sewage.

Excretion and Osmoregulation

In Chapter 3 we discussed nephridial organs in invertebrates. Thus far, we have seen various types of protonephridia, especially among the acoelomate and certain blastocoelomate Metazoa. In annelids, metanephridia are typically found in adults, and these structures commonly pass through a protonephridial stage during their development. Most annelids possess some type of metanephridia, often serially arranged as one pair per segment, with the pore in the segment posterior to the nephrostome. However, variations on this theme are many, and protonephridia are found in some adult annelids. The success of an animal with segmentally arranged isolated coelomic compartments depends on the physical and physiological maintenance of those separate segments. The removal of metabolic wastes (predominantly ammonia) and the regulation of osmotic and ionic balance must occur in each functionally isolated coelomic chamber. (See also the discussion and figures pertaining to excretion and osmoregulation in Chapter 3). While it was once assumed that annelids had separately derived excretory (nephridial) and gonoduct (coelomoduct) systems, the evidence now suggests that while the ducts exiting the body are for the most part nephridial, they may also function in the spawning of gametes.

Protonephridia are found in certain adult annelids mostly in groups within Phyllodocida, and these appear to be metanephridia that have altered their development such that the funnel opening to the coelom connects to a nephridioduct (Figure 15.14A) that also leads to some flame cells. However, most annelids possess paired metanephridia, each metanephridium opening to the coelom via a ciliated nephrostome. In a few annelids (e.g., capitellids), both metanephridia and separate coelomoducts occur, but in most there are metanephridia only. In certain annelid groups with incomplete or missing septa, the number of nephridia is reduced. In some, such as Terebelliformia, anterior nephridia are excretory only, whereas in the posterior region of the body, where the gametes are formed, nephridia are used for spawning and presumably also excretion. The extreme case of this is found in groups such as acrocirrids, cirratulids, serpulids, siboglinids, and sabellids where there is a single anterior pair of large excretory metanephridia. In sabellids and serpulids these lead to a single fused nephridioduct and common pore behind the head (Figure 15.14C). A typical clitellate nephridium is composed of a preseptal nephrostome (either open to the coelom or secondarily

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closed as a bulb), a short canal that penetrates the septum, and a postsegmental nephridioduct that is variably coiled and sometimes dilated as a bladder (Figure 15.14D). The nephridiopores are usually located ventrolaterally on body segments.

As described in Chapter 3, the open nephrostomes of metanephridia nonselectively pick up coelomic fluids. This action is followed by resorption of materials from the nephridium back into the body, either directly into the surrounding coelomic fluid, or into the blood in cases where extensive nephridial blood vessels are present (e.g., in some nereidids and in aphroditids). In either case the composition of the urine is quite different from that of the body fluids; the difference indicates a significant amount of physiological selectivity along the length of the nephridium.

Osmoregulation presents little problem for subtidal marine annelids living in relatively constant osmotic conditions. Intertidal and estuarine forms, however, must be able to withstand periods of stress associated with fluctuations in environmental salinities. Many species are osmoconformers (e.g., *Arenicola*), allowing the tonicity of their body fluids to fluctuate with changes in the environmental salinity. Most annelid osmoconformers have relatively simple metanephridia, with comparatively short nephridioducts and correspondingly weaker resorptive and regulatory capacities. Some also have relatively thin body-wall musculature, and the

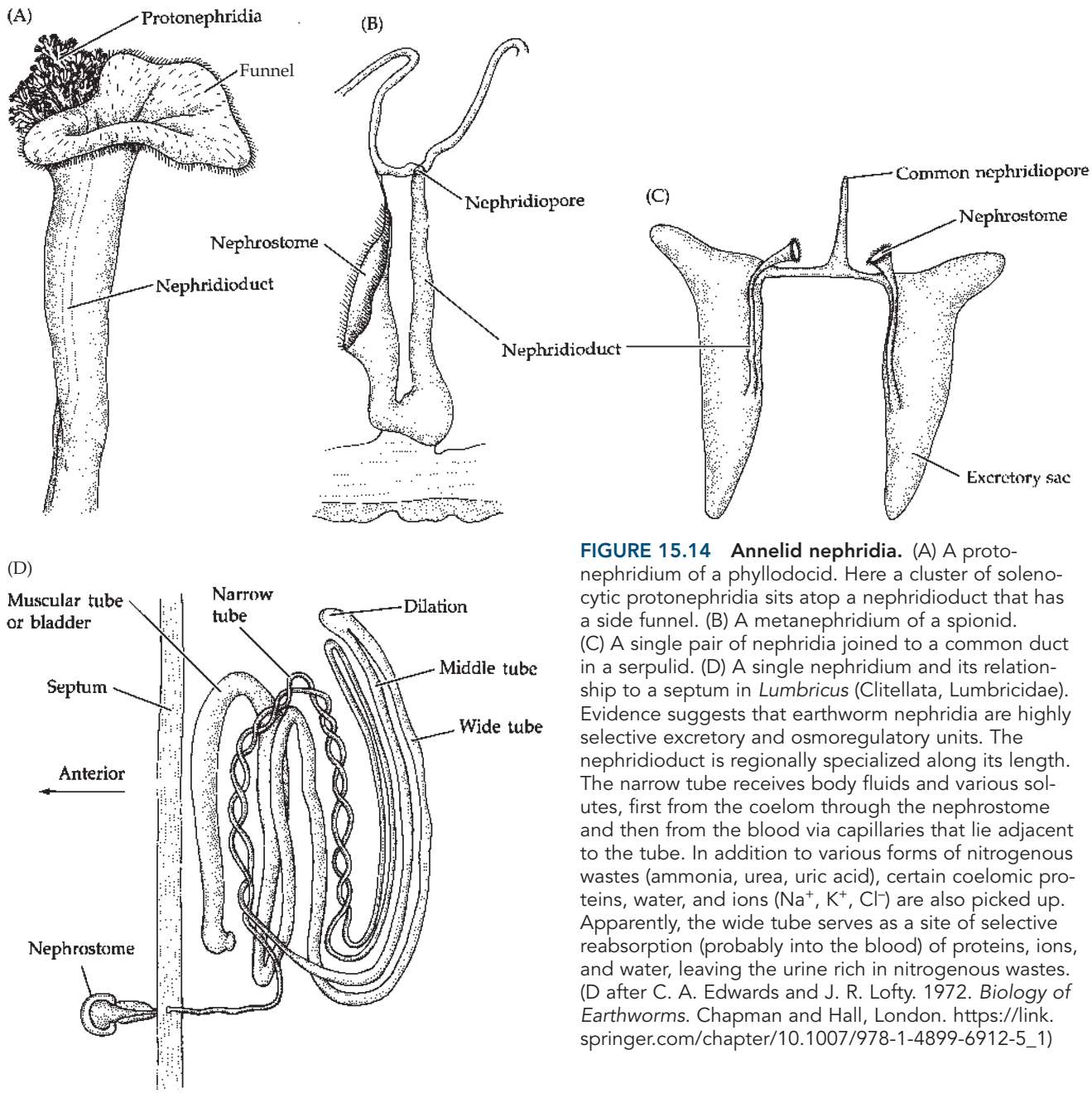

FIGURE 15.14 Annelid nephridia. (A) A protonephridium of a phyllodocid. Here a cluster of solenocytic protonephridia sits atop a nephridioduct that has a side funnel. (B) A metanephridium of a spionid. (C) A single pair of nephridia joined to a common duct in a serpulid. (D) A single nephridium and its relationship to a septum in *Lumbricus* (Clitellata, Lumbricidae). Evidence suggests that earthworm nephridia are highly selective excretory and osmoregulatory units. The nephridioduct is regionally specialized along its length. The narrow tube receives body fluids and various solutes, first from the coelom through the nephrostome and then from the blood via capillaries that lie adjacent to the tube. In addition to various forms of nitrogenous wastes (ammonia, urea, uric acid), certain coelomic proteins, water, and ions (Na^+, K^+, Cl^-) are also picked up. Apparently, the wide tube serves as a site of selective reabsorption (probably into the blood) of proteins, ions, and water, leaving the urine rich in nitrogenous wastes. (D after C. A. Edwards and J. R. Lofty. 1972. *Biology of Earthworms*. Chapman and Hall, London. https://link.springer.com/chapter/10.1007/978-1-4899-6912-5_1)

body swells when in a hypotonic medium. It is likely that burrowers and tube dwellers face less osmotic stress than epibenthic forms, because the water in their tubes may be less subject to ionic variation than the overlying water. Osmoregulators, such as several estuarine nereidids, often have thicker body walls that tend to resist changes in shape and volume. When water enters the body from hypotonic surroundings, the increased hydrostatic pressure generated within the coelom works against that osmotic gradient. In addition, regulators can maintain (within limits) a constant internal fluid tonicity because of the greater selective capabilities of their more complex nephridia.

Ionic and osmotic regulation are major challenges for annelids in freshwater and terrestrial habitats, and few evolutionary lineages have solved these problems, the main example being the Clitellata. The moist, permeable surface necessary for gas exchange, and the severe osmotic gradients across the body wall, present potentially serious problems associated with water loss in terrestrial forms and with water gain in freshwater forms. Both situations threaten the loss of precious diffusible salts. Passive diffusion of water and salts also occurs across the gut wall. The major organs of water and salt balance in freshwater annelids are, of course, the nephridia. Excess water is excreted, and salts are retained by selective and active resorption along the nephridioduct. The problem in terrestrial species is more serious. Surprisingly, earthworms are not absolute osmoregulators; rather, they lose and gain water according to the amount of water in their environment. Various species can tolerate a loss of 20% to 75% of their body water and still recover. Under normal conditions, water conservation by earthworms is probably accomplished in several ways. The production of urea allows the excretion of a relatively hypertonic urine compared with that of a strictly ammonotelic animal. There may also be active uptake of water and salts from food across the gut wall. Certainly, there are behavioral adaptations for remaining in relatively moist environments, in addition to the physiological adaptations that allow these animals to tolerate temporary partial dehydration of their bodies.

Aquatic clitellates are ammonotelic, but most terrestrial forms are at least partially ureotelic. These wastes are transported to the nephridia via the circulatory system and by diffusion through the coelomic fluid. Uptake of materials into the nephridial lumen is partly nonselective from the coelom (in those worms with open nephrostomes) and partly selective across the walls of the nephridioduct from the afferent nephridial blood vessels. A significant amount of selective resorption occurs into the efferent blood flow along the distal portion of the nephridioduct, facilitating efficient excretion as well as ionic and osmoregulation.

Nervous System and Sense Organs

The central nervous system in annelids (as in protostomes in general) includes a dorsal cerebral ganglion, paired circumenteric connectives, and one or more ventral longitudinal nerve cords. The most common ventral nerve cord condition seen in annelids consists of two closely allied cords with segmental ganglia (a **rope ladder nerve cord**; Figure 15.15). This lies inside the body, away from the epidermis (i.e., it is subepidermal). However, a series of annelid groups show a ventral nerve cord that, while somewhat rope-ladder-like, lies within the epidermis (i.e., it is intraepidermal). The occurrence of intraepidermal paired ventral nerve cords in taxa such as Oweniida and Chaetopteridae, as well as Errantia, suggests this might be the plesiomorphic condition for Annelida. The classical rope ladder cord has arguably evolved several times from the intraepidermal nerve cord condition.

The cerebral ganglion of annelids is usually bilobed and lies within the prostomium. One or two pairs of circumenteric connectives extend from the cerebral ganglion around the foregut and unite ventrally in the subenteric ganglion. Commonly, a pair of longitudinal nerve cords arises from the subenteric ganglion and extends the length of the body. Ganglia are arranged along these nerve cords, one pair in each segment, and are connected by transverse commissures. Lateral nerves extend from each ganglion to the body wall, and each bears a so-called **pedal ganglion**. This double nerve cord arrangement is common in certain groups of annelids, including sabellids and serpulids, though these are derived annelids. Other taxa, such as amphinomids, have four longitudinal ventral nerve cords, a medial pair and a lateral pair, the latter connecting the pedal ganglia. Similar, but perhaps nonhomologous, lateral longitudinal cords appear in some other annelid taxa that are relatively derived. In many other annelids there has been fusion of the medial nerve cords to form a single midventral longitudinal cord. The degree of fusion varies among taxa, and some retain separate nerve tracts within the single cord.

The cerebral ganglion is often specialized into three regions, typically called the forebrain, midbrain, and hindbrain. Generally, the forebrain innervates the prostomial palps, the midbrain the eyes and prostomial antennae or tentacles, and the hindbrain the chemosensory nuchal organs (Figure 15.15A,D,E). The circumenteric connectives arise from the fore- and midbrain. The midbrain also gives rise to a complex of motor stomatogastric nerves associated with the foregut, especially with the operation of the proboscis or pharynx. The circumenteric connectives often bear ganglia from which nerves extend to the peristomial cirri, or else these appendages are innervated by nerves from the subenteric ganglion. The subenteric ganglion appears

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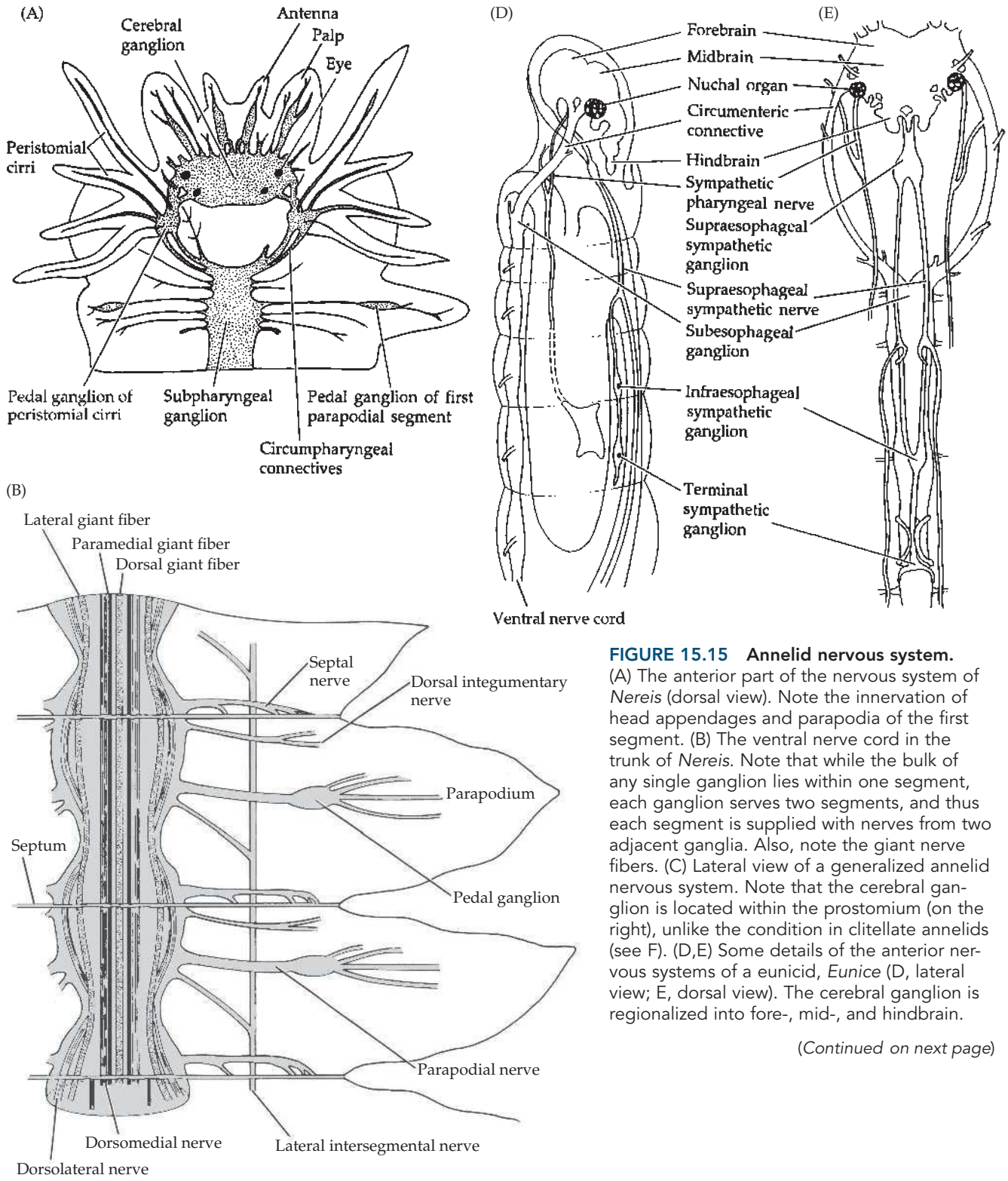

FIGURE 15.15 Annelid nervous system. (A) The anterior part of the nervous system of *Nereis* (dorsal view). Note the innervation of head appendages and parapodia of the first segment. (B) The ventral nerve cord in the trunk of *Nereis*. Note that while the bulk of any single ganglion lies within one segment, each ganglion serves two segments, and thus each segment is supplied with nerves from two adjacent ganglia. Also, note the giant nerve fibers. (C) Lateral view of a generalized annelid nervous system. Note that the cerebral ganglion is located within the prostomium (on the right), unlike the condition in clitellate annelids (see F). (D,E) Some details of the anterior nervous systems of a eunicid, *Eunice* (D, lateral view; E, dorsal view). The cerebral ganglion is regionalized into fore-, mid-, and hindbrain.

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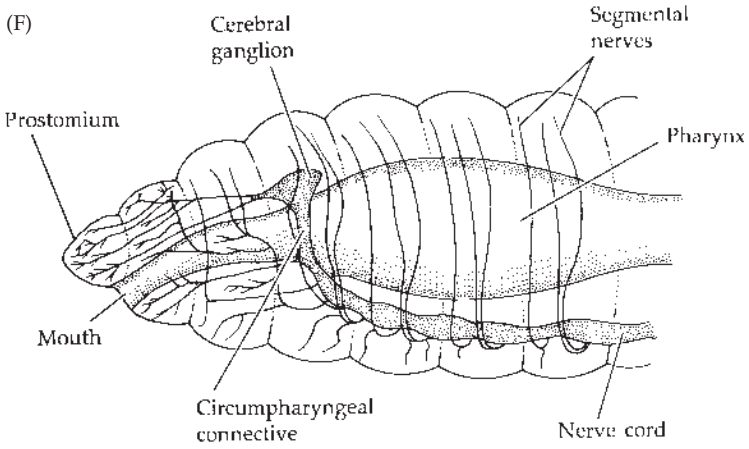

FIGURE 15.15 (*continued*) Annelid nervous system. (F) The nervous system of the clitellate *Lumbricus* in lateral view. Note that the cerebral ganglion is located behind the head, a development apparently associated with a reduction in the size of the prostomium. (D,E after After P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

to exhibit excitatory control over the ventral nerve cord(s) and segmental ganglia.

The nerves that arise from the segmental ganglia innervate the body wall musculature and parapodia (via the pedal ganglia) and the digestive tract. The ventral nerve cord and sometimes the lateral nerves of most annelids contain some extremely long neurons, or giant fibers, of large diameter; these neurons facilitate rapid, "straight-through" impulse conduction, bypassing the ganglia (Figure 15.15B). Giant fibers are apparently lacking in some annelids (e.g., syllids) but are well developed in tube dwellers, such as sabellids and serpulids, permitting rapid contraction of the body and retraction into the tube. The central nervous system of clitellates consists of the usual annelid components: a supraenteric cerebral ganglion joined to a ganglionated ventral nerve cord by circumenteric connectives and a subenteric ganglion (Figure 15.15). With the reduction in head size, especially of the prostomium, the cerebral ganglion occupies a more posterior position than in the other annelids, often lying as far back as the third body segment. The paired ventral nerve cords are almost always fused as a single tract in clitellates, and it usually contains some giant fibers, especially in leeches.

Annelids show an impressive array of sensory receptors. As would be expected, the kinds of sense organs present and the degree of their development vary greatly among annelids with different lifestyles. Certainly, the requirements for sorts of sensory information are not the same for a tube-dwelling sabellid as they are for an errant predatory nereidid or a burrowing arenicolid.

In general, annelids are highly touch sensitive. Crawlers, tube dwellers, and burrowers depend on tactile reception for interaction with their immediate surroundings (locomotion, anchorage within their tube, and so on). Touch receptors are distributed over much of the body surface but are concentrated in such areas as the head appendages and parts of the parapodia. The chaetae are also typically associated with sensory neurons and serve as touch receptors. Some burrowers and tube dwellers have such a strong positive response to contact with the walls of their burrow or tube that the response dominates all other receptor input. Some of these annelids will remain in their burrow or tube regardless of other stimuli that would normally produce a negative response.

Most annelids possess photoreceptors, although these structures are lacking in many burrowers (Figure 15.16). The best-developed annelid eyes occur in pairs on the dorsal surface of the prostomium. In some there is a single pair of eyes (e.g., most phyllodocids); in many there are two or more pairs (e.g., nereidids, polynoids, hesionids, many syllids). These prostomial eyes are direct pigment cups. They may be simple depressions in the body surface lined with retinular cells, or they may be quite complex, with a distinct refractive body or lens (Figure 15.16A–C). In nearly all cases, the eye units are covered by a modified section of the cuticle that functions as a cornea. The eyes of most annelids are capable of transmitting information on light direction and intensity, but in certain pelagic forms (e.g., alciopin phyllodocids) the eyes are huge and possess true lenses capable of accommodation and perhaps image perception (Figure 15.16C,D).

In addition to, or instead of, the prostomial eyes, some annelids bear photoreceptors on other parts of the body. A few species bear simple eyespots along the length of the body (e.g., *Polyophthalmus*). Pygidial eyespots occur in newly settled sabellariids and on some adult fabriciids (e.g., *Fabricia*) and sabellids (small ones such as *Amphiglena*). Interestingly, in these cases the animals crawl backward. Many sabellids and serpulids possess simple ocelli, or even compound eyes remarkably like those of arthropods, on the branchial crown tentacles, and they react to sudden decreases in light intensity by retracting into their tubes (Figure 15.16E). This "shadow response" helps these sedentary worms avoid predators and can easily be demonstrated by passing one's hand to cast a shadow over a live worm.

Nearly all annelids are sensitive to dissolved chemicals in their environment. Most of the chemoreceptors are specialized cells that bear a receptor process extending through the cuticle. Sensory nerve fibers extend from the base of each receptor cell. Such simple chemoreceptors are often scattered over much of the worm's body, but they tend to be concentrated on the head and

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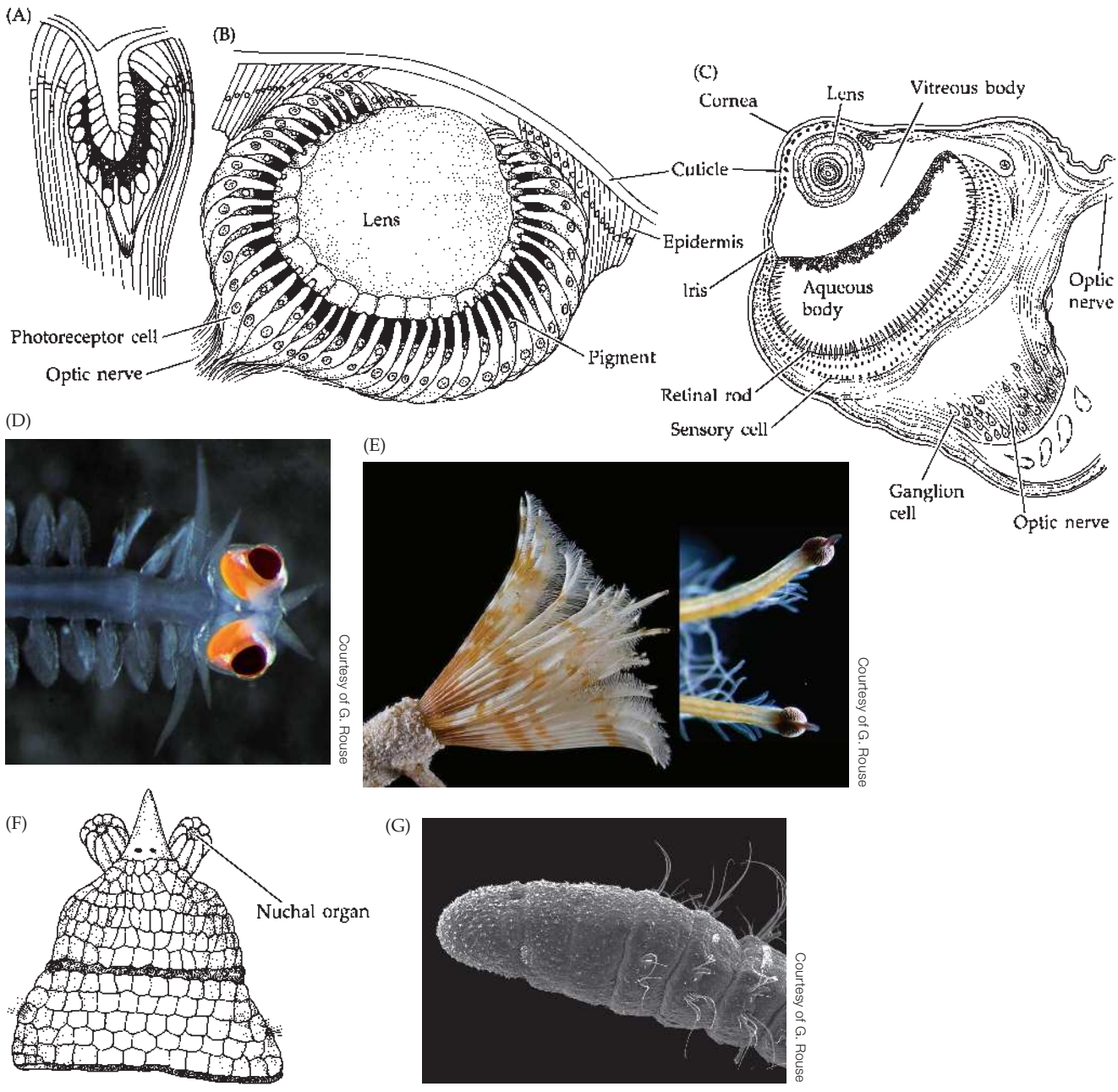

FIGURE 15.16 Annelid photoreceptors and nuchal organs. (A) Simple pigment-cup eye of a chaetopterid. (B) Lensed pigment-cup eye of a nereid. (C) A complex eye (section) of *Vanadis* (Phyllodocidae, Alciopini). (D) Anterior end of an alciopin phyllodocid (ventral view) showing the large eye lobes. (E) *Acromegalomma* (Sabellidae) has compound eyes like, but convergently evolved to, those seen in arthropods. This pair of compound eyes allows the worm to detect potential predators and safely withdraw into the tube. (F) Nuchal organs of *Notomastus* (Capitellidae). (G) SEM of *Proscoloplos* (Orbiniidae) showing nuchal organs on the prostomium.

its appendages. Some annelids also possess ciliated pits or slits called **nuchal organs,** which are presumed to be chemosensory (Figure 15.16F,G). These structures are typically paired and lie posteriorly on the dorsal surface of the prostomium. In some forms (e.g., certain nereidids) the nuchal organs are simple depressions, whereas in others (e.g., opheliids) they are rather complex eversible structures equipped with special retractor muscles. In members of Amphinomidae, the nuchal organs are elaborate outgrowths of an extension of the prostomium called the **caruncle**.

Statocysts are common in some burrowing and tube-dwelling annelids (e.g., certain terebellids, arenicolids, and sabellids). A few forms possess several pairs of statocysts, but most have just a single pair, located near the head. These statocysts may be closed or open to the exterior, and the statolith may be a secreted structure or formed of extrinsic material,

such as sand grains. It has been demonstrated experimentally that the statocysts of some annelids do serve as georeceptors and help maintain proper orientation when the bearer is burrowing or tube building.

Several other structures of presumed sensory function occur in some annelids. These structures are often in the form of ciliated ridges or grooves occurring on various parts of the body and associated with sensory neurons. A variety of names have been applied to these structures, but in most cases their functions remain unclear. Annelids also possess organs or tissues of neurosecretory or endocrine functions. Most of the secretions appear to be associated with the regulation of reproductive activities, as discussed in the Reproduction and Development section.

Reproduction and Development

Regeneration and asexual reproduction Annelids show various degrees of regenerative capabilities. Nearly all of them are capable of regenerating lost appendages such as palps, tentacles, cirri, and parapodia. Most of them can also regenerate posterior body segments if the trunk is severed. There are numerous exceptional cases of the regenerative powers of annelids. While regeneration of the posterior end is common, most cannot regenerate lost heads. However, sabellids, syllids, and some others can regrow the anterior end. The most dramatic regenerative powers among the annelids occur, oddly, in a few forms with highly specialized and heteronomous bodies. In *Chaetopterus*, for example, the anterior end will regenerate a normal posterior end if the regenerating part (the anterior end) includes not more than 14 segments; if the animal is cut behind the fourteenth segment, regeneration does not occur. Furthermore, any single segment from among the first 14 can regenerate anteriorly and posteriorly to produce a complete worm (Figure 15.17A). An even more dramatic example of regenerative power is known among certain species of *Dodecaceria*, which can fragment their bodies into individual segments, each of which can regenerate a complete individual! A similar situation is seen in another cirratulid, *Ctenodrilus*, where segments transform into a series of heads that then proliferate further segments behind, resulting in a chain of individuals that eventually separates. A chain of six is shown in Figure 15.17B. Such clonal reproduction has been maintained by *Ctenodrilus* in culture for decades without any instances of sexual reproduction.

Regeneration appears to be controlled by neuroendocrine secretions released by the central nervous system at sites of regrowth. It is initiated by severing the elements of the nervous system. Initiation has been demonstrated experimentally by cutting the ventral nerve cord while leaving the body intact; the result is the formation of an extra part at the site of cutting (e.g., two "tails"). The actual mechanism of regeneration has been studied in a variety of annelids, and although the results are not entirely consistent, a general scenario can be outlined. Normal growth and addition of segments (in young worms) take place immediately anterior to the pygidium, in a region known as the growth zone. However, this growth zone is obviously not involved in regeneration. Rather, when the trunk is severed, the cut region heals over and then a patch of generative tissue, or blastema, forms. The blastema comprises an inner mass of cells, originating from nearby tissues that were derived originally from mesoderm, and an outer covering of cells from ectodermally derived tissues such as the epidermis. Somewhat like a growth zone analogue, these two cell masses proliferate new body parts according to their tissue origins. This process is coupled with the growth of the gut, which contributes parts of endodermal origin.

In addition, research has shown that relatively undifferentiated cells from mesenchyme-like layers of the body migrate to injured areas and contribute, to various (and uncertain) degrees, to the regenerative process. These so-called neoblast cells are ectomesodermal in origin and arise embryonically from presumptive ectoderm. During regeneration, they apparently contribute to tissues and structures normally associated with true mesoderm, and perhaps other germ layers as well. The implication here is that the germ layer of the precursor of a regenerated part may not correspond to the normal origin of that part. For example, regenerated coelomic spaces may be lined with tissue derived originally from ectoderm rather than from mesoderm.

Several annelid groups use their regenerative powers for asexual reproduction. A few reproduce asexually by multiple fragmentation. We have discussed the ability of *Dodecaceria* to regenerate complete individuals from isolated segments; this phenomenon occurs spontaneously and naturally in these animals as a highly effective reproductive strategy. Spontaneous transverse fragmentation of the body into two or several groups of segments also occurs in certain syllids, chaetopterids, cirratulids, and sabellids (Figure 15.17B). The point (or points) at which the body fragment is typically species specific and can be anticipated by an ingrowth of the epidermis that produces a partition across the body called a **macroseptum**. Asexual reproduction results in a variety of regeneration patterns, including chains of individuals, budlike outgrowths, or direct growth to new individuals from isolated fragments. Asexual reproduction in annelids may be under the same sort of neurosecretory control as that postulated for nonreproductive regeneration.

Sexual reproduction The majority of annelids are gonochoristic. Hermaphroditism is known in some sabellids, serpulids, certain freshwater nereidids, and isolated cases in other clades, but it is notably found across all Clitellata. The gametes arise by

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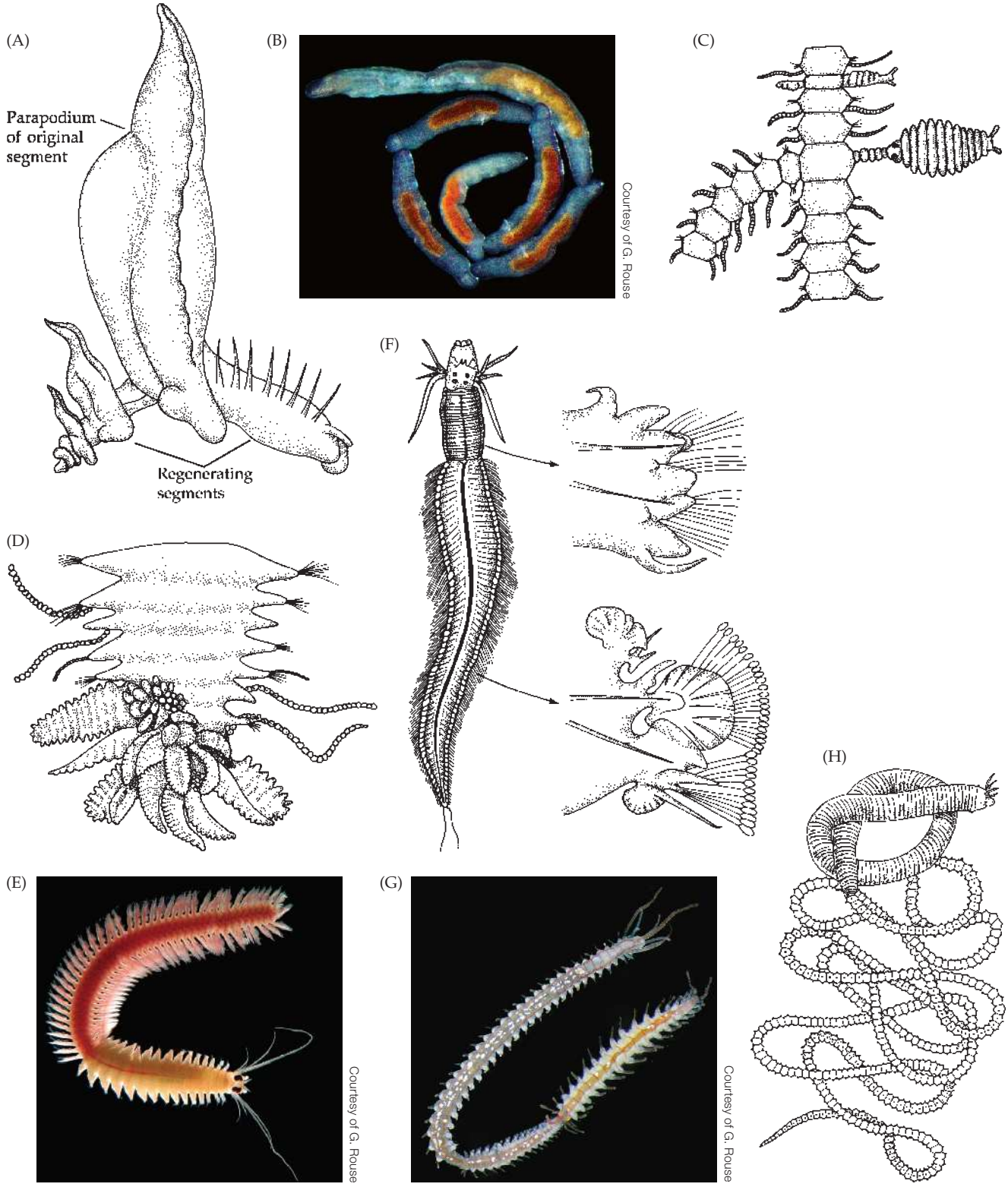

FIGURE 15.17 Regeneration, asexual reproduction, and epitoky in annelids. (A) The remarkable regeneration of a chaetopterid from a single excised segment (in this case, a fan parapodia segment). (B) Clonal reproduction in *Ctenodrilus* (Cirratulidae). Body segments transform into a series of heads that then proliferate further segments behind, resulting in a chain of individuals that eventually separates. (C) A portion of a syllid (*Syllis ramosa*, but this also occurs in *Ramisyllis*) in which reproductive individuals are budded (cloned) from the parent's parapodia. (D) The posterior end of *Typosyllis* (Syllidae) bearing a cluster of epitokes. (E) A heteronereid (Nereididae). Note the enlarged eyes. (F) An epitokous nereidid, *Neanthes nubila*. Note the dimorphic condition of the anterior and posterior parapodia. (G) Another syllid, *Myrianida gidholmi*, where there are two epitokes being produced in a series. The more mature epitoke (posterior) is full of eggs and has enlarged eyes. (H) The epitokous palolo worm, *Palola viridis* (Eunicidae). (A,C after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

proliferation of cells from the peritoneum, these being released into the coelom as gametogonia or primary gametocytes. Formation of gametes may occur throughout the body or only in particular regions of the trunk. Within a reproductive segment, the production of gametes may occur all over the coelomic lining or only on specific areas.

The gametes generally mature within the coelom and are released to the outside by mechanisms such as metanephridia or a simple rupture of the parent body wall. Many species release eggs and sperm into the water, where external fertilization is followed by indirect development with planktotrophic trochophore larvae. Others display mixed life history patterns. In these latter forms, fertilization is internal, followed by brooding or by the production of floating or attached egg capsules. In most instances the embryos are released as free-swimming lecithotrophic trochophores. Some species brood their embryos on the body surface or in their tubes.

Many of the free-spawning annelids have evolved methods that ensure relatively high rates of fertilization. One of these methods is the fascinating phenomenon of **epitoky**, characteristic of many syllids, nereidids, and eunicids (Figure 15.17D–H). This phenomenon involves the production of a sexually reproductive worm called an **epitokous individual**. Epitokous forms may arise from nonreproductive (**atokous**) animals by a transformation of an individual worm, as in nereidids, or by the asexual production of new epitokous individuals, as in many syllids. In nereidids, the whole body may transform into a sexual **epitokous** individual called a heteronereid. In these heteronereids the posterior body segments are swollen and filled with gametes and the associated parapodia become enlarged and natatory, while the head develops large eyes and the gut atrophies (Figure 15.17E,F). In syllids, where the epitokous worm is clonally produced, the epitokes are formed as single clones, in a linear series (Figure 15.17G), or even as clusters of outgrowths from certain body regions (Figure 15.17C,D).

In any event, the epitokes are gamete-carrying bodies capable of swimming from the bottom upward into the water column, where the gametes are released. Epitoky is controlled by neurosecretory/hormonal activity, and the upward migration of the epitokes is precisely timed to synchronize spawning within a population. The reproductive swarming of epitokes is linked with lunar periodicity. This activity not only ensures successful fertilization but establishes the developing embryos in a planktonic habitat suitable for the larvae. Perhaps the most famous of the epitokous worms are eunicids in the genus *Palola*, commonly known as palolo worms based on the Samoan name for them. Native Polynesian islanders have long been known to predict the swarming (typically to the day and hour) and collect the ripe epitokes, which are the released posterior ends of the worms' bodies, under a full moon to feast on them (Figure 15.17H).

Clitellates are hermaphroditic, and the various parts of the reproductive apparatus are restricted to certain anterior segments (Figure 15.18). The arrangement of the reproductive system facilitates mutual cross-fertilization followed by encapsulation and deposition of the zygotes. The male system includes one or two pairs of testes located in one or two specific body segments. Sperm are released from the testes into the coelomic spaces, where they mature or are picked up by storage sacs (seminal vesicles) derived from pouches of the septal peritoneum (Figures 15.12G and 15.18B). There may be a single seminal vesicle or as many as three pairs in some earthworms. When mature, the sperm are released from the seminal vesicles, picked up by ciliated seminal (sperm) funnels, and carried by sperm ducts to paired gonopores. The female reproductive system consists of a single pair of ovaries located posterior to the male system (Figures 15.12G and 15.18B). Again, the ova are released into the adjacent coelomic space and sometimes stored until mature in shallow pouches in the septal wall; these pouches are called ovisacs. Next to each ovisac is a ciliated funnel that carries the mature ova to an oviduct and eventually to the female gonopore. Most clitellates also possess one or two or more pairs of blind sacs called spermathecae (seminal receptacles) that open to the outside via separate pores (Figure 15.18A,B).

Of major importance to the overall reproductive strategy of clitellates is the unique region of glandular tissue called the **clitellum** (Latin for "saddle") (Figure 15.18A,C–G,I), a principal anatomical feature giving rise to the name Clitellata. The clitellum has the appearance of a thick sleeve that partially or completely encircles the worm's body. It is formed of secretory cells within the epidermis of several segments. The exact position of the clitellum and the number of segments involved are consistent within any given species. In freshwater forms the clitellum is located around the position of the gonopores, but in most earthworms it is posterior to the gonopores. There are three types of gland cells within the clitellum, each secreting a different substance important to reproduction: mucus that aids in copulation, the material forming the outer casing of the egg capsule (or cocoon), and albumin deposited with the zygotes inside the cocoon.

During copulation in most clitellates, the mating worms align themselves facing in opposite directions (Figure 15.18C,D,I), and mucous secretions from the clitellum hold them in this copulatory posture. Many clitellates position themselves so that the male gonopores of one are aligned with the spermathecal openings of the other. In such cases, special copulatory chaetae near the male pores or eversible penislike structures aid in

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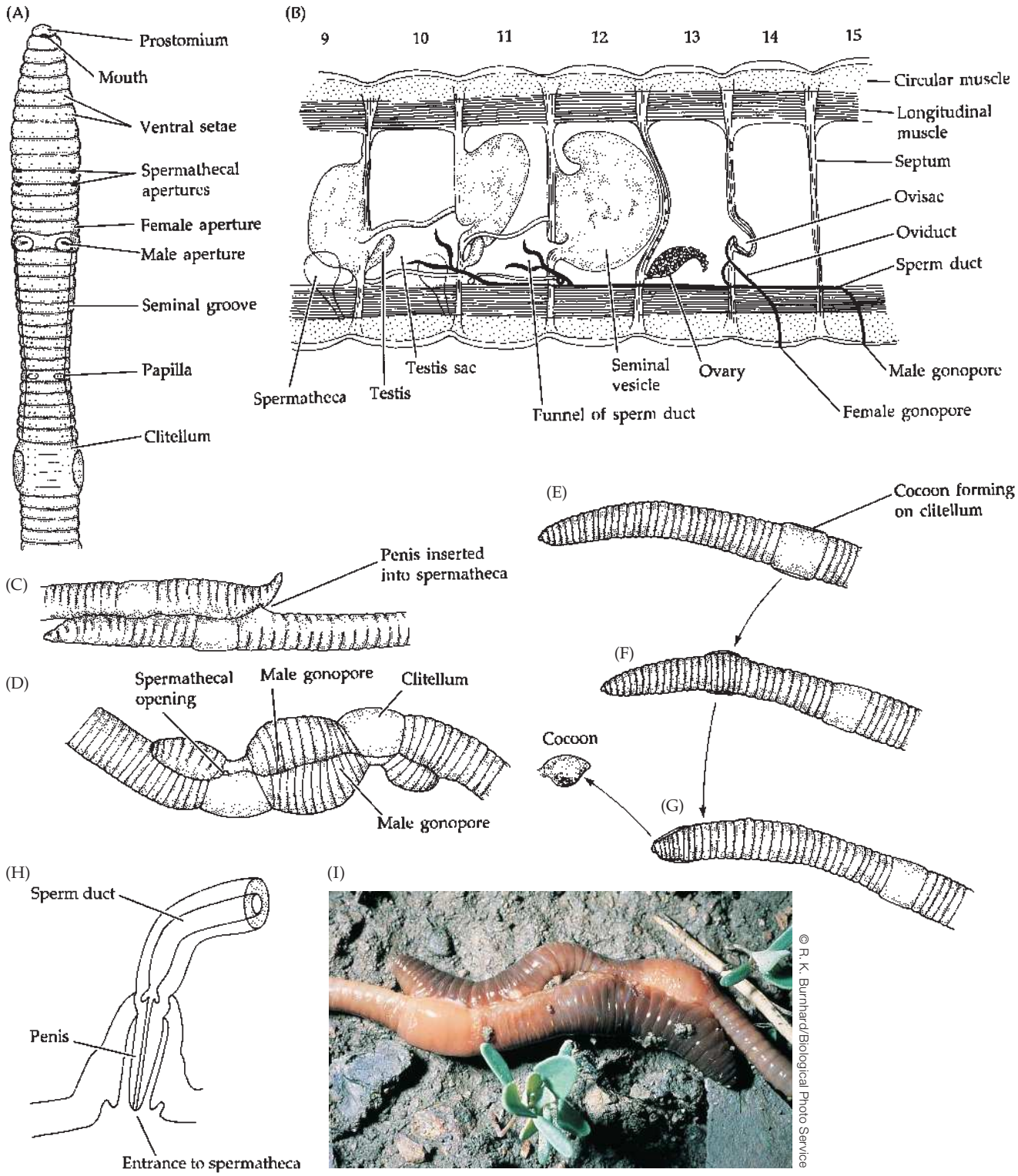

FIGURE 15.18 The reproductive system of *Lumbricus* (Clitellata) and mating in earthworms. (A) External structures associated with reproduction of *Lumbricus* (ventral view). (B) Segments 9–15 of *Lumbricus* (composite lateral view). (C,D) Copulating earthworms. (C) *Pheretima* (Crassiclitellata, Megascolecidae) transfers sperm directly from the male pore, through a penis, into the mate's spermatheca. (D) *Eisenia* uses indirect sperm transfer. As in *Lumbricus*, the sperm leave the male pores and travel along paired seminal grooves to the spermathecal openings of the mate. (E–G) An earthworm forming and releasing a cocoon. As the cocoon slides over the worm, it receives ova and sperm. (H) Engaged copulatory apparatus of *Rhynchelmis*, a lumbriculid with direct sperm transfer. (I) Copulating earthworms (*Lumbricus*). (A,B,D–G after C. A. Edwards and J. R. Lofty. 1972. *Biology of Earthworms*. Chapman and Hall, London. https://link.springer.com/chapter/10.1007/978-1-4899-6912-5_3)

anchoring the mates together (Figure 15.18H). Some earthworms (Crassiclitellata) are not so accurate with their mating, and their copulatory position does not bring the male pores against the spermathecal openings. Instead, they develop external sperm grooves along which the male gametes must travel prior to entering the spermathecal pores. These grooves are formed temporarily by muscle contraction and are covered by a sheet of mucus. Underlying muscles cause the grooves to undulate, and the sperm are transported along the body to their destination. Following the mutual exchange of sperm to the seminal receptacles of each mate, the worms separate, each functioning as an inseminated female.

From several hours to a few days following copulation between clitellate annelids, a sheet of mucus is produced around the clitellum and all the anterior segments. Then the clitellum produces the cocoon itself in the form of a leathery, proteinaceous sleeve. The cocoons of terrestrial species are especially tough and resistant to adverse conditions. Albumin is secreted between the cocoon and the clitellar surface. The amount of albumin deposited with the cocoon is much greater in terrestrial species than in aquatic forms. Thus formed, the cocoon and underlying albumin sheath are moved toward the anterior end of the worm by muscular waves and backward motion of the body. As it moves along the body, the cocoon first receives eggs from the female gonopores, and then sperm previously received from the mate and stored in the seminal receptacles. Fertilization occurs within the albumin matrix inside the cocoon (though not in leeches). The open ends of the cocoon contract and seal as they pass off the anterior end of the body (Figure 15.18E–G). The closed cocoons are deposited in benthic debris by aquatic clitellates. Terrestrial forms deposit their cocoons in the soil at various depths, depending on the moisture content of the substratum.

Development Early annelid development exemplifies a classic protostomous, spiralian pattern (Figures 15.19, 15.20, and 15.21). The eggs are telolecithal with small to moderate quantities of yolk. Those with a period of encapsulation or brooding prior to larval release generally contain more yolk than those that free-spawn.

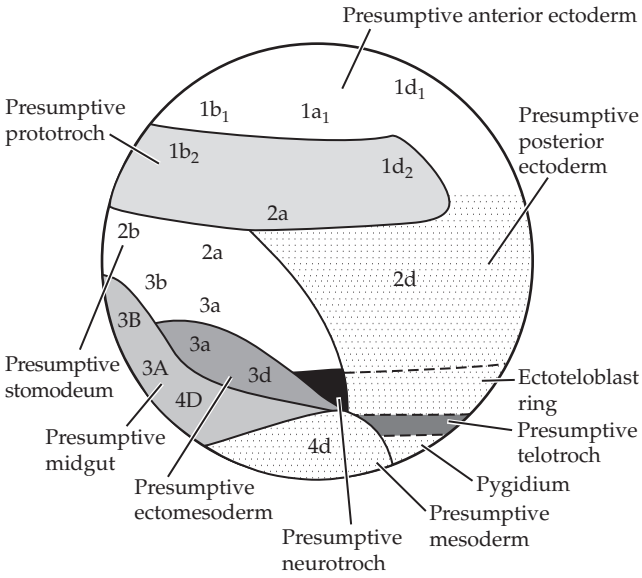

FIGURE 15.19 Fate map of a *Scoloplos* (Orbiniidae) blastula (viewed from the left side).

In any case, cleavage is holoblastic and clearly spiral. A coeloblastula or, in the cases of more yolky eggs, a stereoblastula develops and undergoes gastrulation by invagination, epiboly, or a combination of these two events. Gastrulation results in the internalization of the presumptive endoderm (the 4A, 4B, 4C, 4D and the 4a, 4b, 4c cells) and presumptive mesoderm (4d micromere). The derivatives of the first three micromere quartets give rise to ectoderm and ectomesoderm, the latter producing various larval muscles between the body wall and the developing gut. As the endoderm hollows to produce the archenteron, a stomodeal invagination forms at the site of the blastopore and a proctodeal invagination produces the hindgut.

In most annelids, these early ontogenetic events result in a clearly recognizable trochophore larva characterized by a locomotory ciliary band just anterior to the region of the mouth (Figures 15.20 and 15.21). Trochophores are also seen in Mollusca and Nemertea (and possibly some other phyla). This ciliary band, the **prototroch**, arises from special cells, called trochoblasts,

FIGURE 15.20 Some annelid larvae—trochophores and beyond. (A–C) Opposed-band planktotrophic trochophores of serpulid polychaetes. (A) *Spirobranchus giganteus* (Serpulidae) trochophore showing complete gut (g), apical tuft (a), eye (e), prototroch (p), and metatroch (m) (differential interference contrast micrograph). (B) SEM of *S. giganteus* trochophore in side view showing apical tuft (a), episphere (epi), and prototroch (p). (C) SEM of *S. giganteus* trochophore in posterior view showing prototroch (p), metatroch (m), and ciliated food groove (shown by arrow). (D) SEM of a planktonic six-segmented nectochaete larva of a chrysopetalid. (E) SEM of a planktonic five-segmented nectochaete larva of a glycerid. (F) Lecithotrophic trochophore of *Marphysa* (Eunicidae) with first segment developing and showing chaetae. (G) Some annelid larvae that show little, if any, metamorphosis. After nine days in the tube a young juvenile of *Echinofabricia alata* (Fabriciidae), with a fully developed radiolar crown and gut, as well as anterior and posterior eyes, is ready to crawl away. (H–J) Others show dramatic metamorphosis, sometimes in just a few minutes, as seen here in *Owenia* (Oweniidae). (H) Lateral view of an oweniid mitraria larva, taken from plankton off Belize, showing long larval chaetae and episphere with ciliated margin. (I) Closeup of mitraria episphere showing juvenile inside larval body. (J). Juvenile immediately after metamorphosis (taken only a few seconds after the previous micrograph). Larval chaetae have been shed, as has the episphere. ▶

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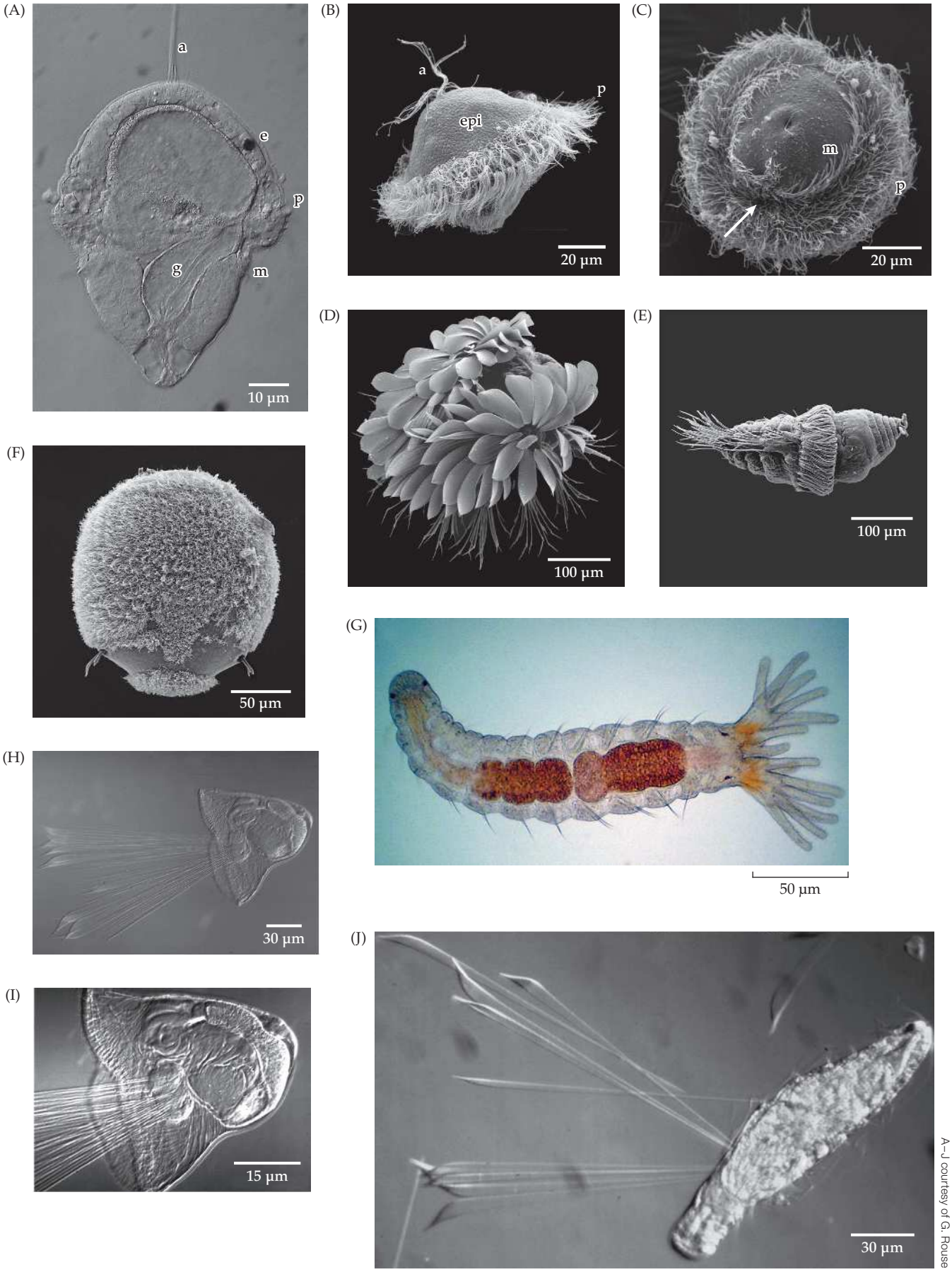

A–J courtesy of G. Rouse

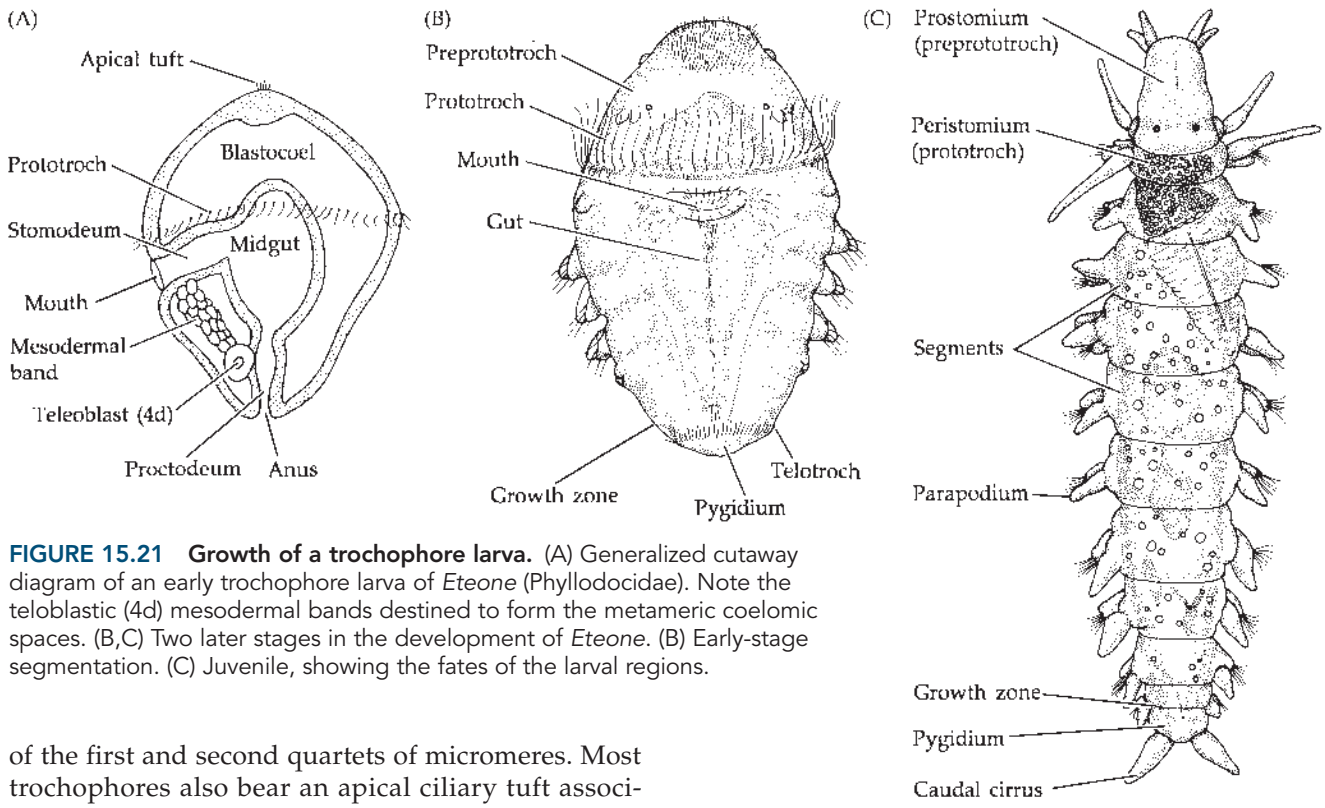

FIGURE 15.21 Growth of a trochophore larva. (A) Generalized cutaway diagram of an early trochophore larva of *Eteone* (Phyllodocidae). Note the teloblastic (4d) mesodermal bands destined to form the metameric coelomic spaces. (B,C) Two later stages in the development of *Eteone*. (B) Early-stage segmentation. (C) Juvenile, showing the fates of the larval regions.

of the first and second quartets of micromeres. Most trochophores also bear an apical ciliary tuft associated with an apical sense organ derived from a plate of thickened ectoderm at the anterior end. In addition, there is often a perianal ciliary band called the telotroch and/or a midventral band called the neurotroch. Some trochophores may also have a band called a metatroch. The mesentoblast divides to form a pair of cells called teloblasts, which in turn proliferate a pair of mesodermal bands, one on each side of the archenteron in the region of the hindgut, an area known as the growth zone (Figure 15.21B). Many trochophores bear larval sense organs such as ocelli, as well as a pair of larval protonephridia, and develop bundles of mobile chaetae that are known to serve as a defense against predators and to help retard sinking. Several annelid larvae are shown in Figure 15.20.

The larva grows and generally elongates by proliferation of tissue in the growth zone and may initially form several segments simultaneously (Figure 15.21C), while subsequent segments are produced by the anterior proliferation of mesoderm from the teloblast derivatives on either side of the gut. These packets of mesoderm hollow (the process known as schizocoely) and expand as paired coelomic spaces, which eventually obliterate the blastocoel. Thus, the production of serially arranged coelomic compartments and the formation of segments are one and the same; the anterior and posterior walls of adjacent coelomic compartments form the intersegmental septa. Proliferation of segments by this process is called **teloblastic growth**. Externally, additional ciliary bands are added at each segment. These metatrochal bands aid in locomotion as the animal increases in size. Such segmented larvae are sometimes called **polytroch larvae**.

The fates of the various larval regions are now apparent (Figures 15.19 and 15.21). The region anterior to the prototrochal ring (the **episphere**) becomes the prostomium, while the prototrochal area itself forms the peristomium. Note that these two parts are not involved in the proliferation of segments and are thus presegmental. However, in some annelids, one or more of the anterior trunk segments may be incorporated into the peristomium during growth. The segmental, metatrochal portion of the larva forms the trunk, and the growth zone and postsegmental pygidium remain as the corresponding adult body parts. The apical sense organ becomes the cerebral ganglion, which is eventually joined with the developing ventral nerve cord by the formation of circumenteric connectives. The body continues to elongate as more segments form, and the juvenile worm finally drops from the plankton and assumes the lifestyle of a young annelid. This whole affair was beautifully described in verse by the late Walter Garstang (1951), where he explained the development of *Phyllodoce* in the first part of his classic poem, "The Trochophores":

The trochophores are larval tops the Annelids
set spinning
With just a ciliated ring—at least in the beginning—
They feed, and feel an urgent need to grow more like
their mothers,
So sprout some segments on behind, first one,
and then the others.

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And since more weight demands more power,
each segment has to bring
Its contribution in an extra locomotive ring:
With these the larva swims with ease, and,
adding segments more,
Becomes a Polytrochula instead of Trochophore.
Then setose bundles sprout and grow,
and the sequel can't be hid:
The larva fails to pull its weight, and sinks—
an Annelid.

Clitellates produce telolecithal ova, but the amount of yolk varies greatly and inversely with the amount of albumin secreted into the cocoon. The eggs of freshwater forms often contain relatively large amounts of yolk but are encased with only a small quantity of albumin. Conversely, the eggs of terrestrial species tend to have little yolk but are supplied with large quantities of albumin on which the developing embryos depend for a source of nutrition. In any case, cleavage is holoblastic and unequal. And, although highly modified, evidence of the ancestral spiralian pattern is still apparent in cell placement and fates (e.g., an identifiable 4d mesentoblast homologue gives rise to the presumptive mesoderm). Development is direct, with no trace of a trochophore larval stage. However, the teloblastic production of coelomic spaces and segments is an obvious retained characteristic of the basic annelid developmental program. Development time varies from about one week to several months, depending on the species and environmental conditions. In climates where relatively severe conditions follow cocoon deposition, development time is usually long enough to ensure that the juveniles hatch in the spring. Under more stable conditions, development time is shorter, and reproduction is less seasonal.

Sipuncula: The Peanut Worms

In the past, the coelomate worm phyla Sipuncula and Echiura were often dismissed in short fashion as "minor" or "lesser" groups. However, thanks to recent molecular phylogenetic research, we now know that these two groups are remarkably modified spiralian clades embedded within the phylum Annelida. Sipunculans and echiurans (Thalassematidae) resemble one another in several respects, although they are not closely related, and they are often found in similar habitats. For these reasons, biologists who find interest in one of these groups often study both. Sipunculans are never as abundant or important ecologically as some other worms, especially the polychaetes and nematodes. Nonetheless, they display body plans that are different from any we have discussed so far and provide important lessons in functional morphology—and thus deserve special attention.

The clade Sipuncula (Greek *siphunculus*, "little tube") includes about 150 species in 16 genera and 6 families. Usually called "peanut worms," adult sipunculans show no evidence of segmentation or chaetae (two features viewed as characteristic of annelids). The body is sausage shaped and divisible into a retractable introvert and a thicker trunk (Figure 15.22). It is when the introvert is retracted and the body is turgid that some species resemble a peanut. The anterior end of the introvert bears the mouth and feeding tentacles. The tentacles are derived from the regions around the mouth (**peripheral tentacles**) and around the nuchal organ (**nuchal tentacles**); differences in tentacular arrangements are of taxonomic importance. The gut is characteristically U-shaped and highly coiled, and the anus is located dorsally on the body near the introvert-trunk junction. The body surface is usually beset with minute bumps, warts, tubercles, or spines. Sipunculans range in length from less than 1 cm to about 50 cm, but most are 3–10 cm long. With the exception of the coiled gut, the body plan of sipunculans has remained largely unchanged since the early Cambrian, as judged by two fossil species from the Maotianshan Shales of southwest China.

The coelom is well developed and unsegmented, forming a spacious body cavity. Metanephridia are present, with nephridiopores on the ventral body surface. There is no circulatory system, but the coelomic fluid includes cells containing a respiratory pigment. Most sipunculans are gonochoristic and reproduce by epidemic spawning. Development is typically spiral, usually indirect, and includes a free-swimming larva.

Sipunculans are benthic and exclusively marine. They are usually reclusive, either burrowing into sediments or living beneath stones or in algal holdfasts. In tropical waters sipunculans are common inhabitants of coral and littoral communities, where they often burrow into hard, calcareous substrata. Some inhabit abandoned gastropod shells, annelid tubes, and other such structures. They are found from the intertidal zone to depths of over 5,000 m, and some deep-burrowing species may play an important role in influencing the ecology and geochemistry of the Nordic Seas region. In Southeast Asia (e.g., Vietnam), large sand-burrowing species are occasionally consumed as human food, and others are used as fishing bait in Europe.

The sipunculan body plan is founded on the qualities of the spacious body coelom. Uninterrupted by transverse septa, the coelomic fluid provides an ample circulatory medium for these sedentary worms. The coelom and associated musculature function as a hydrostatic skeleton and as a hydraulic system for locomotion, circulation of coelomic fluid, and introvert extension.

The embryonic and adult characteristics of sipunculans place them solidly within the spiralian protostomes,

FIGURE 15.22 Representative sipunculans. (A) *Phascolosoma*, with the tip of the introvert turned inward. (B) *Sipunculus nudus*. (C) *Thysanocardia nigra*. (D) *Aspidosiphon cristatus*. (E) *Sipunculus norvegicus*. (F) *Phascolion* sp. in a gastropod shell. (G) Feeding tentacles of *Themiste dyscrita*.

and molecular data have provided strong evidence for their membership in the phylum Annelida, despite the lack of adult segmentation. One might view the absence of segmentation as a secondary loss of a partitioned coelom associated with the exploitation of a sedentary, burrowing lifestyle. The reduction in sensory receptors and simplification of the nervous system in general are explainable on this same basis. However, many other species of annelids have evolved burrowing lifestyles while retaining their basic segmentation.

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Classification of Sipuncula

The first published illustrations of sipunculans were produced from woodcuts made in the mid-sixteenth century. Linnaeus included these animals in the twelfth edition of his *Systema Naturae* (1767) and placed them in the Vermes, along with so many other odds and ends. In the nineteenth century, Lamarck and Cuvier considered the sipunculans to be relatives of holothuroid echinoderms (sea cucumbers). No separate taxon was established for these worms until 1828, when Henri Marie Ducrotay de Blainville introduced the name Sipunculida and allied the group with certain parasitic helminths.

In 1847 Jean Louis Armand de Quatrefages created the taxon Gephyrea to include sipunculans, echiurans, and priapulans. The Greek root *gephyra* means "bridge," as Quatrefages regarded these animals as intermediate between annelids and echinoderms. The gephyrean concept was founded on superficial characteristics, but it persisted well into the twentieth century even though many authors attempted to raise the constituent groups to individual phylum status. Finally, Libbie Hyman (1959), recognizing the polyphyletic nature of the Gephyrea, elevated the sipunculans to a separate phylum rank. At that time, however, no classes, orders, or families were recognized, and the phylum was divided into only genera and species. The Herculean effort by Alexander Stephen and Stanley Edmonds (1972) and subsequent modifications by other workers (e.g., Mary Rice 1982) led to a classification comprising 4 families and 16 genera. Later, Edward Cutler and Peter Gibbs (1985) applied phylogenetic methods and produced a classification scheme of 2 classes, 4 orders, 6 families, and 17 genera, which has been used until recently. However, with the use of molecular phylogenetics, this classification was challenged, the phylum was subsumed within Annelida, and a new system, consisting of 6 families and 16 genera was proposed by Lemer and collaborators in 2015, a system that is in use today (Figure 15.23).

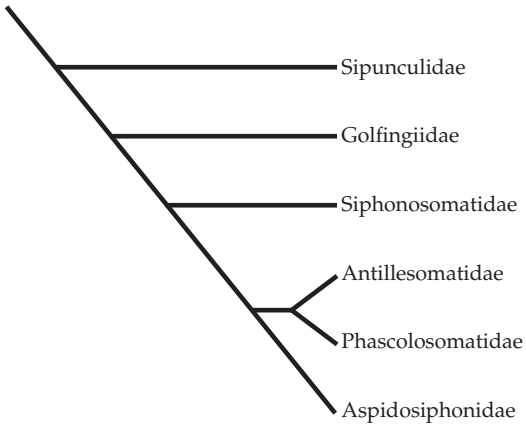

FIGURE 15.23 Phylogenetic relationships of the sipunculan families.

SIPUNCULA

FAMILY SIPUNCULIDAE Large sipunculans, trunk to 45 cm in length (Figure 15.22B,E and Figure 12.25A). Introvert shorter than the trunk, covered with prominent papillae arranged irregularly. Hooks absent. Circular and longitudinal muscle layers divided into distinct bands. Body wall with coelomic extensions in the form of parallel longitudinal canals extending through most of the trunk length, or short diagonal canals limited in length to the width of one circular muscle band. Two protractor muscles may be present. With paired metanephridia. Development proceeds through a planktotrophic pelagosphera larva. Two genera: *Sipunculus*, *Xenosiphon*.

FAMILY GOLFINGIIDAE Heterogeneous group of small to medium-sized sipunculans (trunk no longer than 20 cm) (Figure 15.22C,F,G and Figure 12.25B). Hooks may be deciduous, simple when present, not sharply curved and generally scattered, except in 3 species where hooks are arranged in rings. Body wall with a continuous muscle layer, except in *Phascolopsis*, where the longitudinal muscles are divided in anastomosing bands. With paired or single metanephridia. Seven genera: *Golfingia*, *Nephasoma*, *Onchnesoma*, *Phascolion*, *Phascolopsis*, *Themiste*, *Thysanocardia*.

FAMILY SIPHONOSOMATIDAE Large to medium-sized sipunculans (trunk to 50 cm in length). Introvert much shorter than trunk, with prominent conical papillae and/or hooks arranged in rings. Body wall with small, irregular saclike coelomic extensions. Circular and longitudinal muscle layers gathered into anastomosing, sometimes indistinct bands. With paired metanephridia. Two genera: *Siphonomecus*, *Siphonosoma*.

FAMILY ANTILLESOMATIDAE Medium-sized sipunculans (trunk to 8 cm). Distal part of the introvert smooth and white, proximal portion bears dark papillae and is marked off by a distinctive collar. Hooks absent in adults, but a few hooks present in small individuals (<1 cm). Oral disc consisting of nuchal organ enclosed by numerous tentacles, which vary in number according to size (from 30 to 200 in adults). Body wall with longitudinal muscle layer gathered into anastomosing bands. Contractile vessel with many villi. Four introvert retractor muscles with the lateral pair often extensively fused. With paired metanephridia. Without an anal shield. Single genus: *Antillesoma*.

FAMILY PHASCOLOSOMATIDAE Small to medium-sized sipunculans (trunk to 12 cm in length) (Figure 15.22A). Hooks recurved, usually with internal structures, and closely packed in regularly spaced rings (absent in *Apionsoma trichocephalus*). External trunk wall rough with obvious papillae. In *Apionsoma*, papillae are concentrated at the posterior end of the trunk. Internally, the longitudinal muscle is generally subdivided into anastomosing bands except in two subgenera—*Phascolosoma* (*Fisherana*) and *Apionsoma* (*Apionsoma*)—where this layer is thinner and continuous. Contractile vessel is

smooth but may be large with bulbous pouches or swelling in a few *Phascolosoma*. With paired metanephridia. Two genera: *Apionsoma*, *Phascolosoma*.

FAMILY ASPIDOSIPHONIDAE Generally small (to 30 mm) sipunculans with smooth trunk and 2 retractor muscles (Figure 15.22D). Introvert protruding at 45°–90° angle ventral to main axis of trunk. Muscle layers generally smooth and continuous, or with longitudinal muscle layer separated in anastomosing bundles. Trunk with anterior, and sometimes posterior, anal shields derived from thickened cuticle or calcareous deposits. With paired metanephridia. Two genera: *Aspidosiphon*, *Cloeosiphon*.

The Sipunculan Body Plan

Body Wall, Coelom, Circulation, and Gas Exchange

The sipunculan body surface is covered by a well-developed cuticle that varies from thin on the tentacles to quite thick and layered over much of the trunk (Figures 15.22 and 15.24). The cuticle often bears papillae, warts, or spines of various shapes. Beneath the cuticle lies the epidermis, the cells of which are cuboidal over most of the body but grade to columnar and ciliated on the tentacles. The epidermis contains a variety of unicellular and multicellular glands called epidermal organs, some of which project into the cuticle and produce some of the surface papillae or knobs. Some of these glands are associated with sensory nerve endings; others are responsible for producing the cuticle or for mucus secretion. In both larval and adult sipunculans, epidermal organs are externally encapsulated by a cuticle and internally delimited by regular epidermal cells. If pocketed deeply into the body ball, epidermal organs are also delimited by subepidermal musculature.

Beneath the epidermis, especially where it is raised, is a dermis composed of connective tissue fibers and loose cells. From one to four large introvert retractor muscles extend from the body wall into the introvert where they insert on the gut just behind the mouth (Figure 15.25A,B). All species so far studied go through developmental stages with four retractor muscles, which are eventually reduced to a lower number in the adult. Species with crawling larvae have more strongly developed body wall musculature than those with swimming larvae.

In Sipunculidae, which are mostly large and include some warm-water species, the dermis also houses a system of coelomic extensions or channels (Figure 15.24). These **coelomic channels** may extend entirely through the muscle layers and into the epidermal layer, and they have a gas transport function in some species. They are connected to the trunk coelom by pores. The muscles of the body wall include outer circular and inner longitudinal layers and sometimes a thin middle layer of diagonal fibers. The longitudinal muscles form a continuous sheet in many sipunculans, but in some genera these muscles

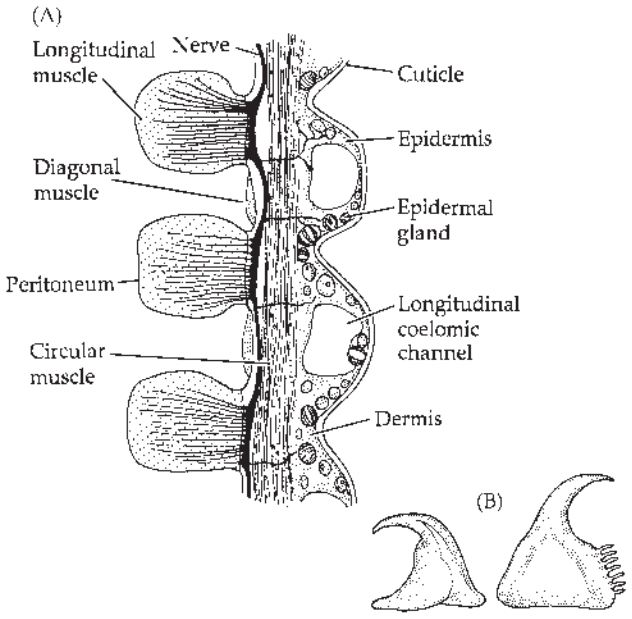

FIGURE 15.24 The sipunculan body wall. (A) The body wall of *Sipunculus nudus* (cross section). (B) Two types of cuticular hooks from sipunculans.

form distinct bundles or bands (e.g., *Phascolosoma*, *Phascolopsis*, *Siphonomecus*, *Siphonosoma*, *Sipunculus*, and *Xenosiphon*). This arrangement gives the internal surface of the body wall a ribbed appearance that is often visible through the animal's cuticle. While this character was once the basis for the family Sipunculidae, the family now has a more restricted definition, and it has been shown that this feature is homoplastic.

A peritoneum lines the body wall and the internal organs. The coelom is a continuous space, but peritoneal mesenteries form incomplete partitions supporting the organs. In addition to the main body coelom and the coelomic channels in the body wall, a separate fluid-filled "coelom" called the compensation system is associated with the tentacles. The hollow tentacles contain lined spaces that are continuous with one or two sacs (the **compensation sacs**) that lie next to the esophagus (Figure 15.25A,B). Upon eversion of the introvert, circular body muscles apply pressure on these sacs and force the contained fluid into the tentacles, causing their erection.

The fluid of the body cavity contains a variety of cells and other inclusions. There are both granular and agranular amebocytes of uncertain function, and red blood cells containing hemerythrin. Also contained in the coelomic fluid are unique and fascinating multicellular structures called **urns**, some of which are fixed to the peritoneum and some of which swim free in the fluid (Figure 15.25C,D). The urns accumulate waste materials and dead cells by trapping them with cilia and mucus.

Gas exchange apparently varies among species. It has been suggested that rock borers (e.g., *Phascolosoma*) and those that burrow in sediments of low oxygen content (e.g., *Themiste*) exchange gases largely across

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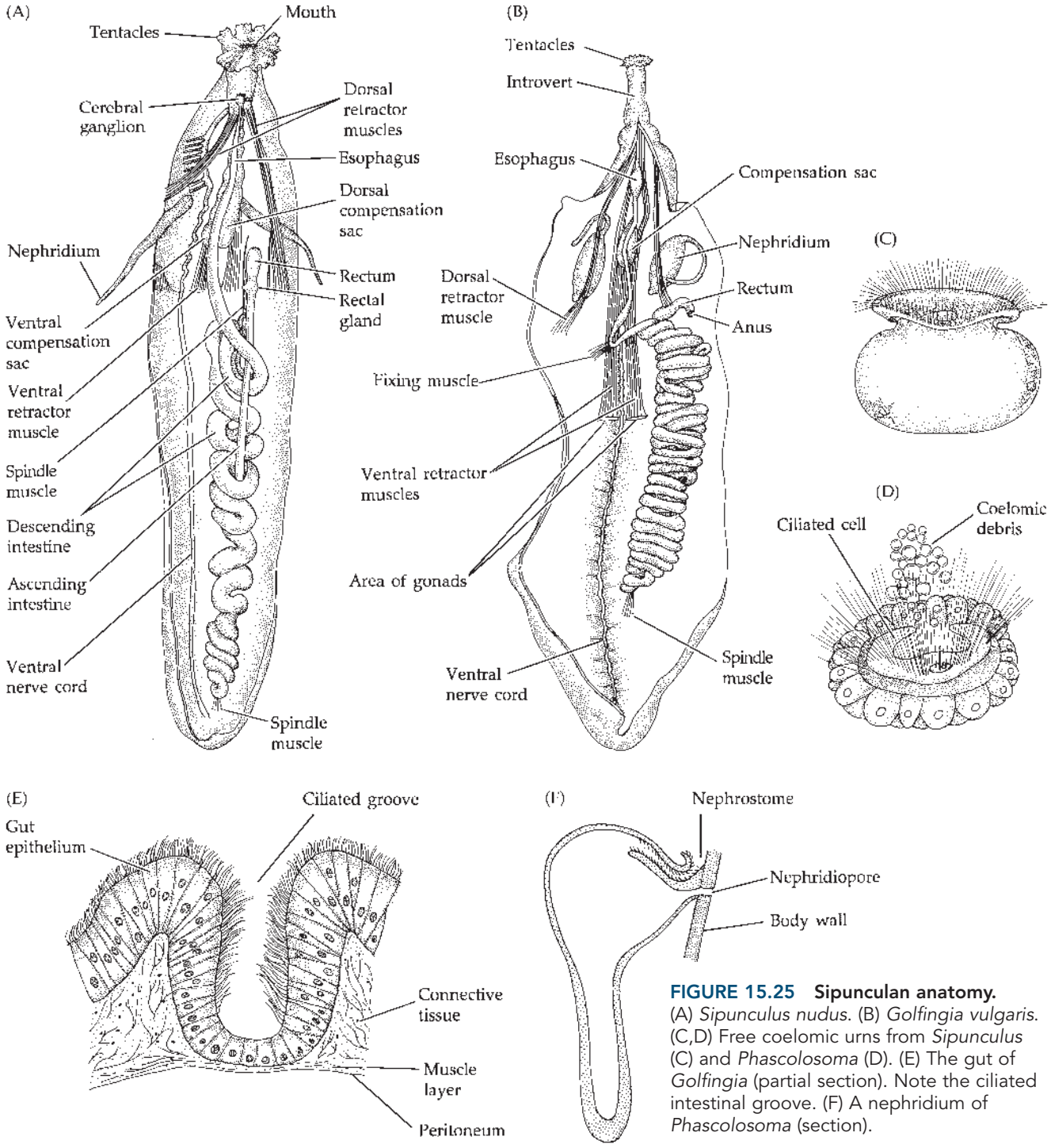

FIGURE 15.25 Sipunculan anatomy. (A) *Sipunculus nudus*. (B) *Golfingia vulgaris*. (C,D) Free coelomic urns from *Sipunculus* (C) and *Phascolosoma* (D). (E) The gut of *Golfingia* (partial section). Note the ciliated intestinal groove. (F) A nephridium of *Phascolosoma* (section).

the tentacles, which extend into the overlying water. Other burrowers with long introverts may use the body surface of both the tentacles and the introvert for gas exchange, whereas others, such as the large-bodied species of the genus *Sipunculus*, may use the entire body surface. The coelomic fluid in the body cavity and in body wall channels provides a circulatory medium, aided by diffusion and body movements. The erythrocytes that circulate in the coelomic fluid of sipunculans contain intracellular polymeric hemerythrin for storing and transporting oxygen.

Support and Locomotion

Sipunculans are sedentary creatures. The general body shape is maintained by the muscles of the body wall and the hydrostatic skeleton established by the large coelom. The body is essentially a fluid-filled bag of constant volume, so any constriction at one point is accompanied by an expansion at another. Burrowing in soft substrata is accomplished by peristalsis, driven by the circular and longitudinal muscles of the body wall and by the action of the introvert. Movement through algal holdfasts and

bottom rubble occurs in a similar manner. Some species with an anterior cuticular shield burrow into hard substrata and use the shield as a functional operculum to close the burrow entrance. Burrowing into hard substrata is probably accomplished by both mechanical and chemical means, the former using cuticular structures (such as spines and the posterior shield) as rasps, the latter facilitated by the secretions of epidermal glands.

The introvert is extended when the coelomic pressure is increased by contracting the circular muscles of the body wall. Withdrawal is accomplished by the retractor muscles, which pull from the mouth end, turning the introvert inward as the body wall muscles relax. When the introvert is fully extended, the tentacles are erected by increasing the pressure on the compensation sacs.

Sipunculans are highly tactile and strongly thigmotactic, requiring contact with their surroundings. Placed alone in a glass dish, they are rather inactive except for rolling the introvert in and out. However, if several sipunculans are placed together or with small stones or shell fragments, they soon respond by making contact with each other or surrounding objects.

Feeding and Digestion

There is surprisingly little information on the details of sipunculan feeding mechanisms. Indirect evidence from anatomy, gut contents, and general behavior suggests that these animals use different feeding methods in different habitats. Most of the sipunculans that can place their tentacles at a substratum-water interface are selective or nonselective detritivores (e.g., shallow burrowers, algal holdfast dwellers); they use the mucus and cilia on the tentacles to obtain food. Deeper burrowers in sand are direct deposit feeders. Some appear to be ciliary-mucus-suspension feeders, using the tentacles to extract organic material from the water. Sipunculans that burrow in calcareous substrata use spines or hooks on their introverts to retrieve organic detritus within reach and ingest the material by retracting the introvert. Limited data suggest that at least some sipunculans take up dissolved organic compounds directly across the body wall. Some workers have speculated that up to 10% of these animals' nutritional requirements may be met in this fashion.

Because the anus is located anteriorly on the dorsal side of the body, the digestive tract is basically U-shaped, although highly coiled (Figure 15.25A,B)—the coiled gut is unknown in any other annelid or invertebrate group. The mouth is terminal, located at the end of the introvert, and is wholly or partially surrounded by the peripheral tentacles (e.g., Sipunculidae) or lies near the nuchal tentacles (e.g., Phascolosomatidae). The mouth leads inward to a short, muscular stomodeal pharynx, which is followed by an esophagus that extends through the introvert and into the trunk. The midgut consists of a long intestine composed of descending and ascending portions coiled together, although this coiling is not observed in the Cambrian species. Studies comparing the expression patterns of regulatory "gut genes" of *Themiste* and other annelids (with uncoiled guts) revealed differences in persistence and extension of endodermal expression of *FoxA*, which could be related to the U-shaped gut and coiling. The gut is usually supported by a threadlike spindle muscle that extends from the body wall near the anus through the coils to the end of the trunk and by several fixing muscles connecting the gut to the body wall. The ascending intestine leads to a short proctodeal rectum, terminating in the anus.

The intestine is ciliated and bears a distinct groove along its length (Figure 15.25E). This ciliated groove leads ultimately to a small pouch or diverticulum (the rectal gland) off the rectum. The function of this groove and diverticulum is unknown. The lumen epithelium of the descending intestine contains a variety of gland cells that are presumably the sources of digestive enzymes.

Excretion and Osmoregulation

Most sipunculans possess one pair of elongate, saclike, tubular metanephridia with the coelomoducts becoming fused with the nephridia (a condition known as nephromixia; Figure 15.25A,B,F) located ventrolaterally at the anterior end of the trunk. Two genera (*Onchnesoma* and *Phascolion*) have but a single nephridium. Species in these genera tend to be asymmetrically coiled. The nephridiopores are located ventrally on the anterior region of the trunk. The nephrostome lies close to the body wall, near the pore, and leads to a large nephridial sac that extends posteriorly in the trunk.

Sipunculans are ammonotelic. Nitrogenous wastes accumulate in the coelomic fluid and are excreted via the nephridia. The urns also play a major excretory role by picking up particulate waste material in the coelom. The fate of wastes accumulated by urns is unknown, but at least some are probably transported to the nephridia. Urns originate as fixed epithelial cell complexes in the peritoneum, where they trap and remove particulate debris. They are also known to secrete mucus in response to pathogens in the coelomic fluid. Fixed urns regularly detach and become free-swimming in the coelomic fluid. Not only do urns effectively cleanse the coelomic fluid, but they also participate in a clotting process when a sipunculan is injured. Free urns can be seen by preparing a wet slide of fresh coelomic fluid. They are usually obvious, moving about like little bumper cars, trailing strands of mucus and bits of particulate matter.

Sipunculans are basically osmoconformers, and they are unknown from brackish and freshwater habitats. Under normal conditions, the coelomic fluid is nearly isotonic to the surrounding seawater. However, when sipunculans are placed in hypotonic or hypertonic environments, their body volume increases or decreases, respectively. Interestingly, the rates of volume change differ when the animal is exposed to these opposing

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environments, suggesting that sipunculans are better at preventing water loss than at preventing water gain. This situation may be due to a differential permeability of the cuticle or, perhaps, to some active mechanism of the nephridia. In any case, sipunculans rarely face severe osmotic problems in their usual environments, and even in laboratory experiments they are able to recover nicely from most conditions of osmotic stress.

Nervous System and Sense Organs

The general structure of the sipunculan nervous system is similar in many respects to that in other annelids. A bilobed cerebral ganglion lies dorsally in the introvert, just behind the mouth. Circumenteric connectives extend from the cerebral ganglion to a ventral nerve cord running along the body wall through the introvert and trunk (Figures 15.25A,B and 15.26). The adult ventral nerve cord is single, and there is no evidence of segmental ganglia. In *Phascolosoma agassizii*, a double ventral nerve cord forms initially but later fuses into a single cord, and neurogenesis initially follows a segmental pattern similar to that of annelids. Starting out with paired FMRFamidergic and serotonergic axons, four pairs of associated serotonergic perikarya and interconnecting commissures form one after another in an anterior–posterior progression. In late-stage larvae, the two serotonergic axons of the ventral nerve cords fuse, the commissures disappear, and one additional pair of perikarya is formed. These cells (ten in total) migrate toward one another, eventually forming two clusters of five cells each. These neural-remodeling processes result in the single nonmetameric central nervous system of the adult sipunculan. This ontogenetic example suggests that the ancestral sipunculan condition may have been a double ventral nerve cord like that found in some primitive annelids. Lateral nerves arise from the nerve cord and extend to the body wall muscles and sensory receptors in the epidermis.

Sensory receptors are widespread in sipunculans, but many are poorly understood. Tactile receptor cells are scattered over the body within the epidermis, as would be expected, and are especially abundant on and around the tentacles. Chemosensory **nuchal organs** are located on the dorsal side of the introvert in many species (Figure 15.26B). Many possess a pair of pigment-cup ocelli on the dorsal surface of the cerebral ganglion, and some have a so-called cerebral organ, consisting of a ciliated pit projecting inward to the cerebral ganglion. The cerebral organ may be involved in chemoreception or perhaps neurosecretion, as is similar in structure to that seen in nemerteans.

Reproduction and Development

Sipunculans possess reasonable powers of regeneration. Most species are able to regrow lost parts of the tentacles and even the introvert, and some can

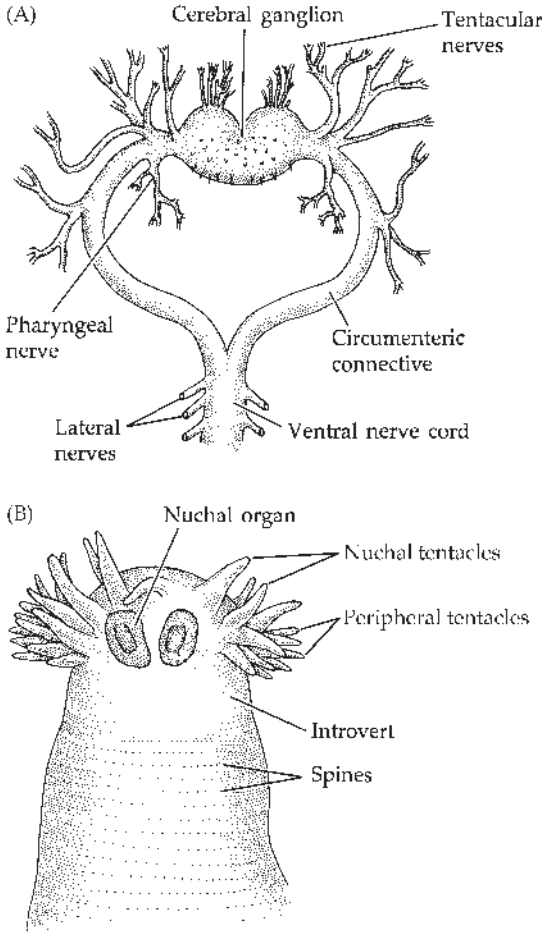

FIGURE 15.26 Sipunculan brains and nuchal organs. (A) Anterior portion of the central nervous system of *Golfingia*. (B) Anterior end of *Golfingia*. Note the nuchal organs.

regenerate portions of the trunk and the digestive tract. It was long believed that sipunculans could not reproduce asexually. However, in the 1970s it was discovered that at least some species do possess this capacity. The process takes place by transverse fission of the body, whereby the worm divides into a small posterior fragment and a larger anterior portion. Both portions then regrow the missing parts. Regeneration from the small posterior part is quite remarkable, since most of the trunk, anterior gut, retractor muscles, nephridia, introvert, and so on must be regrown.

Except for *Nephasoma minutum*, sipunculans are gonochoristic. (Facultative parthenogenesis has been reported in one species, *Themiste lageniformis*.) The gametes arise from the coelomic lining, often near the origins of the retractor muscles. Gametes are released into the coelom, where they mature. Ripe eggs and sperm are picked up selectively by the nephridia and stored in the sacs until released. The eggs are encased in a layered, porous covering. Males spawn first, probably in response to some environmental cue, and the presence of sperm in the water stimulates females to spawn.

Following external fertilization, the zygotes pass through typical spiralian development. In *Golfingia*

cleavage is spiral and holoblastic, but the relative sizes of micromeres and macromeres differ among species, depending on the amount of yolk in the egg. Although traditionally sipunculan embryos were described as having a "molluscan cross," which suggested a close relationship with the Mollusca, this character is now known to have been misinterpreted, and sipunculans are now considered to be an early but highly derived offshoot of Annelida.

The cell fates are the same as those in most typical spiralians. The first three quartets of micromeres become ectoderm and ectomesoderm; the 4d cell produces endomesoderm; and 4a, 4b, 4c, and 4Q form the endoderm. The mouth opens at the site of the blastopore, and the surrounding ectodermal cells grow inward as a stomodeum. The anus breaks through secondarily on the dorsal surface (Figure 15.27). The 4d mesoderm proliferates as two bands, as it does

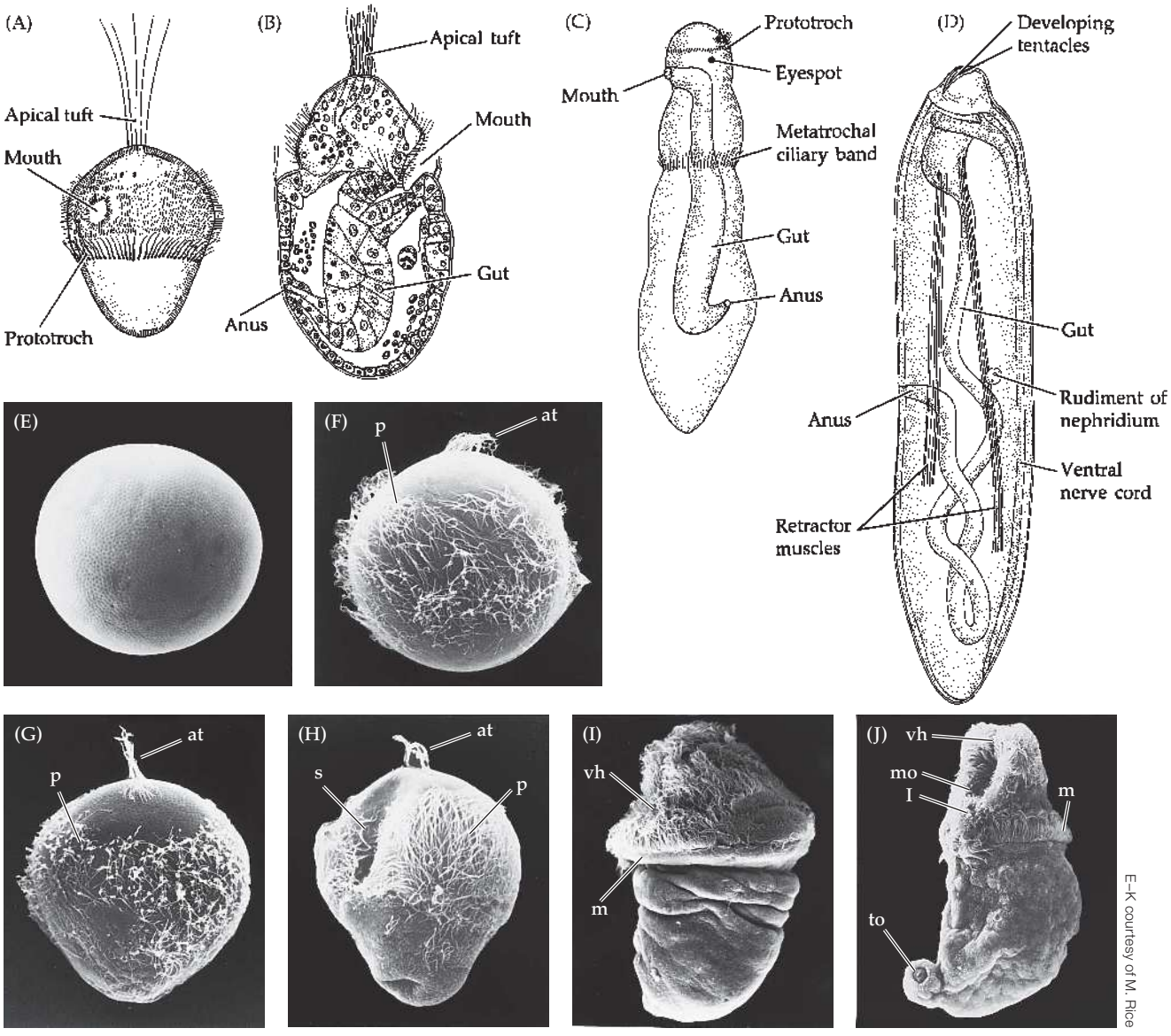

FIGURE 15.27 Sipunculan development. (A) Young trochophore of *Golfingia*. (B) A later larva of *Golfingia* (section), showing gut shape and placement of the anus. (C) The pelagosphera larva of *Phascolosoma* has an enlarged metatroch. (D) A juvenile sipunculan. (E–J) A series of SEMs showing growth from blastula to trochophore, and metamorphosis to the pelagosphera in *Siphonosoma*. Labels show apical tuft (at), lower ciliated lip (l), metatroch (m), mouth region (mo), prototroch (p), stomodeum (s), terminal attachment organ (to), ventral ciliated head (vh). (K) One-day-old juvenile of *Siphonosoma*. Note the coiled gut.

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in other annelids, but yields the major trunk coelom without segmentation.

Four different developmental sequences have been recognized among the sipunculans, including direct (e.g., *Nephasoma minutum*, *Phascolion cryptum*, *Themiste pyroides*) and indirect development. In direct development, the eggs are covered by an adhesive jelly and attached to the substratum after fertilization. The embryo develops directly to a vermiform individual that hatches as a minute juvenile sipunculan. The other three developmental patterns are indirect, involving various combinations of larval stages. In some species (e.g., *Phascolion strombus*), a free-living lecithotrophic trochophore larva develops and metamorphoses into a juvenile worm. The other two developmental patterns involve a second larval stage, the **pelagosphera larva**, that forms after a metamorphosis of the trochophore (Figure 15.27C). In some species, both the trochophore and the pelagosphera forms are lecithotrophic and relatively short-lived (e.g., some species of *Golfingia* and *Themiste*), while in others the pelagosphera larva is planktotrophic and may live for extended periods of time in the plankton (e.g., *Aspidosiphon parvulus*, *Sipunculus nudus*, members of the genus *Phascolosoma*).

The transformation of the trochophore to the pelagosphera larva involves a reduction or loss of the prototrochal ciliary band and the formation of a single metatrochal band for locomotion. The pelagosphera eventually elongates, settles, and becomes a juvenile sipunculan (Figure 15.27D).

Since the pelagosphera larva of some species are estimated to spend several months in the plankton and sipunculans display little morphological variation, a disproportionate number of species, when compared with any other marine worm groups, have been suggested to be cosmopolitan. However, detailed developmental and molecular analyses of several supposed cosmopolitan species have shown that cosmopolitanism cannot be the norm and that, instead, sipunculans have many cryptic or pseudocryptic species remaining to be properly described.

Thalassematidae: The Spoon Worms

Thalassematidae is a group of about 220 species of secondarily unsegmented annelids that, until recently, were regarded as their own phylum, Echiura. With their accepted placement as the sister group to Capitellidae within Annelida, it was recommended by Ryutaro Goto and colleagues in 2020 that the group be known by the first family-ranked taxon that was made for the group, Thalassematidae. The vermiform body is divided into an anterior, preoral proboscis and an enlarged trunk (Figure 15.28). The mouth is located at the anterior end of the trunk at the base of a proboscis groove, or gutter. The body surface may be smooth or somewhat warty, and it often bears chaetae (e.g., *Protobonellia*). The trunk may terminate in an anal lobe, which can contain glands, the secretions of which might be used during burrow construction. Most thalassematids are quite large. The trunk may be from a few to as many as 40 cm long, but the proboscis may reach lengths of 1–2 m (e.g., in *Ikeda*, Figure 15.29B). Some forms, such as the beautiful emerald green *Metabonellia*, show drastic sexual dimorphism, wherein "dwarf" males are less than 1 cm long (Figure 15.28E,F). *Bonellia,* and relatives such as *Metabonellia,* are also notable for females producing the compound bonellin, which appears to act as an antibiotic for the worm but also as a sex hormone to create dwarf males (see the Reproduction and Development section). Thalassematids are always benthic and marine, though a few species are known from brackish-water habitats. Most burrow in sand or mud or live in surface detritus or rubble. Some species typically inhabit rock galleries excavated by boring clams or other invertebrates. They are known from intertidal regions to a depth of 10,000 m.

Body Wall and Coelom

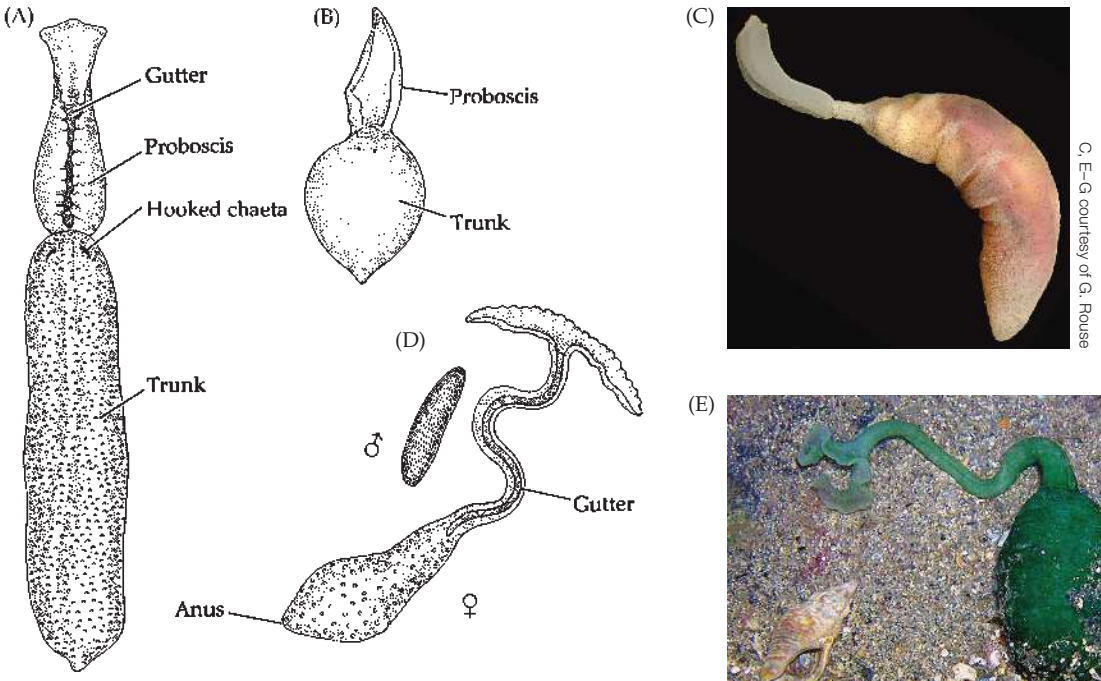
The body wall of thalassematids has an outer thin cuticle covering the epidermis, which is composed of a cuboidal epithelium and contains a variety of gland cells. Epidermal chaetae occur in some species at either the anterior trunk or the posterior trunk, or at both locations. Layers of circular, longitudinal, and oblique muscles form the bulk of the body wall, which is lined internally by the peritoneum. The epidermis is ciliated along the proboscis groove, or gutter. The coelomic cavity is spacious and occupies most of the trunk—it is interrupted only by partial mesenteries between the gut and the body wall. The coelomic fluid contains red blood cells, with hemoglobin in some species, and various types of amebocytes.

Support and Locomotion

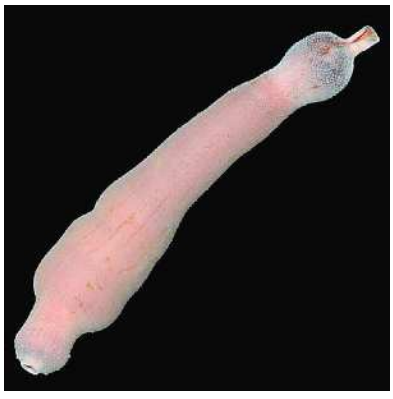
The large trunk coelom provides a hydrostatic skeleton against which the body wall muscles operate. The nonseptate coelom allows peristaltic movements as the animal burrows or moves through various sediments, gravel, or rubble. The proboscis can shorten and lengthen, but it does not roll in and out as does the introvert of sipunculans. This characteristic and the more conventional posterior position of the anus allow one to easily distinguish the two groups.

Feeding and Digestion

Most thalassematids feed on epibenthic detritus. Typically, the animal lies with the trunk buried in the substratum, with the proboscis extended over the



C, E–G courtesy of G. Rouse



Courtesy of A. Anker

FIGURE 15.28 Representative thalassematids. (A) *Echiurus*, anatomy. (B) *Listriolobus*, with the proboscis somewhat contracted. (C) *Anelassorhynchus porcellus* removed from under a rock, with proboscis somewhat contracted. (D) *Bonellia viridis*. Note the extreme sexual dimorphism between the large female (with proboscis extended) and the tiny male. (E) Female *Metabonellia haswelli* removed from the burrow, with forked and somewhat contracted proboscis and 15 cm trunk. The green color comes from the pigment bonellin. (F) A 1 cm long dwarf male of *Metabonellia haswelli*, removed from the nephridium of a female. (G) *Urechis caupo*, the "fat innkeeper." (H) *Onchestoma* sp., from Papua New Guinea. Montage sequence of an individual with peristaltic waves along its body.

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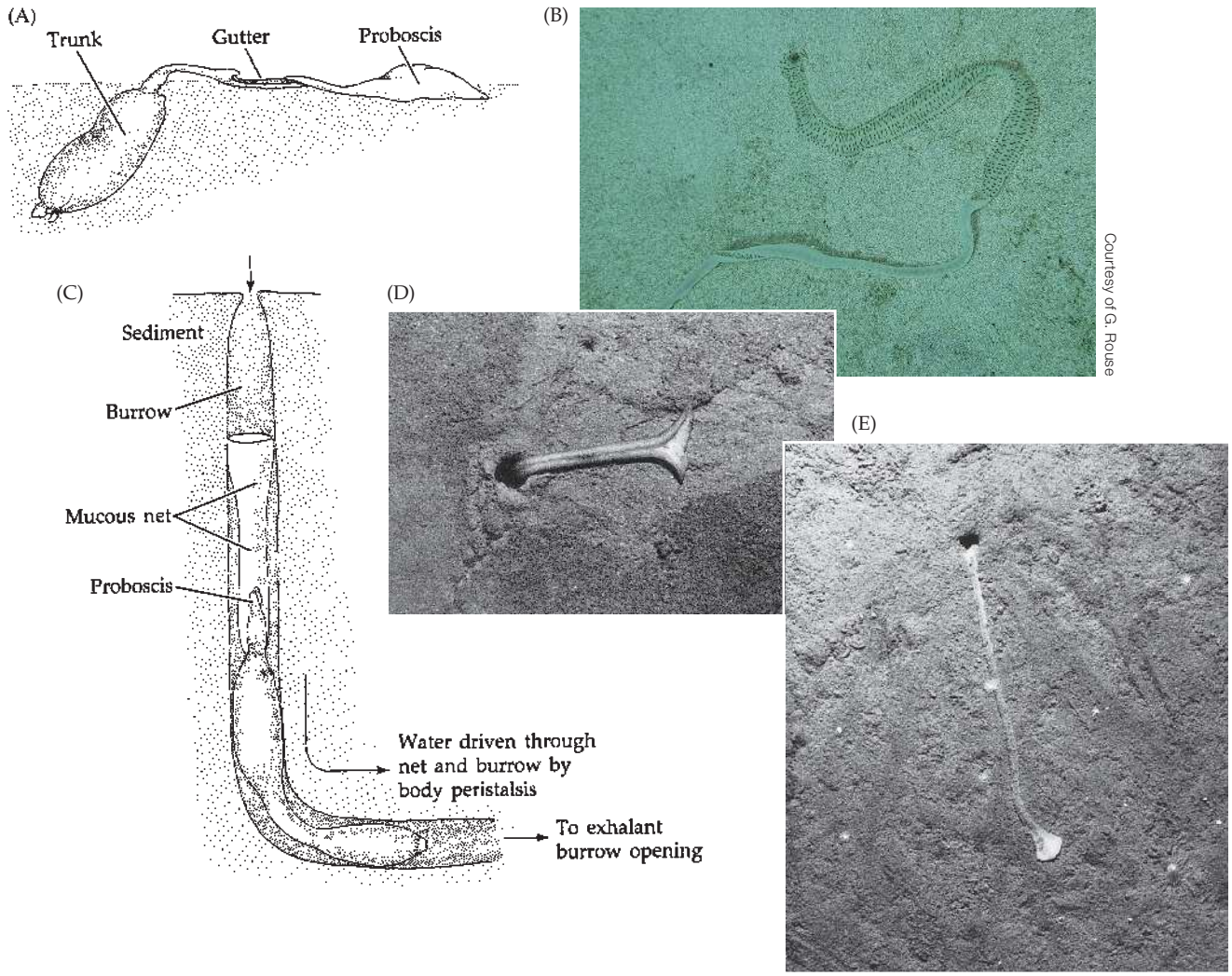

FIGURE 15.29 Feeding in thalassematids. (A) *Prometor grandis* in a "typical" thalassematid feeding posture, with the proboscis extended over the surface of the substratum. (B) *Ikeda* sp., with its long proboscis extending from burrow in sediment. (C) A portion of the burrow of *Urechis caupo*. The worm is in its feeding position. (D,E) The proboscides of deep-sea thalassematids living at depths of 2,635 m and 7,570 m, respectively.

sediment (Figure 15.28C,E,G,H and 15.29). Densely packed gland cells of the proboscis epithelium secrete mucus, to which organic detrital particles adhere. The mucous coating and the food are moved along a ventral proboscis groove, often called the gutter, by ciliary action into the mouth.

An interesting exception to the this feeding method occurs in *Urechis*, worms that live in U-shaped burrows in soft substrata (Figure 15.28G). They have a short proboscis, unlike those of more typical echiurans, and engage in mucous-net filter feeding. A ring of glands located near the proboscis-trunk junction produces a funnel-shaped mucous net, which is attached to the burrow wall by the proboscis. Water is drawn through the burrow and the sheet of mucus by peristaltic movements of the body, and suspended food particles as small as 1 μm are caught in the fine-meshed net. Periodically the animal grasps the food-laden net with its proboscis and ingests it. The whole process is somewhat like the feeding behavior of another annelid, *Chaetopterus*, as previously described.

The digestive tract is generally very long and coiled, leading from the mouth at the base of the proboscis to the posterior anus (Figure 15.30). The foregut may be regionally specialized as pharynx, esophagus, gizzard, and stomach, or it may be uniform along its length. The midgut usually bears a longitudinal ciliated groove, the **siphon**, which probably aids the movement of materials through the gut. It may also shunt excess water from the main midgut lumen, thereby concentrating food and facilitating digestion. The hindgut, or cloaca, varies in structure among

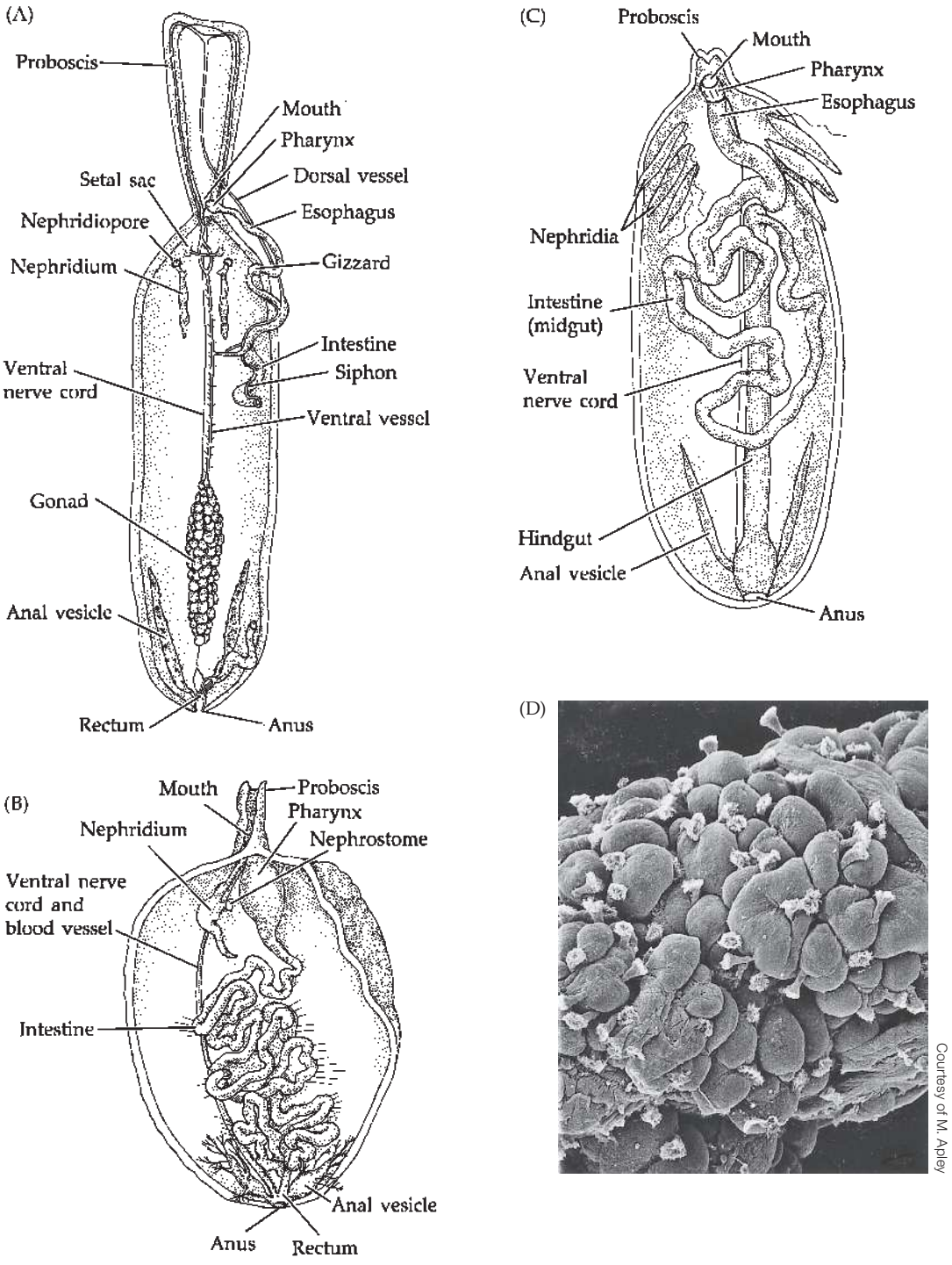

FIGURE 15.30 Internal anatomy of three thalassematids. (A) General internal anatomy, as seen in *Echiurus*. (B) A dissected *Bonellia viridis* female (proboscis cut off). (C) Internal organs of *Urechis*. Note especially the enlarged midgut. (D) SEM of anal vesicles and excretory funnels of *Urechis* at 60×. (B after P. A. Meglitsch.1972. *Invertebrate Zoology*. Oxford University Press, London.)

different species. In most thalassematids, the cloaca bears a pair of large excretory diverticula called anal vesicles (see the Excretion and Osmoregulation section). In some species of *Urechis* the cloaca is enlarged and thin walled. In such cases water is pumped in and out of the hindgut for gas exchange. Not much is known about digestive physiology in thalassematids. The epithelium of the midgut is rich in gland cells that presumably produce and secrete digestive enzymes. Digestion and absorption occur mainly in the midgut.

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Circulation and Gas Exchange

Most thalassematids possess a simple closed circulatory system, although it is absent from some forms (e.g., *Urechis*), in which case the coelomic fluid contains red blood cells with hemoglobin. The circulatory system generally includes dorsal and ventral longitudinal vessels in the trunk and median and lateral vessels in the proboscis (Figure 15.30A). There is no major pumping organ (except in *Ikeda*); the blood is transported by pressures generated from body movements and by the weak musculature of the vessel walls. The main site of gas exchange in *Urechis* is provided with oxygenated water by cloacal irrigation—water being pumped in and out of the anus by muscle action. In other thalassematids gas exchange also occurs across the surface of the proboscis.

Excretion and Osmoregulation

The excretory structures of thalassematids include paired metanephridia and anal vesicles (Figure 15.30). The number of nephridia varies: one pair in *Bonellia* and *Metabonellia*; two pairs in *Echiurus*; three pairs in *Urechis*; and hundreds of pairs in *Ikeda*. When only one or a few pairs are present, the nephridia are in the anterior region of the trunk and lead to nephridiopores on either side of the ventral midline. The degree to which these nephridia function in excretion is debatable; they seem to function primarily in picking up gametes from the coelom, having relinquished the major excretory responsibility to the anal vesicles. Thalassematids are relatively poor osmoregulators, providing an explanation as to why they are only generally in fully marine habitats.

The **anal vesicles** are hollow sacs arising as evaginations of the cloaca near the anus (Figure 15.30). Each vesicle bears from about a dozen to as many as 300 ciliated funnels that open to the coelom. Few studies have been conducted on the function of these structures, but they apparently pick up wastes from the coelomic fluid and remove the material to the hindgut and anus.

Nervous System and Sense Organs

The nervous system of thalassematids is simple, although constructed in a fashion generally like other annelids. An anteriorly located nerve ring extends around the gut and dorsally forward into the proboscis. Ventrally, in the trunk, the nerve ring meets at a subesophageal ganglion that connects with a seemingly single ventral nerve cord extending the length of the body (Figure 15.30A–C). There are no ganglia in this system and no obvious evidence of segmentation in adults. However, immunohistochemical methods and confocal laser-scanning microscopic studies have proposed a metameric organization of the nervous system in different larval stages of *Urechis caupo* and *Bonellia viridis*, which corresponds to the segmental arrangement of ganglia seen in other annelids. Lateral nerves arise from the ventral nerve cord and extend to the body wall muscles. Associated with the simple nervous system and infaunal sedentary lifestyle of thalassematids is the absence of major sensory receptors. These animals are touch sensitive, especially on the proboscis, which can retract quickly upon detecting vibrations or water movements.

Reproduction and Development

Asexual reproduction is unknown in thalassematids, and little work has been done on the powers of regeneration. At least a few have remarkable healing capabilities. For example, *Urechis caupo* (Figure 15.28G)—the "fat innkeeper"—is often found in bay muds that are subjected to heavy pressure from clam diggers. In some of these tidal flats, nearly every *Urechis* specimen bears scars, some nearly completely across the body—signs that the animal has survived cuts from the clammers' shovels.

Thalassematid sexes are separate. The gametes are produced in special "gonadal" regions of the ventral peritoneum and released into the coelom to mature. When ripe, the gametes accumulate in the nephridia (or nephridium, Figure 15.30A–C) until spawning occurs. The nephridia often swell enormously when packed with eggs or sperm. In most cases, epidemic spawning takes place and is followed by external fertilization.

Echiuran development is like that of most other annelids, with spiral cleavage and lecithotrophic trochophore larvae (Figure 15.31C) that may drift in the plankton for up to three months as they gradually elongate to produce young worms (Figure 15.31D). The prototroch and the episphere regions develop into the proboscis, which is thus equivalent to the prostomium and peristomium in other annelids. The region behind the proboscis forms the trunk. As with other annelids the 4d mesentoblast proliferates the main trunk coelom.

Thalassematids are well known for the sexual dimorphism and environmental sex determination found in a clade that includes genera such as *Bonellia*, *Ikeda*, and *Metabonellia*. In such species, the females are quite large, reaching lengths of up to 2 m, including the proboscis. The males, however, which can be from a few millimeters to a centimeter or so long, are simple bodied, and they often retain remnants of larval ciliation. They live on the female's body or in her nephridia (Figures 15.28D,F and 15.31A). Experiments have shown that when exposed to females, the larvae usually metamorphose into dwarf males, but they normally differentiate into females when developing in the absence of other females. This sexual determination is apparently caused by a masculinizing hormone produced by the skin of the female worm.

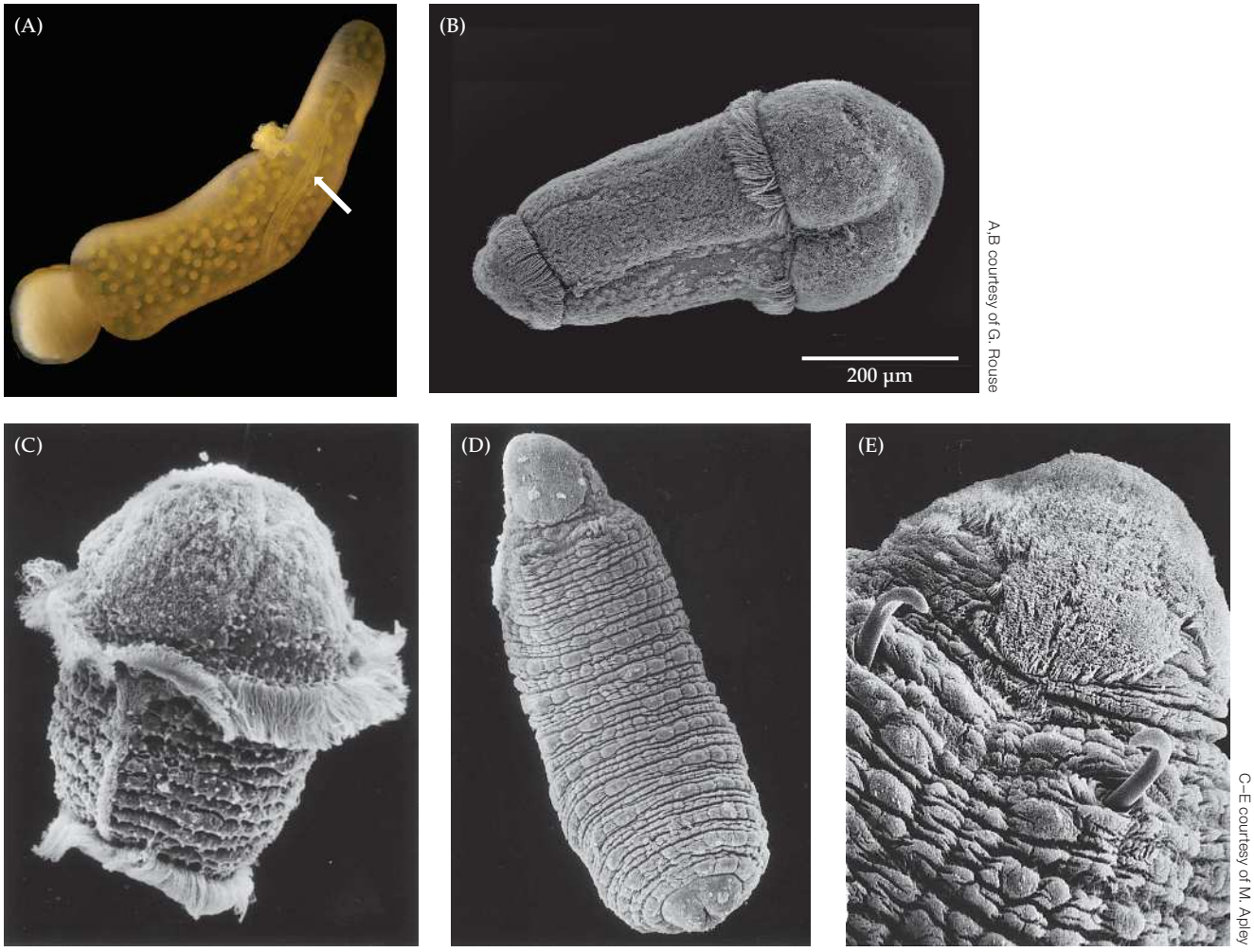

FIGURE 15.31 Reproduction in thalassematids. (A) A dwarf male (arrow) of *Metabonellia haswelli* inside the nephridium of a female, which is also packed with mature oocytes (yellow spheres). (B) *Metabonellia haswelli* trochophore larva in ventrolateral view, showing prototroch and telotroch and overall ciliation. This larva is sexually undifferentiated and will become a female if it settles on sediment, or a dwarf male if it settles on a female *Metabonellia*. (C) A *Urechis* trochophore larva (15 days) exhibits a prototroch, neurotroch, and telotroch. Note the segmented appearance of the trunk produced by distinct bands of epithelial cells. This has been dismissed previously as superficial but may be real. (D) A juvenile *Urechis*, after settling. (E) The anterior end of a juvenile (ventral view). Note the pair of hooked chaetae.

Siboglinidae: Vent Worms and Their Kin

Siboglinidae is an enigmatic family of tube-dwelling marine annelids containing four groups: Frenulata (Latin *frenulum,* "little bridle"), Vestimentifera (Latin *vestimentum*, "garment"; *ferre*, "to bear"), the genus *Sclerolinum* (Latin, *sclera,* "hard"; *linum*, "thread"), and the genus *Osedax* (Latin *Os*, "bone"; *edax*, "to devour"). Together these four worm groups comprise around 180 species of strange creatures that have been the subject of taxonomic and phylogenetic debate since their discovery some 100 years ago (Figures 15.1E, 15.32, and 15.33). We recognize the family name Siboglinidae, although for a while these worms were classified in two distinct phyla, Pogonophora and Vestimentifera. Frenulata (e.g., *Lamellisabella*, *Siboglinum*, *Polybrachia*), which contains most of the described species, live in thin tubes buried in sediments at ocean depths from 100 to 10,000 m. Most frenulates are less than 1 mm in diameter but can be 10 to 75 cm in length (Figure 15.32A–F). The tubes may be three or four times as long as the worm's body. The other main group, Vestimentifera (e.g., *Riftia*, *Tevnia*), is generally found at methane seeps or hydrothermal vents (Figure 15.32G–I). These can be very large worms, with *Riftia pachyptila* reaching well over 1 m in length and several cm in diameter. The anterior trunk of the body has a collar and two lateral extensions, which together make up the vestimentum, from which the group gets its name. One genus that is close to Vestimentifera, *Sclerolinum*, resides in wood fragments or other plant material or at seafloor mud volcanoes. A recently discovered group of siboglinids belongs to *Osedax* (Figure 15.32J–L), and all the more

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than 25+ known species consume the bones of vertebrates that have come to rest on the seafloor.

The body of most siboglinid species is divided into four regions (Figure 15.32A). The head (prostomium, as in other annelids) bears from 1 to over 200 separate thin palps or an elaborate crown of fused palps. These bear tiny side branches called **pinnules**. The **prostomium** (obscured in Vestimentifera) is followed by a short **peristomium** (possibly a segment) and then an elongate **trunk**, which is a single very lengthy segment

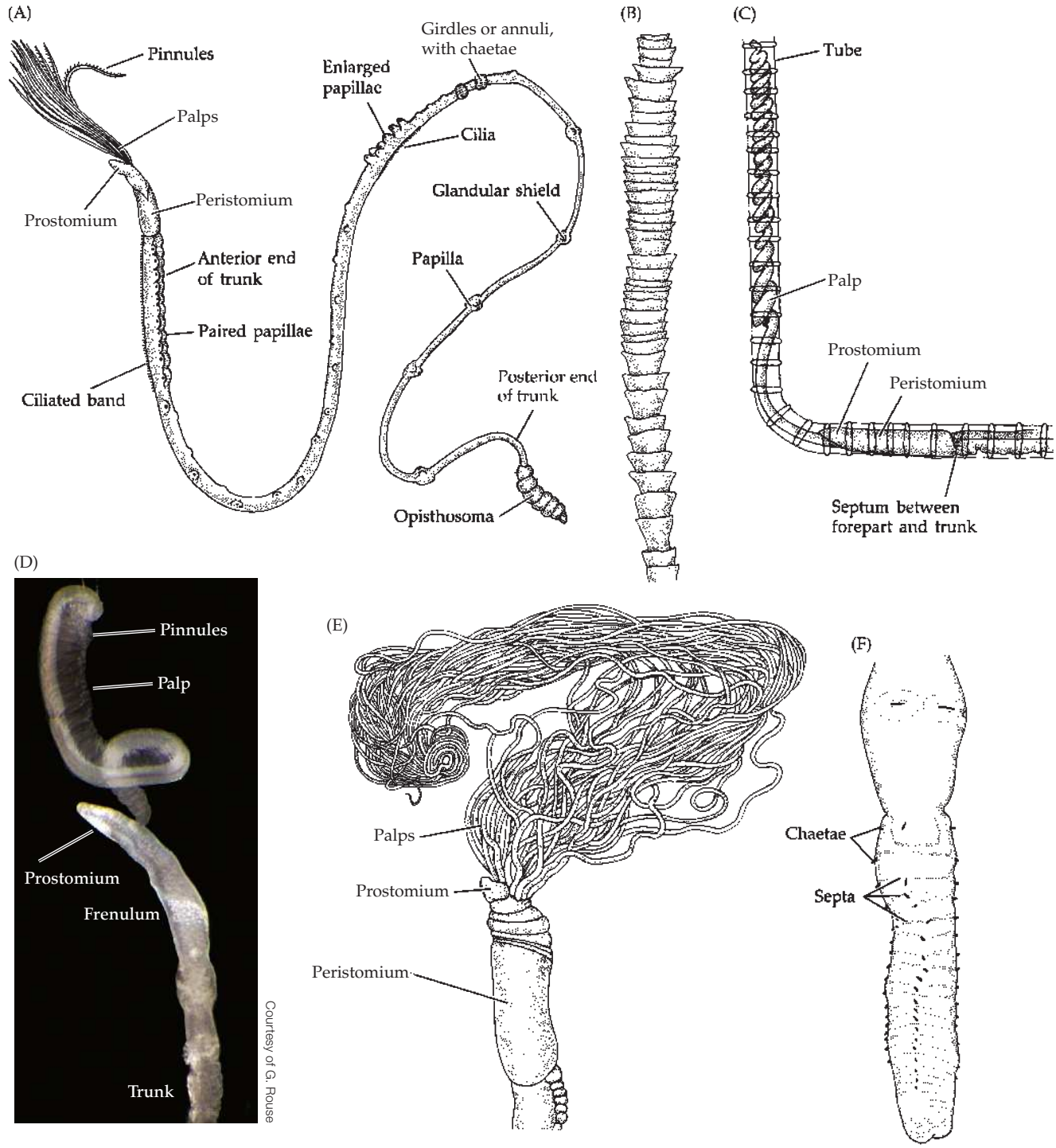

FIGURE 15.32 Siboglinidae. (A) A generalized frenulate siboglinid. (B) The tube of the frenulate *Lamellisabella*. (C) Anterior end of the single-palped frenulate *Siboglinum* in its tube. (D) Anterior end of living specimen of the frenulate *Siboglinum veleronis*. (E,F) Anterior and posterior ends of the frenulate *Polybrachia*. (E) The peristomium gives rise to multiple palps in *Polybrachia*. (F) Enlarged view of the opisthosoma of *Polybrachia*.

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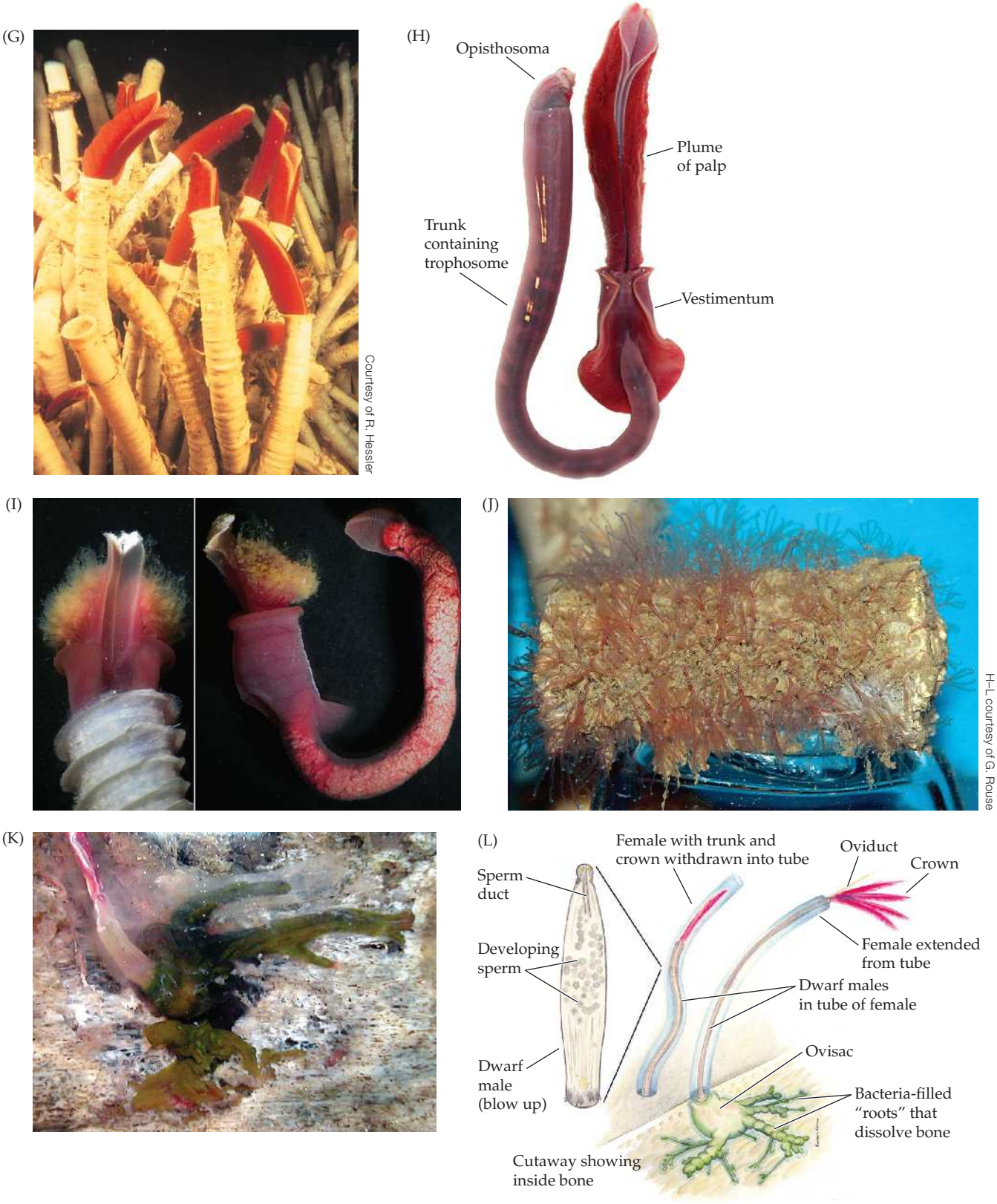

FIGURE 15.32 (*continued*) Siboglinidae. (G) Living specimens of the deep-sea, hydrothermal vent vestimentiferan *Riftia pachyptila*. (H) *Riftia pachyptila* dissected from tube showing body regions. (I) The vestimentiferan *Tevnia jerichonana*. Anterior end emerging from the white chitinous tube. Whole specimen removed from tube showing vestimentum, long trunk, and segmented opisthosoma. (J) Dozens of female *Osedax* emerging from a phalange (finger bone) of a gray whale. Each female has four palps. Note the large red blood vessels running along the trunk into the palps. (K) Female *Osedax frankpressi* with bone dissected away to reveal the ovisac and roots. (L) Diagram of *Osedax rubiplumus* with bone cutaway showing the major body regions. Note the placement of the harem of males in the transparent tube, where they lie near the female's oviduct. (A after After E. C. Southward 1984. In J. Bereiter-Hahn et al. [Eds.], *Biology of the Integument, Vol. 1*, pp. 376–388. Springer-Verlag, Berlin. https://link.springer.com/chapter/10.1007/978-3-642-51593-4_22; E after A. V. Ivanov. 1954. *Syst Zool* 3: 69–80.)

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often bearing various annuli, papillae, and a ring of chaetae. Behind the trunk is a series of segments with more chaetae called the **opisthosoma**.

Internally, siboglinids possess a closed circulatory system and well-developed nervous system. There is an anterior pair of large nephridia, as seen in close relatives such as Cirratulida and Sabellida. There is no digestive tract in the adults. There has been some confusion about the overall body orientation of these animals. For many years it was unclear whether the main longitudinal nerve cord was dorsal or ventral. Those who argued it was dorsal used this to justify the status of phylum for Pogonophora. Furthermore, developmental studies demonstrated a transitory gut in at least one species. However, it now seems clear that the nerve cord is ventral, as in other annelids and in other protostomes.

Siboglinid Taxonomic History

Siboglinids have a complicated, though interesting, history. They were first studied in the early 1900s, following the expedition of the Dutch research vessel *Siboga* in Indonesia. The dredged, partial specimens (lacking the segmented opisthosoma) were given to the eminent French zoologist Maurice Caullery, who studied them for over 40 years and published several papers describing these strange worms. In 1914, Caullery named the originally collected specimens *Siboglinum weberi* and created the family name Siboglinidae for them, although he was unable to assign them to any known phylum. He suggested they were close to deuterostomes such as hemichordates, as they had what he interpreted to be a dorsal nerve cord. The next species to be described, *Lamellisabella zachsi* some 20 years later by a Russian annelid taxonomist (P. V. Uschakov), was placed as a new subfamily of Sabellidae. However, a Swedish annelid worker (K. E. Johansson) suggested that Uschakov had the worms upside down and said they were not annelids and coined the name Pogonophora for them as a new class of animals (again, without a phylum assignment). The problem in interpreting dorsal and ventral was related to the fact that adult animals lacked a mouth and a gut, features that normally helped with orientation. In 1944, Pogonophora was made a phylum and part of the Deuterostomia. A Russian specialist, A. V. Ivanov, described many new species of frenulate siboglinids in the following decades and developed an elaborate taxonomy of genera and families, strongly emphasizing that Pogonophora were deuterostomes. However, in 1964, the first whole specimens were recovered, with the segmented opisthosoma, and an annelid affinity for the group was again proposed by some workers. The discovery of the very large Vestimentifera in the late 1960s and 1970s, associated with seeps and vents, further complicated the controversies surrounding these animals as they were interpreted by one important worker (M. L. Jones) as being closer to annelids than to Pogonophora, leading to the two separate phyla, Pogonophora and Vestimentifera. By the 1990s, both morphology and DNA data began to make it clear that these worms should all be placed within Annelida. To clear up any lingering confusion, the original name, Siboglinidae (designated by Caullery), is now used for the group.

The Siboglinid Body Plan

The Tube, Body Wall, and Body Cavity

The elongate tubes of most siboglinids are composed of chitin and scleroproteins secreted by the epidermis. The tubes are often fringed, flared, or otherwise distinctively shaped and are frequently banded with yellow or brown pigment rings (Figures 15.1E and 15.32B,G). The upper end of the tube projects above the substratum so the worms' palps can extend into the water. The palps of Siboglinidae can be single, as seen in most species (*Siboglinum*, Figure 15.32C,D), or there can be a pair, or four as in *Osedax* (Figure 15.32J–L), and they also range in number from 14–40 (e.g., *Polybrachia*, Figure 15.32E) to hundreds (e.g., vestimentiferans, Figure 15.32G–I). The palps can be free from each other (e.g., *Osedax*, *Polybrachia*) or partially fused together by the cuticle in frenulates such as *Lamellisabella* and in all vestimentiferans. Vestimentiferans have a paired structure called the obturaculum as part of the crown, and its origin has yet to be resolved.

In frenulates the region immediately behind the prostomium is what appears to be a segment that bears a cuticular structure called the **frenulum**, while in vestimentiferans the equivalent region is called the **vestimentum**. These regions are likely involved in tube secretion. The bulk of the body, the trunk, is a single very elongate segment. In frenulates there is a girdle of chaetae halfway along the trunk (lending support to the idea of a single segment), but in Vestimentifera there are no chaetae on the trunk. The chaetae in front of the first opisthosomal septum in these groups are at the end of the trunk and so correspond to the girdle of uncini-type chaetae on the trunks of other siboglinids (Figure 15.5Q). In most siboglinids (except for *Osedax*) the remainder of the body is a short multisegmented region called the opisthosoma that has peglike or hooked chaetae. The body surface is covered by a typical annelid cuticle. There can be small papillae in various parts of the anterior and trunk-bearing thickenings of the cuticle referred to as **cuticular plaques**. The epidermis is mostly a cuboidal to columnar epithelium and includes various gland cells, papillae, and ciliary tracts. Beneath the epidermis is a thin layer of circular muscle and a thick layer of longitudinal muscle, the latter developed as bands or bundles in some parts of the body. There is a spacious coelom in the trunk, and extensions extend into the head region and palps.

Nutrition

Siboglinidae lack a functional digestive tract, and for many years the method of nutrition of these relatively large worms was puzzling. Early suggestions were that the worms subsist on dissolved organic matter from the seawater flowing across their palps and from the muddy sediments in which the animals are buried. Other suggestions were that suspended particulate organic matter and/or bacteria were being filtered from the water column. These ideas have now been supplanted by the realization that all siboglinids have symbiotic bacteria in their bodies, from which they derive their nutrition. This was first discovered in *Riftia pachyptila* by then graduate student Colleen Cavanaugh and colleagues (1981). *Riftia* and its relatives inhabit the sulfide-rich waters near hydrothermal vents or methane seeps, and symbiotic chemoautotrophic Gammaproteobacteria inhabit a region in the siboglinids' trunk called the **trophosome**. These symbionts generate ATP by carrying out sulfide oxidation and by reducing CO_2 to organic compounds. Transfer of organic matter from symbionts to host occurs through translocation of amino acids and other compounds released from the bacteria and through direct digestion of symbiont cells. It appears that free-living stages of the bacteria are taken in by a transitory digestive tract or through the skin by early juvenile stages of the worms. A trophosome with symbiotic bacteria is now known for all siboglinids that have been examined. *Osedax* is unusual in this regard; rather than chemoautotrophic Gammaproteobacteria, the trophosome houses heterotrophic Gammaproteobacteria (belonging to the Oceanospirillales clade). This is because *Osedax* is relying on the organic material in the bone, such as collagen, and possibly on fats. The Oceanospirillales bacteria can exploit these and then, in turn, be digested by the worms. In *Osedax* there are "roots" of tissue (Figure 15.32J–L) that ramify through the bone, and these roots contain the bacteria. The epidermis of the roots secretes acid to dissolve hard bone, allowing access to the proteins and fats.

Circulation, Gas Exchange, Excretion, and Osmoregulation

All siboglinids possess a well-developed closed circulatory system (Figure 15.33A). The major blood vessels are dorsal and ventral longitudinal vessels that extend nearly the entire length of the body. The dorsal vessel is swollen as a muscular pump in the anterior of the body. As in other annelids, blood flows anteriorly in the dorsal vessel and posteriorly in the ventral vessel. Anteriorly, the vessels branch extensively. Some of these vessels supply parts of the head region and lead to afferent and efferent vessels in the palps (Figure 15.33B). Exchange also occurs in the posterior part of the body through a series of connecting blood rings. In *Osedax* the blood vessels branch into the roots.

The blood contains hemoglobin in solution and a variety of cells and cell-like inclusions. Gas exchange probably takes place across the thin walls of the palps. In the species that live near hydrothermal vents, problems of oxygen supply and sulfur toxicity are especially critical. These worms, such as *Riftia pachyptila*, live where hot, anoxic, sulfurous vent water mixes with the surrounding cold, oxygenated water. The animals are thus exposed to potentially dramatic fluctuations in ambient temperatures and oxygen and sulfide availability. These worms possess very high concentrations of hemoglobin in the fluid of their body cavity as well as in their blood. This hemoglobin appears to retain its high affinity for oxygen across a wide temperature range. Furthermore, their blood contains a unique sulfide-binding protein, which serves to concentrate the sulfur and prevent sulfide toxicity and to transport the sulfur to the chemoautotrophic bacteria. Interestingly, similar adaptations are known in the burrowing annelid *Arenicola*, which typically lives in anoxic muds in shallow marine environments.

A pair of large anterior metanephridia lies in close association with the circulatory system, as seen in the closely related Cirratulida and Sabellida. In some Vestimentifera there may be a single fused exterior pore or two pores.

Nervous System and Sense Organs

The nervous system of siboglinids is largely intraepidermal. A well-developed nerve ring just behind the prostomium bears a large ventral ganglion. A single ventral nerve cord arises from this ganglion and extends through all body regions. In many cases there are ganglia (or at least nerve "bulges") at the junctions of the various body regions, and there is an enlargement of the nerve cord in the anterior part of the trunk. In the frenulates where this has been studied, the opisthosoma contains three distinct nerve cords that apparently bear segmental ganglia. The vestimentiferan nervous system has a single opisthosomal nerve cord without ganglia. The bone-devouring *Osedax* also has an intraepidermal nervous system, including the ventrally located brain! Sense organs are poorly understood. The palps probably contain tactile receptors, as the worms are sensitive to vibrations and can rapidly retract into their tubes if disturbed. No siboglinids are known to have eyes or nuchal organs.

Reproduction and Development

Nothing is known about asexual reproduction or regeneration in these animals. While there is simultaneous hermaphroditism known from one species (*Siboglinum fiordicum*), the sexes in Siboglinidae are otherwise separate, and worms possess a pair of gonads in the trunk. In males of frenulates and vestimentiferans,

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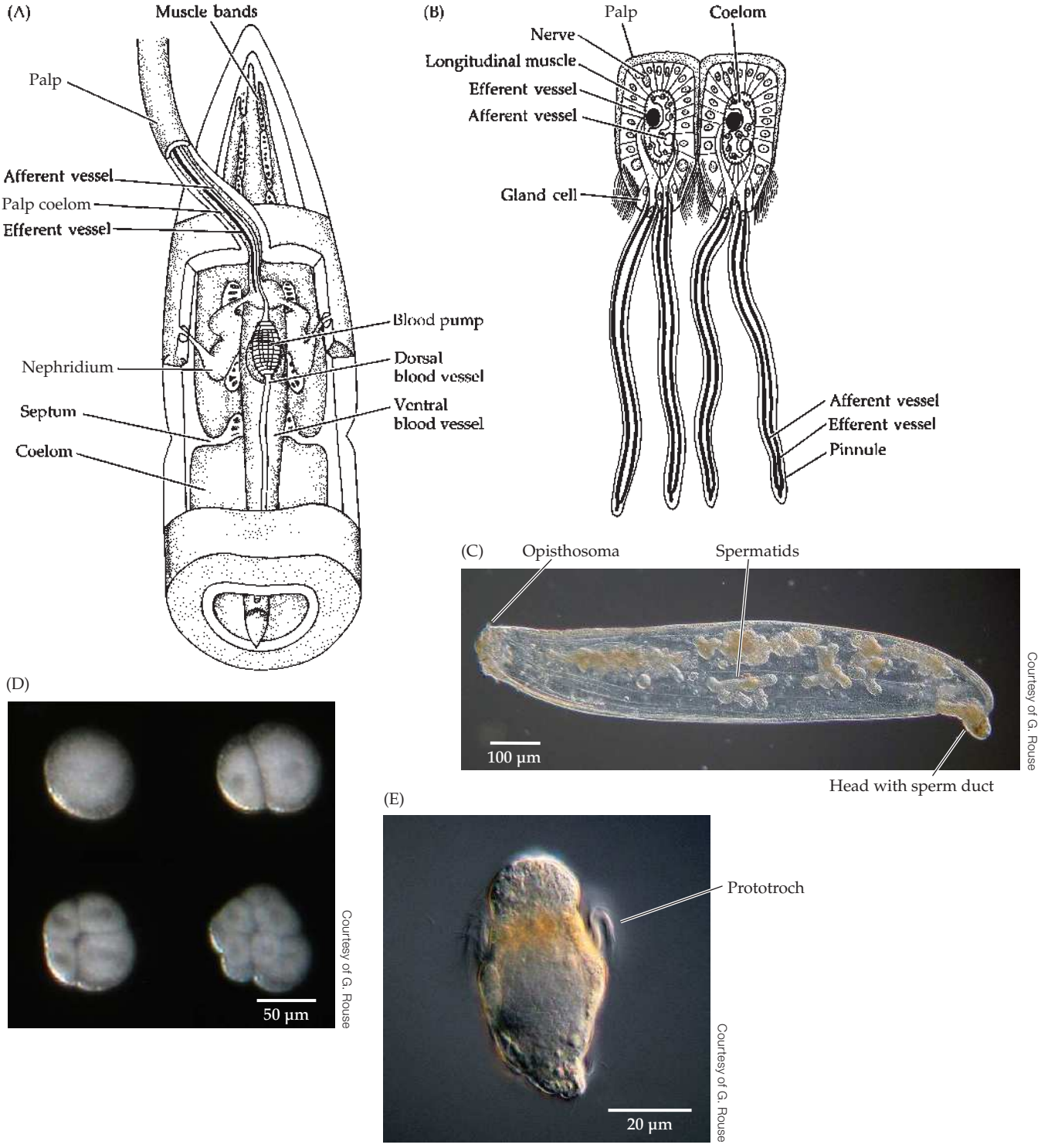

FIGURE 15.33 Siboglinidae anatomy. (A) The anterior end of the frenulate *Siboglinum* (cutaway dorsal view). (B) Two palps of the frenulate *Lamellisabella* (cross sections), showing elements of the circulatory system. (C) Dwarf male of *Osedax rubiplumus*. The male is basically an arrested larva; stage with a two-segmented opisthosoma. The body cavity contains developing sperm. (D) Fertilized egg and first three cleavage stages of *Osedax*. The eight-cell stage clearly shows normal spiral cleavage occurs in Siboglinidae. (E) Trochophore larva of *Osedax* (prior to formation of the opisthosoma). (A after A. V. Ivanov. 1962. *Pogonophora*. Academic Press, London.)

paired sperm ducts extend from the testes to gonopores located near the anterior end of the trunk. As sperm move along these ducts, they are packaged. In frenulates the package is a spermatophore, with an envelope around the sperm, while in vestimentiferans the sperm are in clusters called spermatozeugmata. *Osedax* is unusual in that the males are generally dwarfs (Figures 15.32L and 15.33C), which can be more than 100,000

times smaller than the female—developmentally arrested larvae that develop sperm. These live in the tubes of the females and use their limited yolk supply to make sperm before they die. A female can have up to 600 males in a "harem."

The female system of frenulates and vestimentiferans includes a pair of ovaries from which arise oviducts leading to gonopores on the sides of the trunk. In *Osedax*, the females have a large ovisac that lies in the "host" bone and can be up to one-third of the body mass. This leads to a single oviduct that runs dorsally along the trunk and ends in the plume of palps. The eggs of all siboglinids are spheroidal to elongate, and development is lecithotrophic.

Fertilization is internal in Vestimentifera and *Osedax*, and this is likely also the case for Frenulata. In frenulates and vestimentiferans, males release spermatozeugmata or spermatophores, which drift to the plumes and tubes of nearby females. The sperm end up in the oviduct, which can have sperm storage areas. In *Osedax* the sperm somehow end up in the ovary itself. Brooding of larvae in the tube occurs in some frenulates, while in all vestimentiferans and *Osedax* the fertilized eggs are apparently released into the water column. Individual *Osedax* females can release 400–800 eggs daily, and the larvae can live for several weeks in the plankton. Vestimentifera also produce numerous eggs, and these also live for a month or more as larvae. Such high fecundity is necessary, as the habitats for these worms are very restricted and most larvae are likely unsuccessful in finding a suitable place to settle.

Cleavage is spiral in all siboglinids where this has been studied, and early reports of radial cleavage now appear to be erroneous (Figure 15.33D). Trochophore larvae develop (Figure 15.33E) and add some segments that will later become the opisthosoma. In the dwarf male of *Osedax*, two segments are formed that have hooked chaetae. A transitory digestive tract occurs during development and in juveniles of at least some vestimentiferans and frenulates. Inner cells near the presumptive posterior end of the embryo proliferate spaces within the opisthosomal segments as they develop, a process strikingly like the teloblastic growth and schizocoely seen in other annelids.

Hirudinea: Leeches and Their Relatives

Hirudinea (Figures 15.34–15.40) are clitellate annelids whose closest relatives are Lumbriculidae. They have a fixed number of segments, which are traditionally numbered with Roman numerals (Figure 15.34C). In an unusual tradition with respect to other annelids, the prostomium and peristomium (when present) are counted as segments, and so the bodies of branchiobdellids are counted as having 15 segments (though they lack a prostomium), acanthobdellids have 29 or 30 segments (lacking both a prostomium and peristomium), and hirudinidans (leeches) have 34 segments. These segments are generally obscured by superficial annulations, giving the impression of many more segments (Figure 15.34). Externally, Hirudinea generally feature anterior and posterior suckers and clitellum, while lacking parapodia and chaetae (though Acanthobdellida have chaetae in a few anterior segments). Internally, acanthobdellids have a coelom and segmental septa typical of annelids, while in branchiobdellids there are at least a few segments with coelomic spaces. However, the coelom of leeches is reduced to a series of interconnected channels and spaces, without serially arranged septa.

We usually think of leeches as the bloodsuckers popularized in adventure stories and films, and this is arguably the ancestral state for Hirudinida. However, many hirudinidans are free-living predators, and some are scavengers. Most range from less than 0.5 to about 2 cm in length, although one species from tropical South America, *Haementeria ghilianii*, may reach 45 cm in length. Acanthobdellids and branchiobdellids are exclusively freshwater groups, while leeches occur in both fresh and salt water, and many live in moist terrestrial environments as well. Those that are full- or part-time parasites feed on the body fluids of a variety of vertebrate and invertebrate hosts. Some of these leeches serve as the intermediate hosts and vectors for certain protist, nematode, and cestode parasites.

Many Hirudinea are cylindrical, while others are flattened dorsoventrally. The body is usually divisible into five regions, although the points of division are somewhat arbitrary. The anterior-most head region is composed of the much reduced (or absent) prostomium and peristomium and the anterior body segments. The anterior region usually bears several eyes and a ventral mouth surrounded by the oral or anterior sucker (note the sucker is lacking in *Acanthobdella peledina*). In leeches, segments V–VIII form the preclitellar region, followed by the clitellar region (segments IX–XI). The clitellum is only apparent during periods of reproductive activity. The postclitellar or midbody region comprises segments XII–XXVII. The posterior region of the body includes the ventrally directed posterior sucker formed from seven fused segments (XXVIII–XXXIV). In branchiobdellids and acanthobdellids the counts are different, owing to their smaller numbers of segments.

Other than the suckers, gonopores, and nephridiopores, Hirudinea have few distinctive external features. In a few forms the body surface bears tubercles, and some such as the piscicolid *Branchellion* have lateral gills (Figure 15.34D). Chaetae are present on the first few segments of acanthobdellids, but they do not occur in any other Hirudinea.

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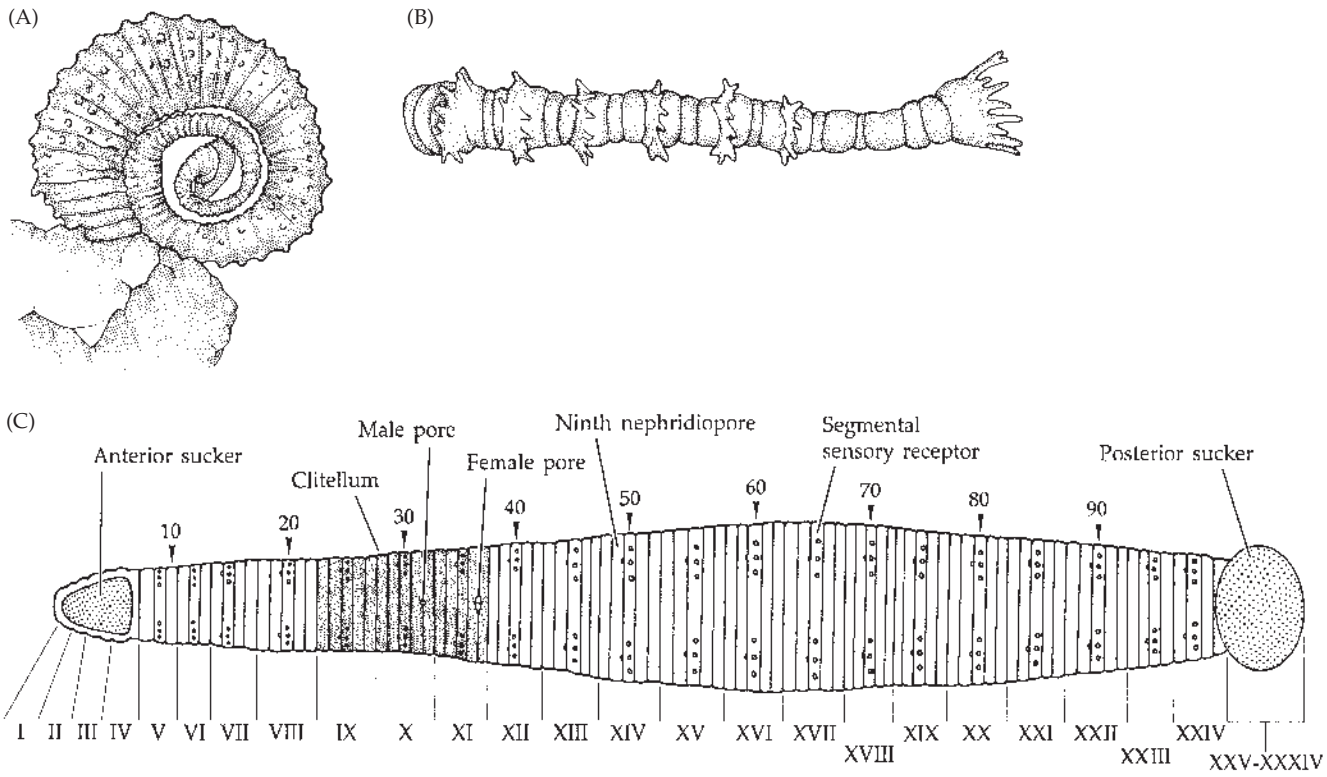

Courtesy of G. Rouse

FIGURE 15.34 Representative Hirudinea. (A) *Acanthobdella peledina* (Acanthobdellida), a part-time parasite of freshwater fishes. (B) *Stephanodrilus* (Branchiobdellida). These small (less than 1 cm) worms live on freshwater crustaceans, especially crayfish. (C) Ventral view of *Hirudo medicinalis* (Hirudinida). Roman numerals indicate true segments; arabic numbers indicate superficial annuli. (D) *Branchellion parkeri* (Branchiobdellida).

The Hirudinean Body Plan

Body Wall and Coelom

A cross-sectional view of a leech is dramatically different from that of other annelids, in large part because of a thick dermal connective tissue layer beneath the epidermis and the reduction of the coelom (Figure 15.35). The typical circular and longitudinal muscles are present, as well as bands of dorsoventral and diagonal (oblique) muscles between the circular and longitudinal layers. The dense dermis fills the areas between the muscle bands. Septate coelomic compartments are present only in acanthobdellids (in the first five segments) and in the midbody region of branchiobdellids. In all Hirudinea, the coelom is limited to various channels and small spaces. These augment the circulatory system in rhynchobdellids (proboscis leeches) and completely replace it in arhynchobdellids (jawed leeches).

Support and Locomotion

Except for acanthobdellids, Hirudinea show a solid body construction, and the absence of a spacious coelom precludes kinds of locomotion seen in other annelids. They do not burrow but are mostly surface dwellers, and the suckers in branchiobdellids and hirudinidans serve as the points of contact with the substratum against which the muscle action can operate (Figure 15.36). Beginning with the posterior sucker attached, the circular muscles are contracted, making the entire body elongate forward, and then the anterior sucker is attached. Then the longitudinal muscles contract, shortening the body and drawing the posterior end forward. Some leeches are also capable of swimming by dorsoventral body undulations; this behavior is an important mechanism for locating and contacting nonbenthic hosts.

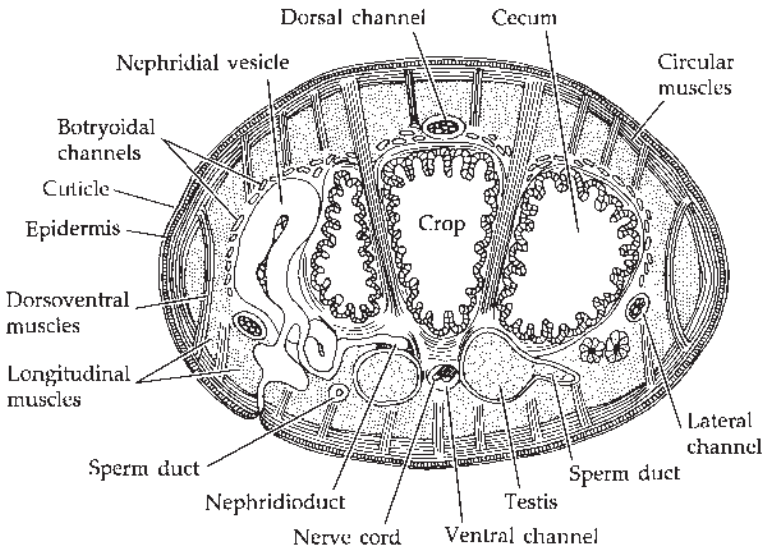

FIGURE 15.35 Body wall and general internal organization of *Hirudo* (cross section). The original circulatory system has been lost and replaced by coelomic channels.

Feeding and Digestion

Like that of most other annelids, the leech digestive tract includes a foregut, midgut, and hindgut (Figure 15.37). The foregut, as mentioned earlier, includes a mouth, buccal cavity, jaws or proboscis, pharynx, and esophagus. There are also masses of unicellular salivary glands that secrete hirudin in the jawed bloodsuckers and may produce enzymes to aid penetration of the proboscis in those parasitic forms that lack jaws. Posterior to the esophagus is the enlarged midgut, usually called the stomach or crop. This region bears large ceca in most leeches, providing a large storage capacity as well as a high surface area. In some kinds of leeches, the posterior midgut is structurally differentiated from the anterior portion. A short rectum connects the midgut to the anus, located dorsally near the junction of the body and the posterior sucker. Little is known about digestion in Hirudinea, except for some fragmentary information on blood-sucking leeches. Midgut enzymes apparently are limited to exopeptidases, which probably accounts for the extremely slow rate of digestion in these animals (a medicinal leech may take several months to digest the contents of a full blood meal).

Assessment of the distribution of blood-feeding and other feeding modes across the phylogeny of Hirudinida has led to the conclusion that blood feeding is the ancestral condition for the group, with several losses of this feeding mode across the group. The acanthobdellids *Acanthobdella peledina* and *Paracanthobdella livanowi* live on the skin, usually of fin rays, of freshwater fishes and suck the blood of their hosts, though they have been shown to also eat insect larvae. *Acanthobdella peledina* is found across northern Europe and Russia with *P. livanowi* limited to the Kamchatka Peninsula. There is a record also from Alaska, though the species identification needs further assessment. Branchiobdellids are tiny worms that live on freshwater crayfish. The anterior end of the pharynx bears a pair of toothed jaws (Figure 15.37). These animals eat other epizoites living on the host, but they also feed on the host's eggs and body fluids.

The majority of Hirudinida lineages ranked as families are ectoparasites that feed by sucking the blood or other body fluids from their hosts. The rest are predators on small invertebrates or scavengers on dead animal matter. Feeding involves either a protrusible pharyngeal proboscis or cutting structures in the form of slicing jaws or stylets. Members of the paraphyletic Rhynchobdellida possess a pharyngeal proboscis but lack jaws, whereas members of the clade Arhynchobdellida lack a proboscis but nearly all have jaws (Figure 15.34). Because of their medical importance, much work has been done on leeches, especially those that affect livestock, game animals, or humans. Blood-sucking leeches are not especially host specific, and most do not remain attached to a single host for long periods of time; many of these leeches may feed by other means when not attached to a suitable host. A few species of leeches feed exclusively on invertebrate hosts, including annelids (even other leeches), gastropods, and crustaceans, but most of them parasitize vertebrates. Some leeches are parasitic on vertebrates. For example, most Piscicolidae (Rhynchobdellida) feed on the blood of fishes (including some deep-sea and hydrothermal vent fishes (Figure 15.37D), whereas Ozobranchidae (another family of

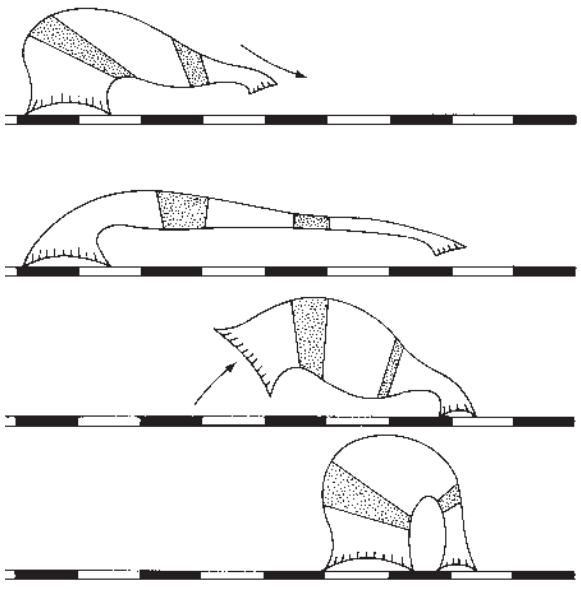

FIGURE 15.36 Locomotion in a leech. Moving left to right, using the anterior and posterior suckers to progress in "inchworm" fashion.

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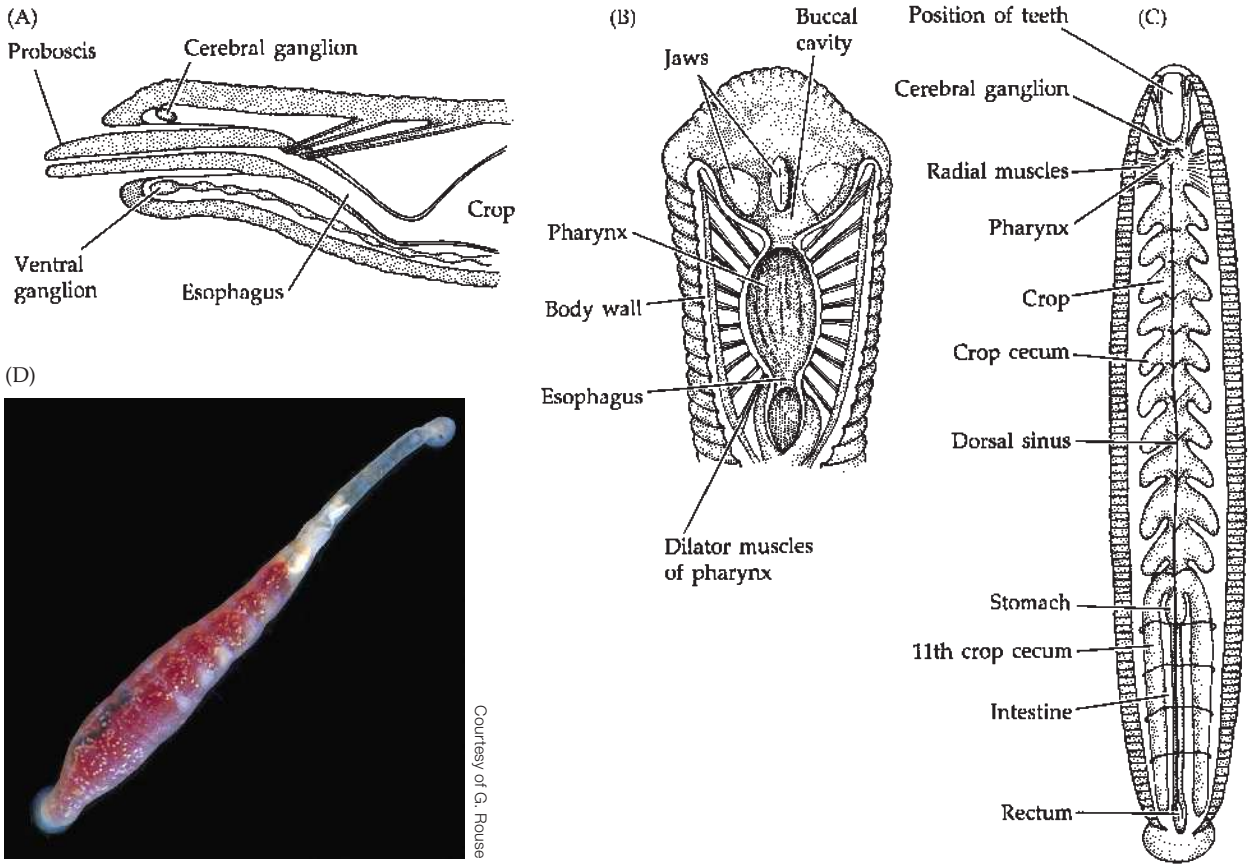

FIGURE 15.37 Feeding structures and digestive tract of leeches. (A) The anterior end (longitudinal section) of a rhynchobdellid leech. (B) The anterior end of an arhynchobdellid leech (cutaway view). Note the arrangement of the jaws and the musculature of the sucking pharynx. The oral aperture is pressed against the host's skin, and the three jaws are rocked to and fro, slicing into the skin. (C) Basic gut structure of *Hirudo*. (D) *Johanssonia*, a piscicolid leech found on the seafloor at a methane seep, full of blood taken from a fish host.

Rhynchobdellida) seem to prefer aquatic reptiles such as turtles and crocodilians.

The European medicinal leeches such as *Hirudo medicinalis* and *H. verbana*, which normally feed on amphibians, will obligingly consume human blood. Overcollecting has meant that *H. medicinalis* is now classified as Near Threatened by the IUCN, and it is protected across much of its range. The North American medicinal leech is *Macrobdella decora*, and other species are used for medicinal purposes in Asia. The common name is derived from using these leeches to draw blood from people afflicted with a wide range of maladies for which such "bleeding" was once thought to be curative or restorative. Today, medicinal leeches are used to reduce hematomas in areas of the body that are difficult to treat surgically, and to avoid leaving scars. The anticoagulant pumped into the wound by the leech (hirudin) allows blood to continue to drain, even after the leech has been removed, and so promotes healing. In addition to the anticoagulant, some leeches produce several other chemicals, including anesthetics and vasodilators. When feeding, the leech anchors to the host by the suckers and presses the mouth against the surface of the host's body. Jawed leeches have three bladelike jaws, each shaped like a half circle. The jaws are set at roughly 120° angles to one another, so the cutting edges form a Y-shaped incision. Muscles rock the jaws to and fro, making slices in the host's skin. The leech releases an anesthetic as it makes its incisions, then it secretes hirudin into the wound, and blood is sucked from the host by the muscular pharynx. The anesthetic desensitizes the victim's skin, so the worms can go unnoticed while they take their blood meal. While the predatory leeches eat frequently, the bloodsuckers feed at widely spaced, very irregular intervals, depending on the availability of hosts. When they do feed, they gorge themselves with several times their own weight in blood (Figure 15.37D).

Circulation and Gas Exchange

Many leeches are relatively large and quite active. The drastic reduction of the coelom has led to a flattening of the body and the formation of extensive gut ceca or diverticula in some lineages. Both reduce internal diffusion distances. In Rhynchobdellida this system is a

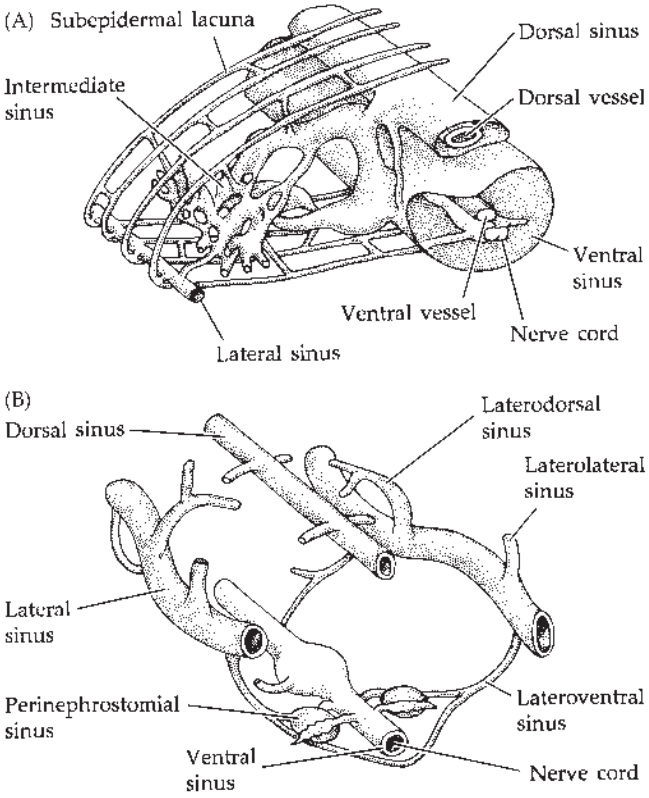

FIGURE 15.38 Coelomic and circulatory systems of two leeches. (A) A portion of the circulatory and coelomic systems of *Placobdella*, a rhynchobdellan leech in which the circulatory system persists and is associated with the coelomic channels. (B) A portion of the coelomic system in *Hirudo*, an arhynchobdellid leech. Here the circulatory system has been completely replaced by coelomic channels.

combination of a true closed circulatory system and the reduced coelomic spaces; in the Arhynchobdellida, the original circulatory system is completely replaced by one derived entirely from the reduced coelom. In both arrangements the circulatory fluid is moved through the system by the action of contractile vessels and by general body movements (Figure 15.38). Gas exchange is accomplished by diffusion across the body wall; gills are present only in some ozobranchids and piscicolids. Some leeches possess hemoglobin in solution in the circulatory fluid, thought to account for about 50 percent of their oxygen-carrying capacity.

Excretion and Osmoregulation

The excretory structures of Hirudinea are paired and segmentally arranged metanephridia that are usually absent from several anterior and posterior segments. The nephrostomes are ciliated funnels associated with coelomic circulatory vessels (where present). Ammonia is the main nitrogenous waste product eliminated via the nephridia. Apparently, particulate waste materials are engulfed by phagocytes, both in the coelomic fluid and in the "mesenchyme," but the eventual disposition of this material is not known.

Nervous System and Sense Organs

The nervous system of leeches has received, and continues to receive, a great deal of attention from biologists. The leech nervous system—even that of large leeches—is composed of very few neurons, and these individual nerve cells are sufficiently large that their circuitry has been traced in detail.

The nervous system includes a cerebral ganglion that is usually set back from the anterior end of the body at about the level of the pharynx (Figure 15.39). The cerebral ganglion, circumenteric connectives, and subenteric ganglion together form a nerve ring around the foregut. Two longitudinal nerve cords arise from the ventral portion of this ring and extend posteriorly through the body. The nerve cords are separate in some areas, but the segmental ganglia are fused. Peripheral nerves include abundant sensory neurons from the cerebral ganglion and segmentally arranged motor and sensory neurons from the ventral nerve cord ganglia.

Leeches are extremely sensitive to certain environmental stimuli, although their sensory receptors are relatively simple. They have from two to ten dorsal eyes of varying complexity, and special sensory papillae that bear bristles extending from the body surface. Except for the eyes, the functions of various leech sense organs are not well understood, and most of the information is based on behavioral responses to different stimuli. Leeches tend to be negatively phototactic. However,

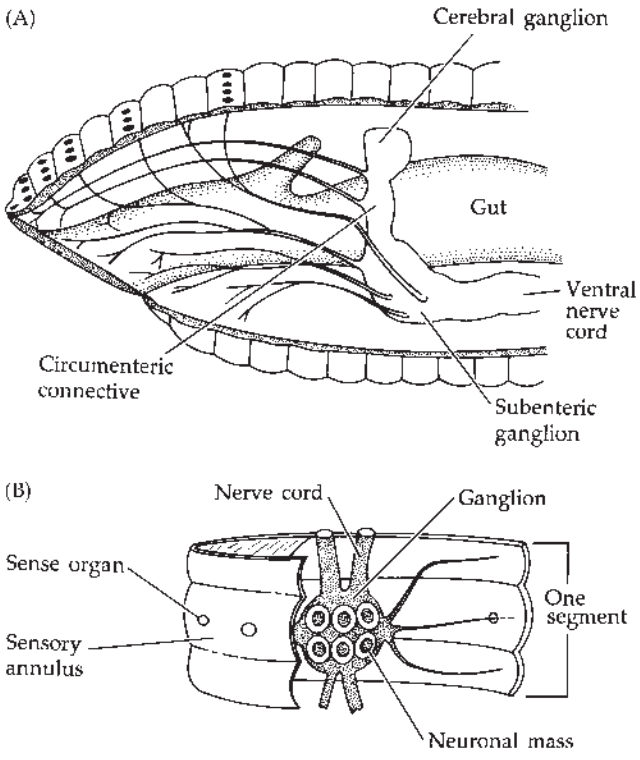

FIGURE 15.39 Leech nervous system. (A) The anterior nervous system (lateral view). (B) A generalized leech segment comprising three annuli, cut away to show segmental ganglion and innervation of epithelial sense organs.

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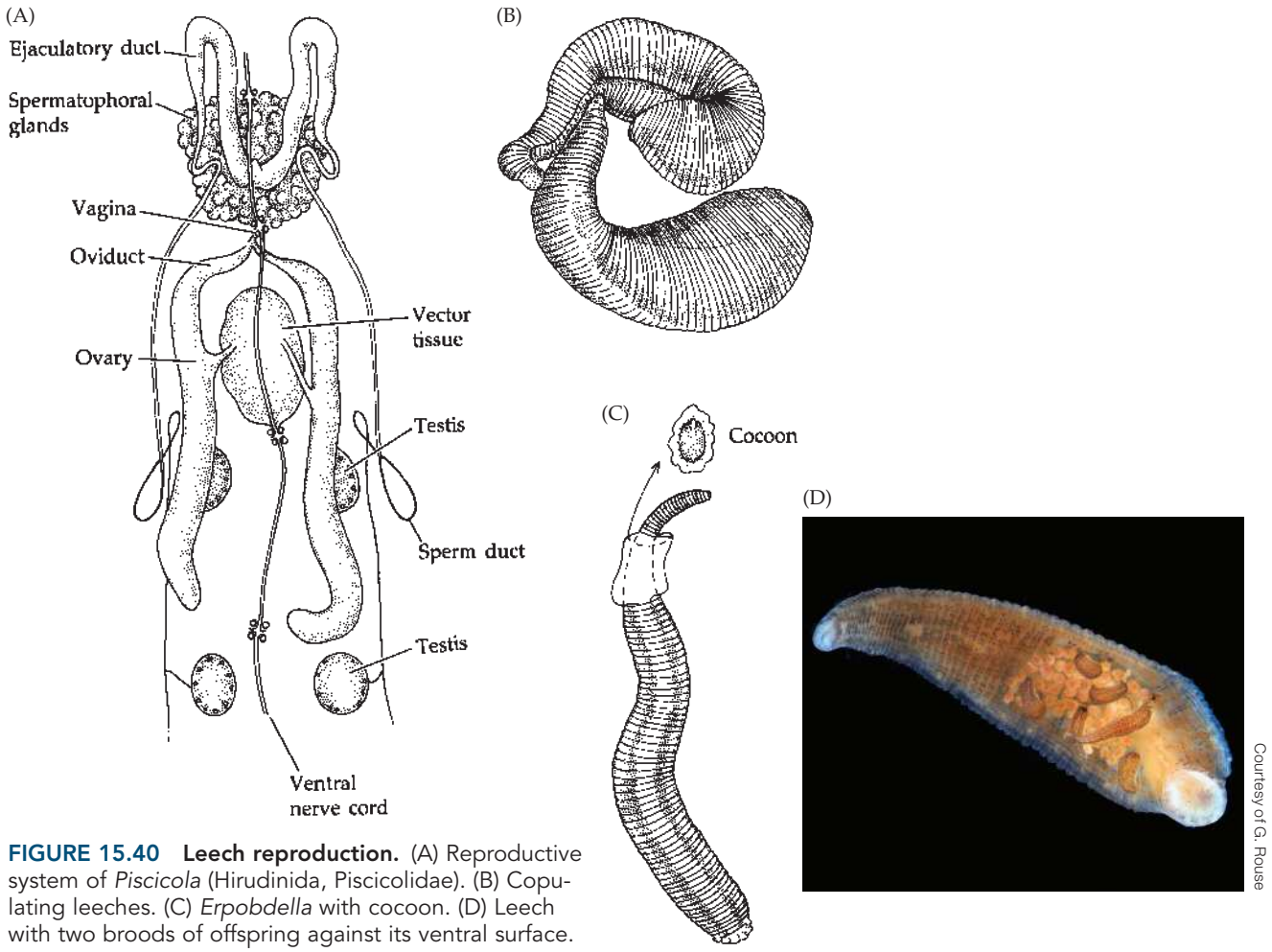
some of the blood-sucking species react positively to light when preparing to feed. This behavioral change likely causes the leech to move into areas where a host encounter is more likely. Most leeches can also detect movement in their surroundings, as evidenced by their responses to shadows passing over them. This reaction has been noted particularly in leeches that attack fishes. Leeches also respond to mechanical stimulation in the forms of direct touch and vibrations in their environments. They are also chemosensitive and attracted to the secretions of potential hosts. Some aquatic and even terrestrial leeches that prefer warm-blooded mammalian hosts are apparently attracted to points of relatively high temperatures in their surroundings, thus aiding in food location. Standing in a leech-inhabited pond is a great way to observe firsthand this rapid response, as these animals will detect your presence and begin swimming or crawling toward you within seconds.

Reproduction and Development

Hirudinea, like all Clitellata, are hermaphroditic and have complex reproductive organs (Figure 15.40) and direct development. The male reproductive system includes a variable number of paired testes, usually from five to ten pairs in leeches, arranged serially beginning in segments XI or XII (Figure 15.34C). The testes are drained by a pair of sperm ducts that lead to a copulatory apparatus and a single gonopore located midventrally on segment X. Leeches have a single pair of ovaries, which may extend through several segments. Oviducts extend anteriorly from the ovaries and unite as a common vagina, which leads to the female gonopore on the midventral surface of segment XI, just behind the male pore.

The copulatory apparatus of leeches is often complex and varies in structure among species. Each sperm duct is coiled distally and enlarges as an ejaculatory duct. The two ducts join at a common glandular, muscular atrium. In arhynchobdellids, the atrium is modified as an eversible penis. The rhychobdellids lack a penis, and the atrium functions as a chamber in which spermatophores are produced. In arhynchobdellids, mating worms align themselves so that the male pore of each rests over the female pore of the other. The penis is everted and inserted into the mate's vagina, where sperm are deposited. Fertilization takes place within the female reproductive system. Rhynchobdellid leeches use hypodermic impregnation. These animals grasp one



Courtesy of G. Rouse

FIGURE 15.40 Leech reproduction. (A) Reproductive system of *Piscicola* (Hirudinida, Piscicolidae). (B) Copulating leeches. (C) *Erpobdella* with cocoon. (D) Leech with two broods of offspring against its ventral surface.

another by their anterior suckers and bring their male pores in alignment with a particular region of the mate's body. The spermatophores are released onto the clitellar region of the mate and then penetrate the body surface of the recipient, and the sperm emerge beneath the epidermis. The sperm migrate to the ovaries by way of the coelomic channels and sinuses. In some of the piscicolid leeches there is a special "target" area, beneath which is a mass of tissue called vector tissue that connects with the ovaries via short ducts.

Cocoon formation in leeches is like that in other clitellates, with the clitellum producing a cocoon wall and albumin (Figure 15.40C). However, as the cocoon slides anteriorly past the female gonopore, it receives the zygotes or young embryos rather than separate eggs and sperm. The cocoons are deposited in damp soil by terrestrial species and even by a few aquatic forms that migrate to land for this process (e.g., *Hirudo*). Most aquatic forms deposit their cocoons by attaching them to the bottom or to algae; a few attach them to their hosts (e.g., some piscicolids). A few freshwater leeches display some degree of parental care for their cocoons. Some of these bury their cocoons and remain over them, generating ventilatory currents. Others attach the cocoons to their own bodies and brood them externally (Fig 15.40D). The development of leeches is like that described for other clitellates. Except for a few species, the amount of yolk is relatively small and development time quite short.

Orthonectida: Extremely Simplified Annelids

Orthonectida was a small phylum of less than 30 marine species that are parasites of Acoela, other Annelida, Echinodermata, Mollusca, Nemertea, Platyhelminthes, and *Xenoturbella*. Their name refers to the adults' behavior in seawater when they leave their host—they swim in a straight line. Inside the host, the parasite forms a plasmodium that asexually generates germinal cells, resulting in clonal embryos and adults (Figure 15.41A). The adults are completely ciliated (Figure 15.41E), can be several hundred microns long, and break out of their host for sexual reproduction (Figure 15.42). For a long period Orthonectida was grouped as "Mesozoa" with another small group of minute parasites of cephalopods called Dicyemida or Rhombozoa (see Chapter 10), although since the late twentieth century dicyemids and orthonectids were usually given separate phylum status. Observations on the cuticle and epidermis raised the possibility of Orthonectida being derived annelids, and this has now been supported by phylogenetic evidence based on molecular data, though their exact placement within Annelida is still uncertain.

The ciliated swimming stages of orthonectids (the short-lived phase outside the host) are ellipsoidal to cylindrical in shape, with the females usually much larger than the males (Figure 15.41E). The smallest

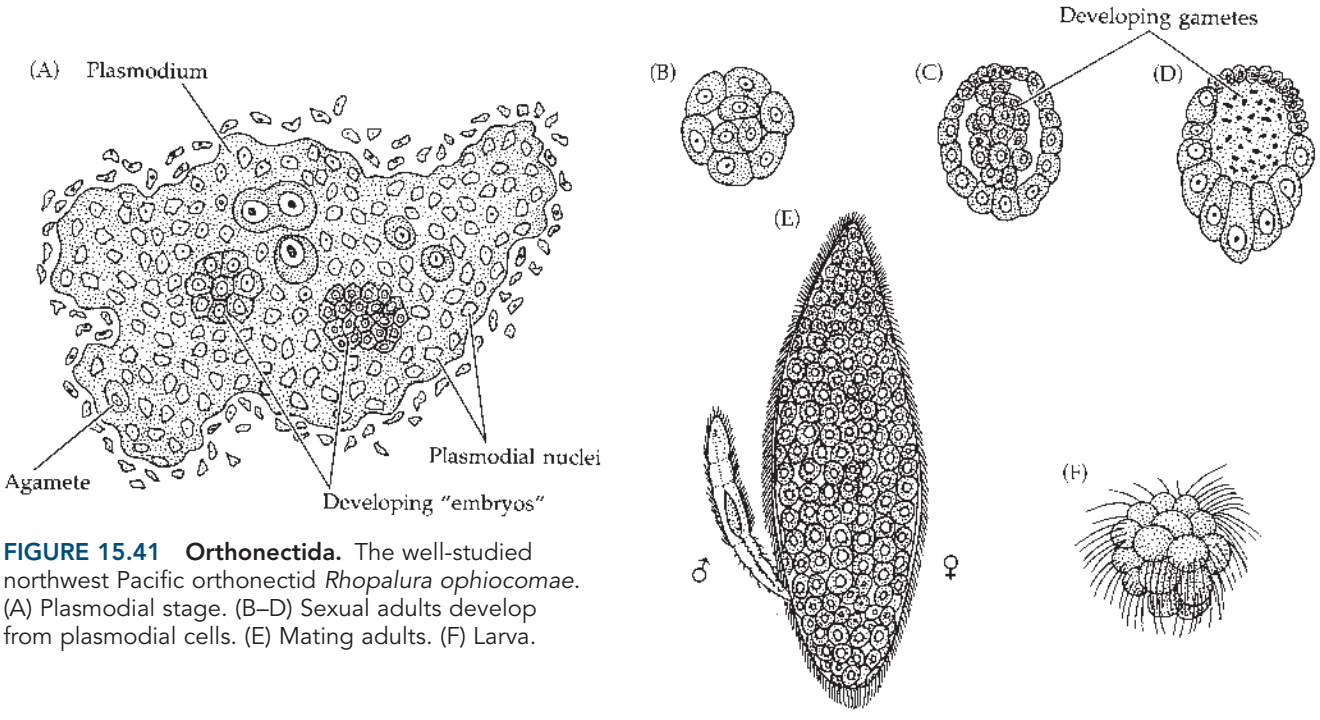


FIGURE 15.41 Orthonectida. The well-studied northwest Pacific orthonectid *Rhopalura ophiocomae*. (A) Plasmodial stage. (B–D) Sexual adults develop from plasmodial cells. (E) Mating adults. (F) Larva.

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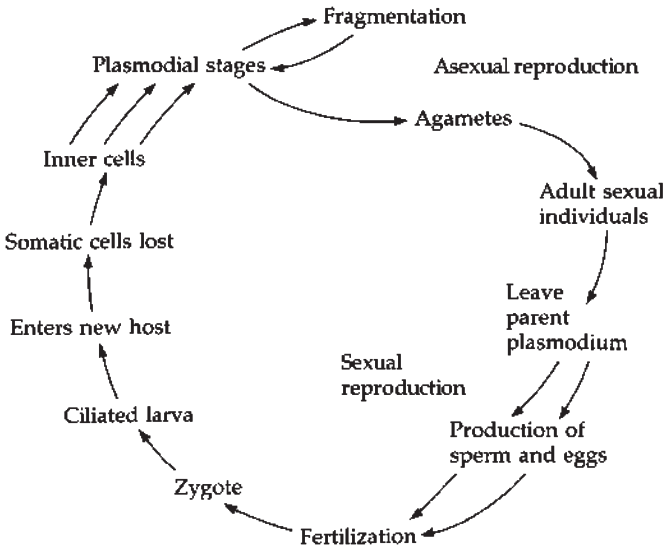

FIGURE 15.42 Orthonectida. Generalized life cyc|e of an orthonectid.

known female, *Intoshia variabili,* reaches just 80 by 20 μm, while the largest, *Ciliocincta sabellariae,* can be 265 by 26 μm. The one hermaphroditic species, *Stoecharthrum monnati*, can be more than 1.5 mm long. The epidermis is made up of ciliated and nonciliated cells and has a cuticle with notable similarities to Annelida, especially during development. A circular and longitudinal muscle system is present but composed of only a few cells. A serotonergic nervous system is also present, but there is no trace of any segmentation, nor excretory organs or a circulatory system. Gametes form in the males and females while they are still developing in the plasmodium (Figure 15.41B–D), and upon release into the seawater they are mature (Figure 15.41E). Females are filled with tiny oocytes 11–13 μm in diameter, and the sperm of males is also uniquely small. Mating occurs via copulation, and fertilization is internal. Females release free-swimming larvae (Figure 15.41F) through a genital pore, and these live for only a few hours before they must find and penetrate a host. The plasmodium phase inside the host has been interpreted as originating from the penetrating larval cells or is the host tissue reacting to such penetration. The plasmodium ramifies through the host, feeding on the host tissues by phagocytosis and pinocytosis. A plasmodium can give rise to daughter plasmodia by budding, and while both males and females can develop in one plasmodium, a single sex is mainly observed. This body miniaturization is also reflected in their genome: orthonectids hold the record of having the smallest animal genome, with one of the smallest numbers of genes recorded.

Annelid Phylogeny

There are undoubted annelid fossils that date back to the Cambrian period, with well-known examples being *Canadia* and *Burgessochaeta*. These show clear evidence of segmentation and chaetae, though it is a subject of debate as to whether they could be classified very closely with any extant lineage of annelids. But these were quite complex annelids, and the early origins of the group are obscure.

In addition to the recognition that the traditional classification (of Polychaeta, Oligochaeta, and Hirudinea) had to be replaced with a phylogenetic classification, the past few decades have seen a series of major changes in annelid membership as well, mainly due to molecular-based phylogenetic studies. Diurodrilidae, Echiura, Myzostomida, Sipuncula, Orthonectida, Pogonophora, and Vestimentifera, all of which were once considered outside Annelida, are now clearly seen as part of this phylum. Hence, Annelida now encompasses many animals that do not conform to the traditionally viewed unique features of the group, such as possession of body segmentation and chaetae. Even more problematic has been resolving the relationships among the groups that have long been regarded as part of the annelid radiation, a work that must still be regarded as very much in progress, especially with respect to the precise position of Myzostomida and many meiofaunal taxa.

While a deep understanding of the origin and evolution of annelids still eludes us, considerable progress has been recently made with the use of high-throughput sequencing technologies, which hold great promise. This means we will likely see a stable annelid phylogenetic tree emerge over the coming years. Our current knowledge of annelid relationships, as used in this chapter, is based on recent phylogenomic studies by Anne Weigert, Sónia Andrade, Torsten Struck, Chema Martín-Durán, and their colleagues (Andrade et al., 2015; Martín-Durán et al., 2021; Struck et al., 2015; Weigert et al., 2014), and these were used to generate the summary tree and classification used in this chapter (Figure 15.43). As future phylogenomic analyses are integrated with increasing knowledge of fossil annelids, we will be able to make better inferences as to the origin and evolution of this diverse group of animals.

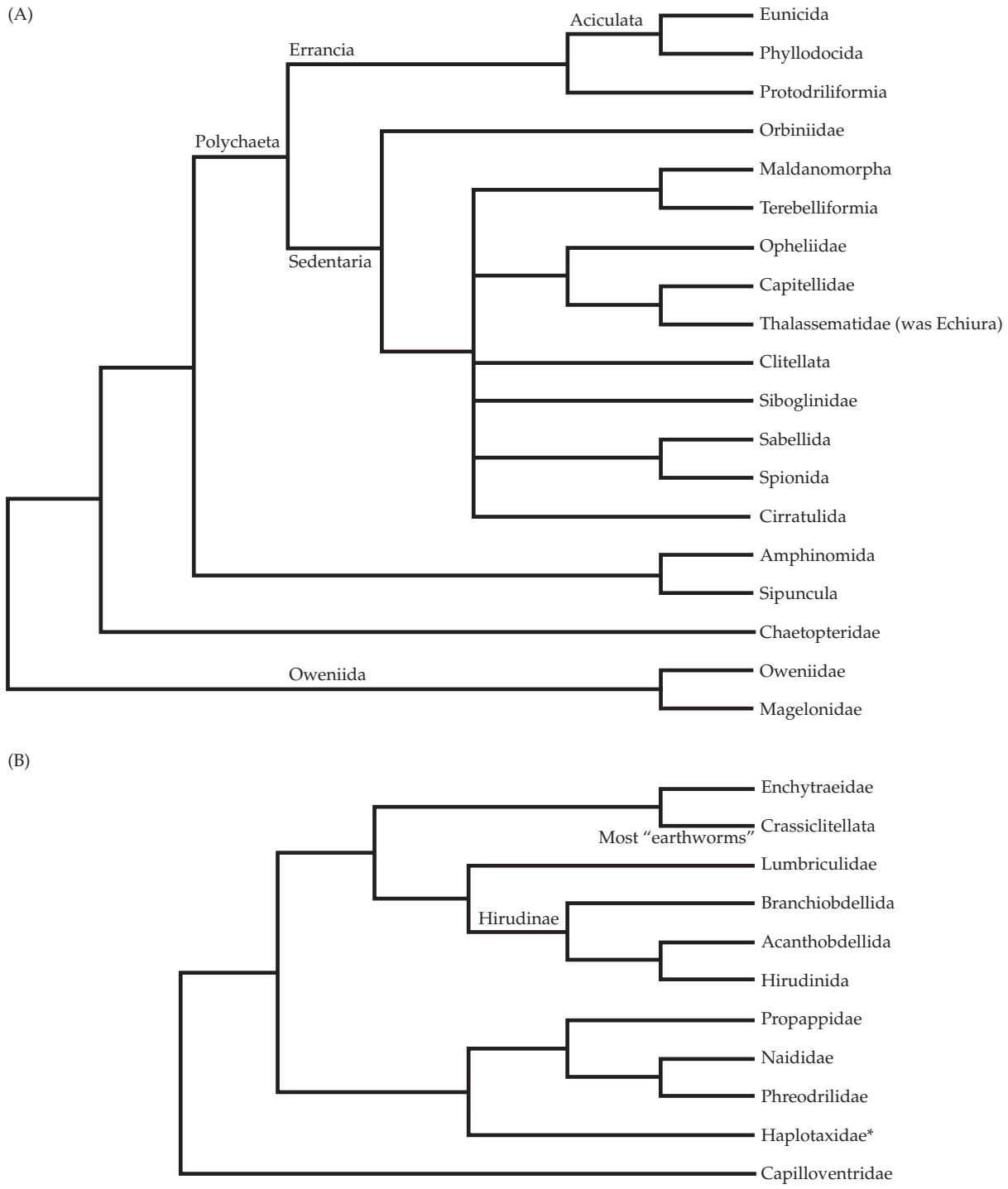

FIGURE 15.43 Phylogenetic relationships of annelids. (A) Annelida, based on areas of agreement in the phylogenomic analyses of Andrade et al. (2015), Weigert et al. (2014), Struck et al. (2015) and Martín-Durán et al. (2021). (B) Clitellata based on topologies in Anderson et al. (2017), Erséus et al. (2020), and Phillips et al. (2019). Haplotaxida is not monophyletic, but only one terminal is shown here.

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Chapter Summary

This chapter introduced you to a large group of primarily segmented spiralian worms, the phylum Annelida. Annelids are lophotrochozoans, closely related to molluscs, nemerteans, and perhaps entoprocts. Annelid segmentation represents true metamerism, the result of teloblastic development—the proliferation of paired, segmental mesodermal bands from teloblast cells at a posterior growth zone in the embryo. The segmented annelid species all show serial homology. Annelids typically have a closed circulatory system, well-developed nervous system, and proto- and/or metanephridia. Development is holoblastic and spiral, and most marine species produce a trochophore larva (a feature shared with molluscs, nemerteans, and entoprocts). Among the better-known, clearly segmented annelids are marine sand worms and tube worms, earthworms, and leeches—the latter two comprising the clade Clitellata. However, a number of lineages in this phylum show secondary loss of obvious segmentation, and molecular phylogenetics has only recently revealed them to be highly modified annelids; these include orthonectids, sipunculans (peanut worms), and thalassematids (spoon worms, or echiurans). Annelids range in size from nearly microscopic marine meiofauna to earthworms exceeding 3 m in length. They can be found in almost all marine, freshwater, and damp terrestrial environments; they are especially common in shallow coastal waters. Many species are symbionts (commensals, mutualists, parasites) with other invertebrates and, in the case of leeches, some vertebrates.

Annelid classification is in a state of flux, and this is reflected in the absence of category names in this chapter (although taxon names ending in *idae* are generally regarded as family names). Because Clitellata (earthworms and leeches) arose from within the other annelids (i.e., from a group once called Polychaeta), the nonclitellates comprise a paraphyletic group. Therefore, many workers now redefine "Polychaeta" as a clade of annelids that includes only the two large groups Errantia and Sedentaria (Clitellata, Siboglinidae, and Thalassematidae are part of Sedentaria). Thus, three major groups of annelids are now viewed as nonpolychaetes: Oweniida, Chaetopteridae, and the Amphinomida + Sipuncula clade.

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CHAPTER 16

The Lophophorates

Phyla Phoronida, Bryozoa, and Brachiopoda

For most of the twentieth century, three phyla—Phoronida, Bryozoa (= Ectoprocta), and Brachiopoda—all of which possess a unique feeding structure called a lophophore, had been regarded as a likely clade within the Deuterostomia. The primary unifying feature of the Lophophorata was the **lophophore** itself, a ciliated tentacular feeding structure, and the associated **epistome** (a muscular flap that functions to move captured food particles from the lophophore to the mouth). Their alliance with the deuterostomes had been based on a suite of developmental features, including radial and indeterminate cleavage, enterocoely, and development of the mouth secondarily rather than from the blastopore (i.e., "deuterostomy"). Further, in all three phyla the adult body is organized into three distinct parts, each with its own coelomic cavity (or paired cavities). This trait was originally termed **archicoely**, in reference to the "archicoelomate" concept, the idea that three regionalized body coeloms is a fundamental feature of Deuterostomia. This archicoelomate condition is also seen in the deuterostome phyla Echinodermata, Hemichordata, and Chordata. The developmental features were viewed as differentiating them from protostomes, in which the blastopore develops into the mouth and radial cleavage typically does not occur. In deuterostomes, the mouth is formed as a secondary opening (i.e., *deutero*, "second"; *stome*, "mouth") on the anterior end of the embryo.

However, with the advent of molecular phylogenetics, it is certain that the three lophophorate phyla are allied with spiralian protostomes, not deuterostomes, and aspects of their development seeming to have deuterostome-like characteristics are

Phoronida was revised by Scott Santagata, Bryozoa was revised by Claus Nielsen, and Brachiopoda was revised by Carsten Lüter.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

likely secondarily derived or have been reinterpreted. It has long been suspected that something akin to radial cleavage might be the primitive cleavage pattern within Bilateria (most demosponges also have radial cleavage), and the discovery that the lophophorate phyla belong to the Spiralia suggests that radial cleavage and deuterostomy are retained plesiomorphic developmental features (or reacquired) of the lophophorate phyla. And in the protostome phylum Phoronida the mouth develops from a portion of the blastopore (protostomously), and both radial cleavage and spiral-like cleavage occur (the cleavage pattern may depend, at least in part, on the size of the egg). Specific brachiopods, on the other hand, develop the mouth by either protostome-like or deuterostome-like developmental patterns. Although bryozoan embryos cleave radially, the resulting blastomere arrangements and cell lineages exhibit several spiralian features. Molecular phylogenetics also places the former deuterostome phylum Chaetognatha within the protostome lineage. In other words, developmental programs appear to be more flexible (and homoplastic) than once thought, and even phyla outside the classic Deuterostomia clade can exhibit a deuterostome type of development

The archicoelomate concept recognizes three distinct body regions (an anterior **prosome**, middle **mesosome**, and posterior **metasome**), each with its own coelomic cavities (**protocoel**, **mesocoel**, and **metacoel**). This condition is also referred to as a tripartite or **trimeric body plan**. However, developmental research since 2000 has shown that the protocoel may not comprise a true coelom in all lophophorate species, or might be absent altogether in many, and we discuss this for each of the phyla. The great American zoologist Libbie Hyman noted in the 1950s that a correspondence between the adult coeloms of lophophorates and the trimeric body of deuterostomes was poorly supported by both embryology and adult morphology. In fact, Hyman was dismayed with the mix of characteristics found in the Lophophorata. She was actually inclined to classify them with protostomes, despite the enterocoelous coelom formation in brachiopods and the lack of spiral cleavage in bryozoans and brachiopods. She eventually found comfort in concluding that "the lophophorates constitute a connecting link between the Protostomia and the Deuterostomia, but the details of this connection cannot be stated." Hardly a more vague phylogenetic statement could be made.

With molecular phylogenetics confirming that lophophorates are protostomes, use of the terms "prosome," "mesosome," and "metasome" to describe their body plan is perhaps ambiguous, and the homology of these regions to those of deuterostomes is now called into question. The same holds for the Entoprocta, another protostome group whose body regions are often referred to as "prosome," "mesosome," and "metasome," despite lacking a coelom. The tentacular crown of pterobranchs (phylum Hemichordata; Chapter 25) also possesses mesosomal tentacles with a coelomic lumen. However, the homology between pterobranch tentacles and a true lophophore is likely invalidated because in the former case the tentacles do not fully surround the mouth.

Even though the lophophorate phyla are no longer considered deuterostomes, molecular phylogenetics does suggest they comprise a monophyletic group, the clade Lophophorata. However, the precise placement of this clade within the Lophotrochozoa remains enigmatic, and whether Entoprocta also belongs with Lophophorata remains unresolved, as some analyses ally them with Bryozoa while others group them with Cycliophora; in the latter case, they are outside the Lophophorata.

At first glance, what we consider here the three lophophorate phyla may not appear closely related to one another. However, in addition to molecular phylogenetic analyses, they are united by their common possession of a lophophore and epistome (although an epistome is absent in most bryozoans); no other animal phylum has these structures. The lophophore is a ciliated, tentacular outgrowth arising from the mesosome and containing extensions of the mesocoel. It surrounds the mouth but not the anus. All lophophorate animals are sessile, have a U-shaped gut, and typically have very simple, often transient, reproductive systems. Nearly all secrete outer casings in the form of tubes, shells, or compartmented exoskeletons, a character that has been used to justify an affinity to the other lophotrochozoans.

With the exception of a few freshwater bryozoans, the lophophorates are exclusively marine. All are benthic, living either in tubes (phoronids) or in secreted shells, or casings. The phoronids are a small group, comprising only two genera and around 15 known species of solitary or gregarious animals. Bryozoans, on the other hand, make up a diverse taxon of about 6,300 living species of colonial forms (with about 15,000 additional species being extinct). The brachiopods, or lamp shells, include about 440 extant species. However, the brachiopods have left a record of thousands of fossil species (over 12,000 described extinct species) as evidence of a greater past, and they were well established by the early Cambrian. Brachiopods flourished in both abundance and diversity from the Ordovician through the Carboniferous, but they have declined in numbers and kinds ever since.

Taxonomic History of the Lophophorates

The lophophorates have had a long and tortuous taxonomic history. The earliest records of lophophorates are of various bryozoans reported in the sixteenth century. With few exceptions, the early zoologists treated them as plantlike and included them in the taxon Zoophyta,

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a misconception that persisted into the 1700s. In 1729, French physician and naturalist Jean-André Peyssonal finally established the animal nature of bryozoans, and in 1742 French naturalist Bernard de Jussieu noted the compartmentalized condition of the colonies and coined the term "polyps" to refer to the individual animals. Still, most well-known workers of the day (e.g., Linnaeus and Cuvier) continued to insist on allying them with the cnidarians in the group Zoophyta.

Eventually (in 1820), French zoologist and anatomist H. M. D. de Blainville noted the complete gut of the bryozoans and "raised" them above the cnidarians. By 1831, two names had been coined for these animals—Bryozoa (by German zoologist Christian Gottfried Ehrenberg) and Polyzoa (by the Englishman J. Vaughan Thompson). Just about the time bryozoans were being recognized as a separate group (under one name or the other), concurrent events confused the issue further. The entoprocts (= Kamptozoa) were described, and most workers included them with the Bryozoa, while others recognized a relationship between bryozoans and other lophophorate phyla. All of this became terribly entangled in 1843 with Henri Milne-Edwards's concept of a taxon Molluscoides, which he established to include bryozoans and compound ascidians (chordates). Hatschek later raised Bryozoa and Entoprocta to distinct phylum ranking in 1891. The brachiopods were known, at least from fossils, in the 1600s and were allied with the molluscs. This mistaken view was held until late in the nineteenth century.

Phoronids were first described from their larvae in 1846 by German zoologist Johannes Müller, who thought they were adults and named them *Actinotrocha brachiata*. In 1854, Karl Gegenbaur recognized these animals as larval stages. The adults were found in 1856 and described by British physician and zoologist T. Strethill Wright, who named them *Phoronis*. Finally, in 1867 the renowned Russian embryologist Alexander Kowalevsky studied the metamorphosis of "Actinotrocha" and established the relationship between the two stages. To this day, the name "actinotroch" persists as a general term for the phoronid larva.

In 1857, Albany Hancock recognized the relationship between brachiopods and bryozoans, but the whole matter was mixed up with confusion over the entoprocts and Milne-Edwards's Molluscoides. Hinrich Nitsche made a valiant attempt in 1869 to separate the entoprocts and bryozoans, and in the 1880s Otis Caldwell and Thomas Masterman both put forth the idea of a close relationship between the three lophophorate phyla. This view was supported by Hatschek in 1888, when he suggested the establishment of a phylum Tentaculata to include the classes Phoronida, Bryozoa, and Brachiopoda (but excluding the entoprocts), thus establishing the grouping we recognize today as Lophophorata. Since that time several attempts to unite some or all of these animals into a single taxon have been made, including Anton Schneider's Lophophorata in 1902 (originally only for phoronids and bryozoans). Hyman (1959) retained separate phylum status for the three groups, an arrangement that has remained popular ever since.

In the recent past, some workers revived the idea of a possible entoproct-ectoproct affinity and argued that the two groups are closely allied with Cycliophora in a grouping called Polyzoa. However, this is not supported by the most recent large-scale phylogenetic work. An alliance between Bryozoa and Entoprocta can also be rejected on the basis of direct comparative grounds. Entoprocts do not possess the lophophore-epistome complex. Furthermore, they lack any vestiges of a coelom or trimeric body plan. The feeding currents are virtually opposite in the two groups, and the methods of food capture and transport are entirely different. Entoprocts possess ducted gonads, and bryozoans do not. Cleavage in entoprocts is spiral, whereas it is radial in bryozoans. Larval forms and particularly metamorphosis are clearly different in the two groups. Similarities such as budding and U-shaped guts are superficial and common to many colonial sessile animals. Thus, we conclude that Bryozoa and Entoprocta are distantly related protostomes, a conclusion supported by some recent molecular phylogenetic studies but not yet fully resolved. The name Ectoprocta is often used in lieu of Bryozoa, acknowledging the fact that the anus lies outside the lophophore ring, whereas in the Entoprocta it lies within the lophophore ring (and the mouth is on the rim carrying the tentacle crown).

The Lophophorate Body Plan

All lophophorates are built for benthic life and suspension feeding, the latter being a primary function of the lophophore itself. The anterior body region, or prosome, is reduced to a small flaplike structure called the epistome (lost in some lineages), which is associated with an overall reduction of the head, the elaboration of the mesosome as the lophophore, and a sessile lifestyle. The metasome houses the bulk of the viscera. The U-shaped gut is clearly advantageous for living encased in tubes, compartments, and shells; such animals do not "foul their nests," as it were. We have seen similar adaptations in some other groups with comparable habits, such as the recurved gut of sipunculans and the ciliated fecal-removal grooves of some tube-dwelling polychaetes. In lophophorates, this condition not only prevents fecal accumulation in the encasement, but generally brings the anus close to rejection currents produced by the cilia on the lophophore. In recent years, it has been shown that an epistome coelom (the protocoel) is absent in some phoronids and brachiopods, and all gymnolaemate bryozoans, whereas in phylactolaemate bryozoans there is an open connection between the epistomal cavity and the lophophoral coelom.

The phoronids most clearly display the mentioned traits and retain the vermiform shape of the probable ancestral form. Evolutionarily, bryozoans have exploited asexual reproduction, colonialism, and small size. Relieved of long-distance internal transport problems, the bryozoans have lost the circulatory and excretory systems. The brachiopods evolved a pair of valves or shells that encase and protect the body, including the lophophore. Thus, instead of exposing the lophophore in the water (as phoronids and bryozoans do), the brachiopods draw water into their mantle cavity for suspension feeding, an action analogous to that in bivalve molluscs. Sessile animals with soft parts (e.g., the lophophore), living on benthic surfaces, are exposed to potentially high levels of predation—thus the selective advantage of the brachiopod shell is clear. The phoronids are motile to the extent that their bodies can be swiftly retracted within their tubes, protecting the soft parts. Bryozoans are entirely anchored in their casings, but the lophophore itself is uniquely retractable into the body, as the result of a unique arrangement of muscles and hydraulic mechanisms.

Phylum Phoronida: The Phoronids

All phoronids occupy a cylindrical tube of their own secretion in which they can move freely. The animals typically occur in aggregations that, in some species, result from asexual reproduction. Their chitinous tubes are usually cemented to hard substrata or buried vertically in soft sediments (Figure 16.1; Box 16A). They are assigned to only two genera, *Phoronis* and *Phoronopsis*, of questionable monophyly, and around 15 widely distributed species. The phylum name was apparently derived from the Latin term *Phoronis*, the surname of Io (who, according to mythology, was changed into a cow and roamed the Earth, eventually to be returned to her former body). Recall that these worms were first described from larval stages drifting in the sea, and only much later were the adults recognized as part of the same life cycle. Adult phoronids are found in intertidal sands or mud flats, and to depths of about 400 m.

BOX 16A Characteristics of the Phylum Phoronida

1. Vermiform lophophorates with two or three coelomic cavities
2. Adult mesoderm derived from both embryonic ectoderm and endoderm
3. Body divided into flaplike epistome (prosome), lophophore-bearing collar (mesosome), and elongate trunk (metasome)
4. Gut U-shaped, anus close to mouth
5. One pair of metanephridia in metasome (trunk)
6. Closed circulatory system
7. Gonochoristic or hermaphroditic, with transient peritoneal gonads
8. With indirect life histories; usually with a unique actinotroch larva
9. Radial and spiral-like, indeterminate cleavage; coeloblastulae gastrulate by invagination; blastopore becoming mouth (protostomous)
10. Marine benthic tube dwellers

The Phoronid Body Plan

Most adult phoronids range from 1 to 25 cm in length. The vermiform body shows little regional specialization, except for the distinct lophophore and a modest inflation of the end bulb, which houses the stomach and also aids in anchoring the animals in their tubes. The slitlike mouth is located between the tentacle-bearing lophophoral ridges and is overlaid by a flap, the epistome. The lateral aspects of the ridges are distinctly coiled and flank the dorsal anus and paired nephridiopores (Figures 16.2 and 16.3). Using the terms "anterior" and "posterior" when referring to phoronids can be misleading. During metamorphosis, the true anterior (mouth-bearing) and posterior (anus-bearing) ends are brought very close together by rapid growth and enlargement of the ventral surface (Figure 16.4). The dorsal surface is reduced to the small area between the adult mouth and anus. Because of these conditions, we refer to the "ends" of the adult worm as the lophophoral end and the stomachic (= ampullar) end (Figure 16.1A).

Body Wall, Body Cavity, and Support

The phoronid body wall includes an epidermis of columnar cells overlaid by a very thin cuticle. Within the epidermis are sensory neurons and various gland cells (Figure 16.2A), the latter being responsible for the production of mucus and chitin for building the tube. The epidermis of the lophophore is densely ciliated. Internal to the epidermis and its basement membrane is a thin layer of circular muscle, some limited diagonal muscle, and a thick layer of longitudinal muscle that allows for fast retraction of the animal into its tube. A peritoneum lines the longitudinal muscles and forms the outer boundary of the coelom.

Although the coelom was long described as being tripartite, there is structural variation among species in the epithelial lining of the most anterior cavity, the "protocoel." Ultrastructural investigations have shown that the myoepithelial lining of the epistome lacks adherent cell junctions (a key component of true epithelial tissues) in at least two *Phoronis* species. However, adherent junctions are present in the myoepithelial lining of the epistome of *Phoronopsis harmeri*. True epithelial layers comprise the coelomic linings of the collar (mesocoel) and trunk

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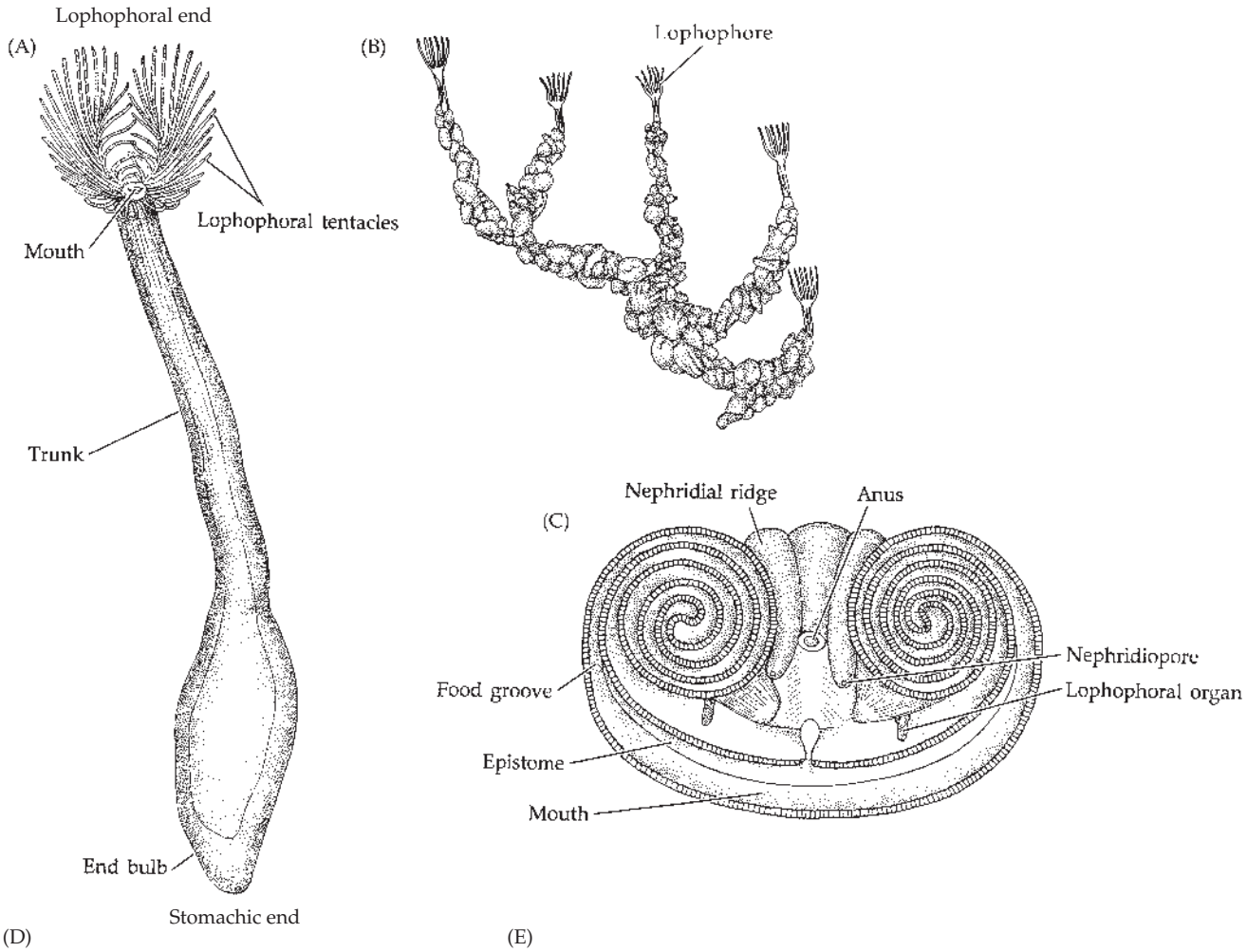

(D)

Courtesy of Greg Jensen

(E)

Courtesy of M. Pennerstorfer

(F)

Courtesy of Scott Santagata

(G)

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FIGURE 16.1 Phoronids. (A) General external form of a phoronid (*Phoronis psammophila*). (B) *Phoronis psammophila* in tubes encrusted with sand grains and shell fragments. (C) A phoronid viewed from the lophophoral end. The tentacles have been cut in cross section. (D) Exposed lophophores of a colony of *Phoronis ijimai*. (E) Anterior end of *Phoronis muelleri* extending from its tube. (F) The lophophore of *Phoronis pallida*, False Bay, Washington State. (G) The phoronid *Phoronopsis californica*, with its spiral lophophore.

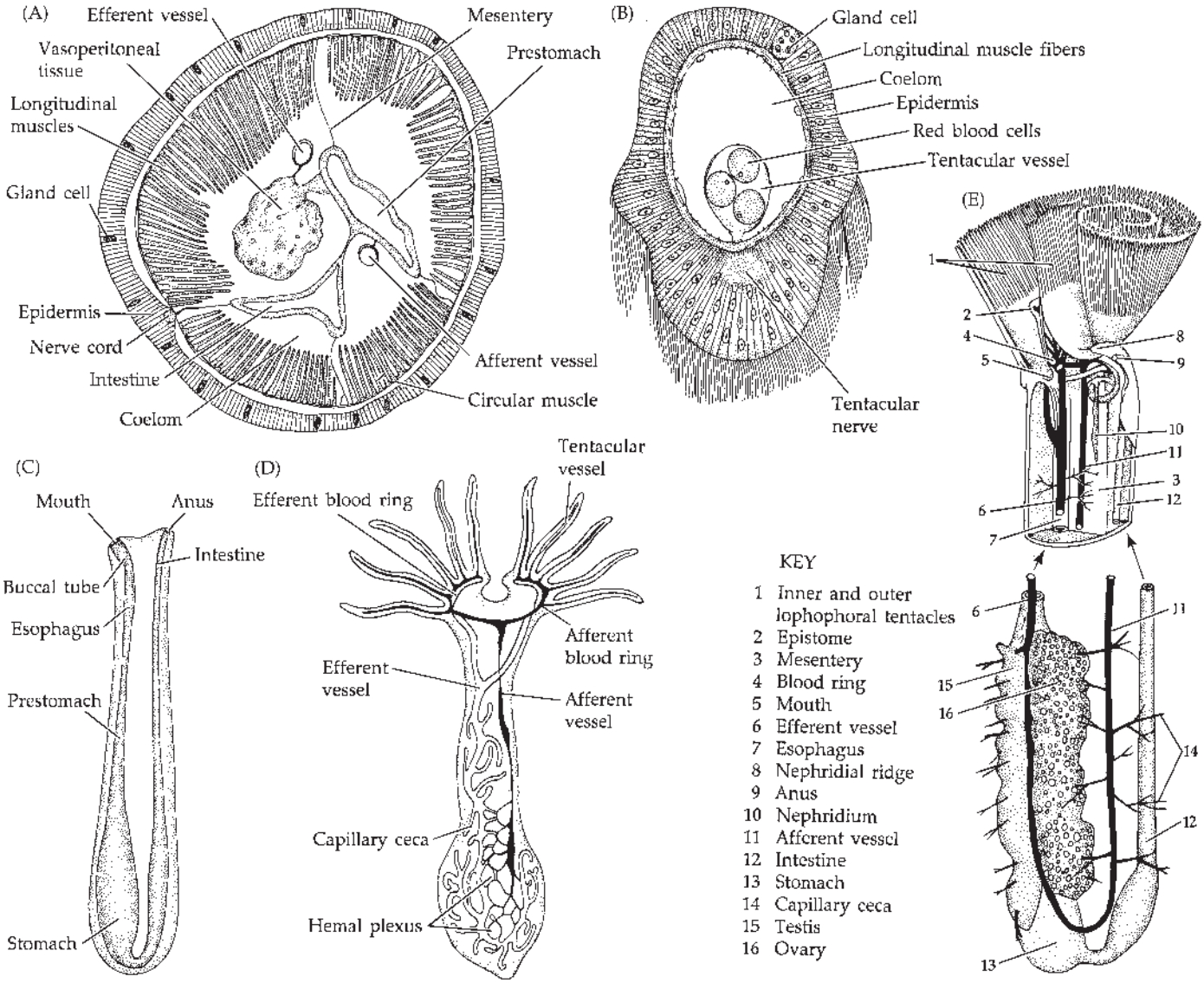

FIGURE 16.2 **Phoronid anatomy.** (A) The trunk of a phoronid in cross section. (B) A tentacle of the lophophore in cross section. (C) The digestive tract. (D) The circulatory system. (E) The major internal organs in the lophophoral and stomachic ends.

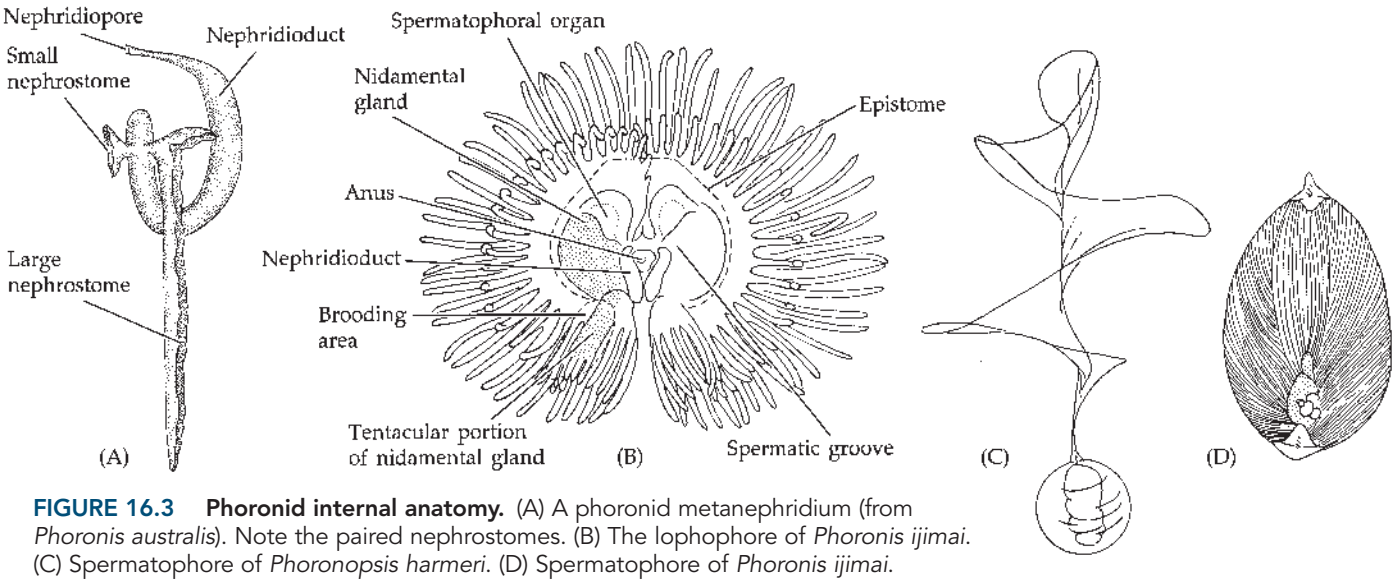

FIGURE 16.3 **Phoronid internal anatomy.** (A) A phoronid metanephridium (from *Phoronis australis*). Note the paired nephrostomes. (B) The lophophore of *Phoronis ijimai*. (C) Spermatophore of *Phoronopsis harmeri*. (D) Spermatophore of *Phoronis ijimai*.

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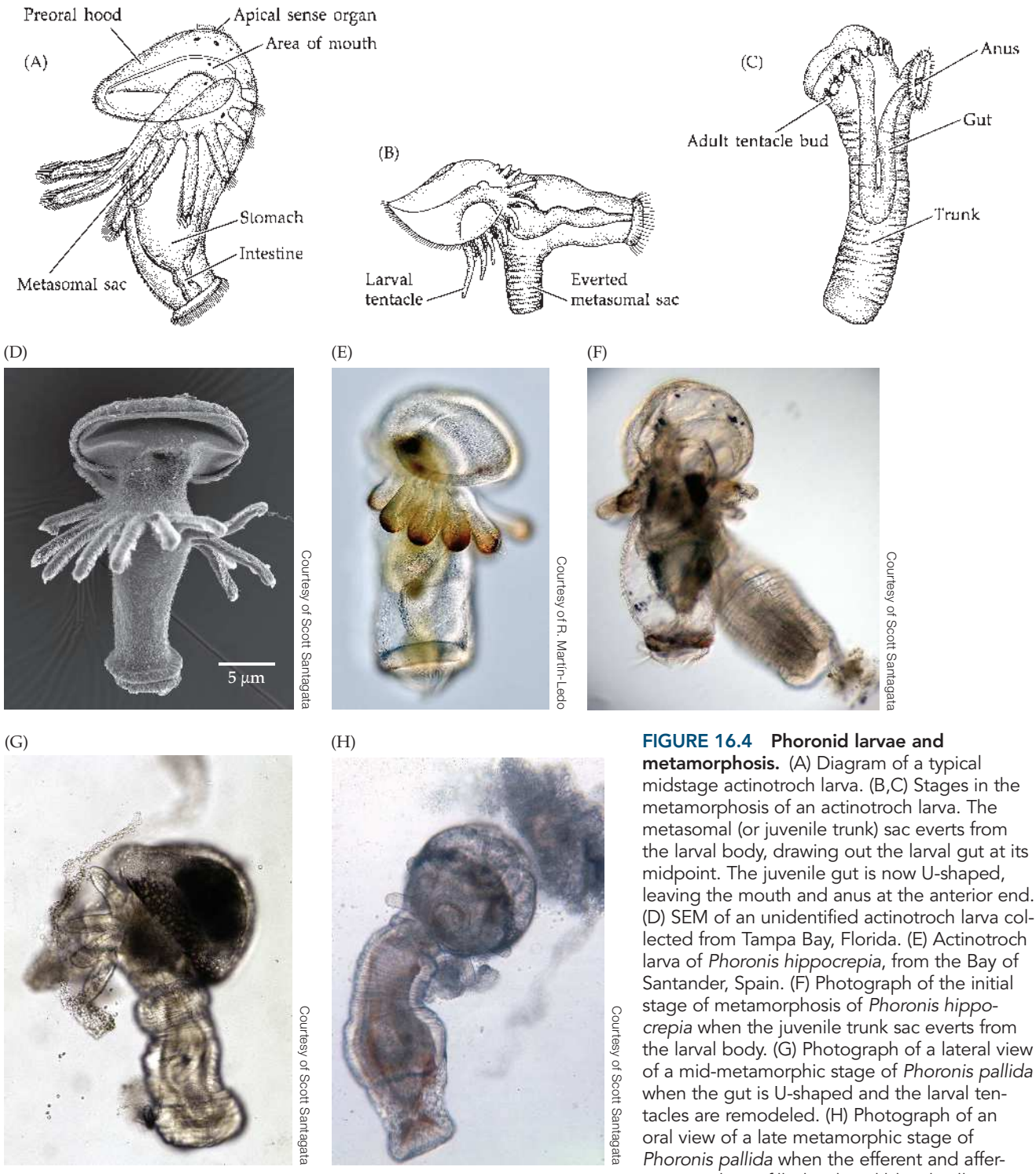

FIGURE 16.4 Phoronid larvae and metamorphosis. (A) Diagram of a typical midstage actinotroch larva. (B,C) Stages in the metamorphosis of an actinotroch larva. The metasomal (or juvenile trunk) sac everts from the larval body, drawing out the larval gut at its midpoint. The juvenile gut is now U-shaped, leaving the mouth and anus at the anterior end. (D) SEM of an unidentified actinotroch larva collected from Tampa Bay, Florida. (E) Actinotroch larva of *Phoronis hippocrepia*, from the Bay of Santander, Spain. (F) Photograph of the initial stage of metamorphosis of *Phoronis hippocrepia* when the juvenile trunk sac everts from the larval body. (G) Photograph of a lateral view of a mid-metamorphic stage of *Phoronis pallida* when the gut is U-shaped and the larval tentacles are remodeled. (H) Photograph of an oral view of a late metamorphic stage of *Phoronis pallida* when the efferent and afferent vessels are filled with red blood cells. Dissociated cells at top are produced from the histolysis of hood tissues.

(metacoel) body regions in both *Phoronis* and *Phoronopsis*. Regardless of the validity of the protocoel as a true coelomic cavity, as an anatomical structure it is limited to a single small cavity within the epistome of only some species. The unpaired mesocoel comprises a coelomic ring in the lophophoral collar and extends into each tentacle (Figure 16.2B). The protocoel and mesocoel are connected to one another along the lateral regions of the epistome. The metacoel forms the main trunk coelom, which is separated from the mesocoel by a transverse septum. Ontogenetically, the metacoel is an uninterrupted cavity with only one midventral mesentery. However, secondary mesenteries form later in development, yielding four longitudinal spaces (Figure 16.2A). The coelomic fluid contains several kinds of freely wandering cells, or coelomocytes, including phagocytic amebocytes.

Body support is provided by the hydrostatic qualities of the coelomic chambers and by the tube. The muscles of the body wall are rather weak, particularly those in the circular layer, and once removed from their tubes, phoronids are capable of only limited movement. Normally, however, the body wall of the end bulb is pressed against the tube, holding the worm in place. When disturbed, the animal simply contracts into the tube; the lophophore itself is not retractable.

The tube is secreted by epidermal gland cells. When first produced, the chitinous secretion is sticky, but upon contact with water it solidifies to a flexible parchmentlike consistency. Sand grains and bits of other material adhere to the tube during the sticky phase of tube formation in those phoronids that inhabit soft substrata (e.g., *Phoronopsis harmeri*). In some species the tubes intertwine with one another, with the whole tangled aggregation attached to a substratum or actually embedded in calcareous stone or shells (e.g., *Phoronis hippocrepia*).

The Lophophore, Feeding, and Digestion

The tentacles of the **lophophore** are hollow, ciliated outgrowths of the mesosome, and each contains a blind-ended blood vessel and a coelomic extension (Figure 16.2B). The tentacles are in a double row, arising from two ridges, in a circle or a spiral as is *Phoronopsis californica* (Figures 16.1, 16.2, and 16.3). The ridges lie close to one another and form a narrow food groove in which the slitlike mouth is located (Figure 16.1C). Because the sides of the lophophoral ridges are coiled, many tentacles are compacted into a small area.

Phoronids are ciliary-mucus suspension feeders. The lophophoral cilia generate a water current that passes down between the two rows of tentacles and then out between the tentacles. Food particles are trapped in mucus lining the food groove and then passed along the groove by cilia to the mouth. As the current passes between the tentacles and out of the area of the food groove, some water flow is directed over the anus and nephridiopores away from the animal (Figure 16.1C).

The digestive tract is U-shaped, but simple and not coiled (Figure 16.2C). The mouth is overlaid by the epistomal flap and leads inward to a short buccal tube, which is followed by an esophagus and a narrow prestomach. Within the end bulb the gut expands into a stomach, from which emerges the intestine. The intestine bends up toward the lophophore and leads to a short rectum and the anus. The gut is supported by peritoneal mesenteries (Figure 16.2A).

The majority of the digestive tract is apparently derived from endoderm, except that the anus and the initial formation of the larval intestine are formed from an ectodermal invagination. Some parts are muscular, but only weakly so, and much of the movement of food is by ciliary action. A middorsal strip of densely ciliated cells arises in the prestomach and extends into the stomach, and it is probably responsible for directing food along that portion of the gut. Gland cells occur in the esophagus, but their function remains uncertain. Transitory syncytial bulges in the stomach walls are the sites of intracellular digestion in that organ.

Circulation, Gas Exchange, and Excretion

Phoronids contain an extensive circulatory system composed of two major longitudinal vessels between which blood is exchanged in the lophophoral and stomachic ends of the body (Figure 16.2D,E). Various names have been applied to these vessels, depending on their positions in the body. These terms are often confusing because the positions of vessels vary along the length of the trunk, and they are not clearly dorsal, medial, lateral, or ventral as the names imply. Therefore, preference is given here to the terms "afferent" and "efferent," which refer to the direction of a vessel's blood flow relative to the lophophore.

The afferent vessel extends unbranched from the region of the end bulb to the base of the lophophore. For most of its length it lies more or less between the descending and ascending portions of the gut. In the mesosome the afferent vessel forks, forming an afferent "ring" (U-shaped) vessel at the base of the lophophoral tentacles. A series of lophophoral vessels, one in each tentacle, arises from the afferent ring. Each of these vessels joins with an efferent "ring" vessel (also U-shaped), which drains blood from the lophophore. Thus, the afferent and efferent blood rings lie against one another, and they generally share openings into the lophophoral tentacles within which blood moves back and forth, as there is just a single vessel in each tentacle. One-way flap valves largely prevent backflow into the afferent ring.

The arms of the efferent ring unite to form the main efferent blood vessel, which extends through the trunk. This vessel connects with numerous branches or simple blind diverticula called capillary ceca, which bring blood close to the gut wall and other organs. In the end bulb, surrounding the stomach and first part of the intestine, blood flows from efferent to afferent vessels through spaces composing the **hemal** (**stomachic**) **plexus** (Figure 16.2D,E). Blood actually leaves the vessels here and flows through spaces between the organs and their bordering layers of peritoneum. Thus, technically speaking, the system is open at this point; however, blood flow is directed within the confines of these passages. Blood is moved through the circulatory system largely by muscular action of the blood vessel walls.

The intimate association of blood and the stomach wall suggests that nutrients are picked up from the stomach by the circulatory fluid and transported throughout

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the body. The tentacles of the lophophore are also probably the most important sites of gas exchange. Oxygenated blood flows from the lophophore into the efferent vessel and is then distributed to all parts of the trunk. The blood contains nucleated red corpuscles, with hemoglobin as the respiratory pigment.

A pair of metanephridia lies in the trunk, and each bears two nephrostomes opening to the metacoel (Figures 16.2E and 16.3A). In each nephridium, the nephrostomes—one large and one small—join a curved nephridioduct, which leads to a nephridiopore adjacent to the anus. Although virtually nothing is known about excretory physiology in phoronids, particulate crystalline matter has been observed exiting the nephridiopores and probably represents precipitated nitrogenous waste products. The nephridia also function as pathways for the release of gametes. Osmoregulatory problems are presumably insignificant in subtidally occurring phoronid species. However, little is known about the osmotic challenges faced by those species inhabiting intertidal and/or estuarine habitats.

Nervous System

The nervous system of phoronids is rather diffuse and lacks a distinct cerebral ganglion. This condition is no doubt related to the sedentary lifestyle and overall reduction in cephalization in these worms. Most of the nervous system is intimately associated with the body wall, being either intraepidermal or immediately subepidermal. Throughout the body a layer of nerve fibers is present between the epidermis and the circular muscle layer. Simple sensory neurons project out from this layer, either singly or in bundles, and extend to the body surface as the only receptor structures. Motor neurons extend inward to the muscle layers.

The central nervous system includes a group of basiepidermal neuronal cell bodies concentrated between the mouth and the anus (the so-called dorsal "ganglion" or neural plexus) connected to a collar nerve ring, which lies at the base of the lophophore and is continuous with the basiepidermal nerve layer. A proposed shared character among the nervous systems of phoronids and bryozoans may be present in the smallest phoronid species, *Phoronis ovalis*, which has two anterior ganglia. One of these ganglia is similar to that of other phoronid species, but the second, inner ganglion may be morphologically similar to the cerebral ganglion of bryozoans, thus retaining a potential plesiomorphic character (since *P. ovalis* is likely to be the sister group to all other living phoronid species). The collar nerve ring connects with frontal and abfrontal nerves of the tentacles and also with motor nerves that innervate some of the longitudinal muscles in the metasome. In addition, a bundle of sensory neurons extends from the nerve ring to each of the lophophoral organs.

Phoronids possess one or two longitudinal giant motor fibers in the trunk (absent in *Phoronis ovalis*). When only one longitudinal fiber is present, it lies on the left side. This fiber actually originates within the right side of the nerve ring, through which it passes to emerge on the left side. This nerve fiber is intraepidermal except where it extends inward along the left nephridium. In those species where two longitudinal fibers are present, the right one originates on the left side of the nerve ring and extends to the opposite side of the body.

Reproduction and Development

Asexual reproduction by transverse fission or by a form of budding has been documented in a few species. Phoronids are also capable of regenerating lost body parts, and various parts of the lophophoral end are capable of autotomy.

Phoronids have benthic adults and planktotrophic larvae, although one, *Phoronis ovalis*, has creeping lecithotrophic larvae. Both gonochoristic and hermaphroditic species of phoronids are known, and in the latter case some are simultaneous hermaphrodites (e.g., *Phoronis ijimai*, = *P. vancouverensis*). Phoronids spawn their fertilized eggs or early embryos into the environment and most brood their embryos among the tentacles of the adults or inside the mother's tubes, although in some species the entire development occurs in the water column. Recently, one species, *Phoronis embryolabi* (which lives commensally in burrows of an axiid shrimp), has been shown to be potentially viviparous, which would result in females releasing fully developed larvae into the environment.

The gonads are transient and form as thickened areas of the peritoneum around the hemal plexus (Figure 16.2D). The resulting mass of gamete-forming tissue and blood sinuses is sometimes called vasoperitoneal tissue. Gametes proliferate into the metacoel and typically are carried to the outside via the nephridia. Fertilization is usually internal, as in *Phoronopsis harmeri* (= *P. viridis*). In this species, the male lophophoral organs produce elaborately shaped spermatophores (Figure 16.3C) that are transferred to the metanephridial opening or tentacles of the females. In these females the lophophoral organs are called **nidamental glands** and serve as brooding areas. The complicated internal fertilization process in *Phoronopsis harmeri* was elucidated by Russel Zimmer. Spermatophores contacting the nephridiopore release ameboid masses of V-shaped sperm, which travel down the metanephridial funnels into the base of the trunk coelom near the ovary. If a spermatophore contacts a female's tentacle instead, the sperm enter the lophophoral coelom by lysis of the tentacular wall and then proceed to digest their way through the septum separating the mesocoel and metacoel into the trunk coelom, where fertilization occurs. Although fertilization has not actually been observed,

Zimmer's experimental data, coupled with the fact that fertilized ova occur internally, suggest that this scenario is the likeliest explanation.

Developmental strategy differs among species, the particular pattern depending in part on the size of the egg and whether or not the embryo is brooded. The ova of broadcast-spawning species contain little yolk and develop quickly to planktotrophic **actinotroch larvae** (Figure 16.4). In species that possess nidamental glands, fertilization is followed by brooding until release at the actinotroch stage. The eggs of these species are moderately rich in yolk, providing nutrients for the embryos during the brooding period. *Phoronis ovalis* lacks nidamental glands, but the yolky eggs are shed into the maternal tube where they are brooded. Development in *P. ovalis* does not include a typical actinotroch; instead, the embryos emerge through the autotomized lophophoral end as ciliated, sluglike larvae that have a short, planktonic life. Based on the expression of some evolutionarily conserved transcription factors, there is support for the idea that the actinotroch is derived from a "head-larva".

Since their first description, the evolutionary affinities of phoronids have been debated, as some developmental and morphological characters seemingly support both a deuterostome and protostome (spiralian) origin. Early reports of spiral-like cleavage in species that broadcast-spawn smaller (~60 μm) eggs have been corroborated by confocal and 4-D time-lapse microscopy. In these species (e.g., *Phoronis pallida*) the embryos have oblique (rather than perpendicular) cell divisions at the third and subsequent cleavages, accompanied by alternating dextral-sinistral twists, as in typical spiral development, although the products of cell division are equal. Species with larger (~100 μm) eggs typically have radial cleavage (e.g., *Phoronis ijimai*). In both cases, a coeloblastula forms and gastrulates largely by invagination. Cell labeling and other embryological experiments show that some of the larval mesoderm is derived from ectodermal cells, especially where the ectoderm is in contact with the endoderm; the remaining mesoderm is derived from the endoderm. Furthermore, a portion of the blastopore forms the mouth. Along with these developmental and morphological features, molecular phylogenetic evidence supports the relation of phoronids to brachiopods and bryozoans as well as more typical spiralians such as annelids, nemerteans, and molluscs (i.e., the Lophotrochozoa).

As noted, all phoronids except *Phoronis ovalis* produce distinctive **actinotroch larvae** (Figure 16.4A,D). The fully formed actinotroch bears a preoral hood, or lobe, over the mouth. As the actinotroch develops, an inpocketing (called the metasomal or juvenile trunk sac) forms on the ventral surface. At settlement and metamorphosis this sac everts, extending the ventral surface such that the anus and mouth remain close to one another as the gut is drawn out into the characteristic U shape. As discussed previously the structure of the hood "coelom" of some *Phoronis* species varies and may obliterate late in larval development. However, the hood coelom of *Phoronopsis harmeri* apparently has a true epithelial lining, at least a portion of which may be carried over during metamorphosis to form the coelomic lining of the juvenile epistome. Metamorphic remodeling of the larva into the juvenile form varies somewhat among species, but, in general, the neural and muscular tissues of the hood undergo histolysis. In some species the larval tentacles are remodeled into the juvenile lophophore during metamorphosis (Figure 16.4), but in other species the larval tentacles are shed, and the initial juvenile lophophore forms from separate tentacle rudiments. All of these dramatic tissue rearrangements can occur in as little as 15–20 minutes, after which the juvenile worms begin to secrete their tubes.

Phylum Bryozoa: The Moss Animals

Bryozoa (Greek *bryon*, "moss"; *zoon*, "animal"), sometimes called Ectoprocta (Greek *ecto*, "outside"; *procta*, "anus"), comprise sessile colonies of zooids living in marine and freshwater environments (Box 16B; Figure 16.5). Most colonies are the product of budding from a single, sexually produced individual called an **ancestrula**, but colonies may also develop from various types of resting bodies. The colony form differs

BOX 16B Characteristics of the Phylum Bryozoa

1. Organisms always colonial, with zooids developing through budding from a metamorphosed larva or from existing zooids
2. Each zooid consists of a polypide, which can be retracted into a cystid
3. Polypide composed of a ciliated tentacle crown used in suspension feeding, a U-shaped gut, a simple nervous system, and various muscles associated with extension and retraction into the cystid
4. Cystid wall consists of an extracellular gelatinous or chitinous cuticle, with a calcified basal layer in some groups, the epidermis, and the peritoneum; various types of muscles associated with the body wall
5. There are no discrete circulatory or excretory organs
6. Zooids are hermaphroditic in many species, but some species have male and female zooids within the same colony; gametes differentiate from transient patches of the body wall peritoneum or the funiculus
7. Cleavage radial and holoblastic; development indirect with planktotrophic cyphonautes larva or with lecithotrophic coronate or shelled larva; all internal larval organs degenerate after settling
8. Mostly sessile (a few colonies are movable or float) in marine or freshwater habitats

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FIGURE 16.5 Bryozoan diversity. (A–C) Ctenostomata. (A) *Triticella* growing on the antenna of a crustacean. (B) *Anguinella*. (C) *Alcyonidium* washed up on the shore. (D–F) Cheilostomata. (D) *Scruparia* growing on a coralline alga. (E) A small colony of *Membranipora* on a piece of kelp. (F) *Pentapora*. (G–I) Cyclostomata. (G) *Crisia*, note the white gonozooids on the two middle branches. (H) *Tubulipora*. (I) *Heteropora*. (J–L) Phylactolaemata. (J) *Plumatella*, part of a colony with many statoblasts in the body cavity. (K) *Cristatella*. (L) *Pectinatella*, large floating colonies (*ojassie*).

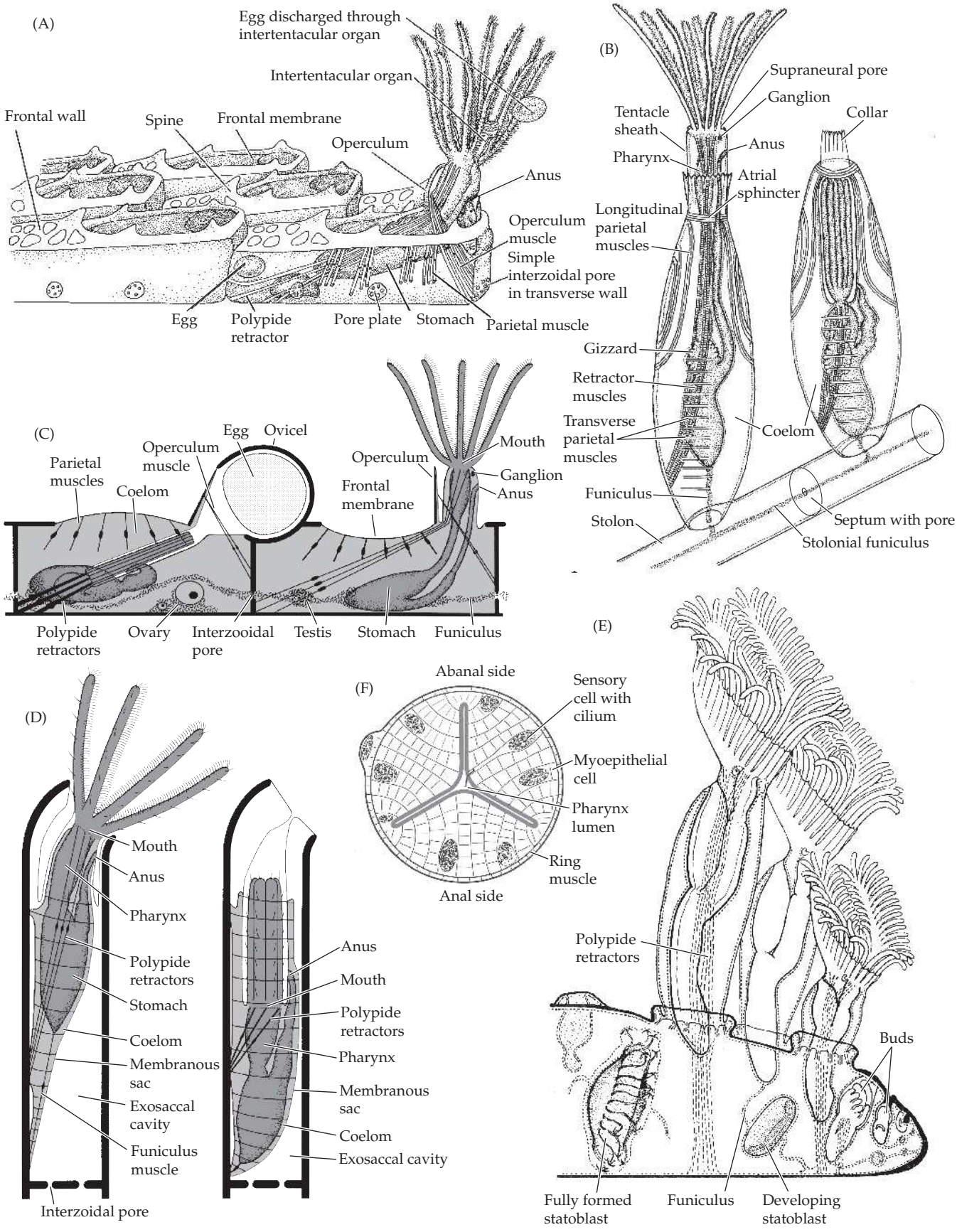

FIGURE 16.6 **Bryozoan morphology.** (A) General bryozoan structure, based on *Electra*. (B) Ctenostome anatomy, based on *Bowerbankia*. (C) Generalized cheilostome. Note constant volume of body cavity plus polypides in extended and retracted states. (D) Cyclostome, based on *Crisia*. Note constant volume of the exosaccal cavity and of body cavity plus polypide in extended and retracted states. (E) Phylactolaemate anatomy, based on *Cristatella*. (F) Diagram of transverse section of the myoepithelial pharynx of *Crisia*. (E,F after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

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greatly among species, and the bushy species were earlier treated as plants, so specimens can be found in older herbariums. Each zooid typically consists of a **polypide**, with a tentacle crown and the gut. These can be retracted into a **cystid**, which is the body wall of the individual zooid or the wall that is common to several zooids (Figure 16.6). Marine bryozoans are known from all depths and latitudes, mostly growing on or attached to solid substrata. A few species form free colonies that creep on the bottom (see Figure 16.8E). An Antarctic species forms gelatinous colonies on floating pieces of ice. A few species occur in fresh and brackish water. Large gelatinous colonies of *Pectinatella magnifica* are frequently encountered in streams and ponds in North America east of the Mississippi River. Meter-large floating colonies of the same species occur in Lake Shoji in Japan, where they are called *ojassie* (Figure 16.5L). Marine littoral regions in most parts of the world harbor luxuriant growths of bryozoans that often cover large areas of rock surfaces and algal fronds. Some species have coral-like growth forms that can create miniature "reefs" in shallow-water habitats. Others form dense bushlike colonies or gelatinous spaghetti-like masses. Many encrusting forms grow on the shells or exoskeletons of other invertebrates, and some bore into calcareous substrata. Most members of the gymnolaemate family Hippoporidridae grow on mollusc shells inhabited by hermit crabs, where evidence suggests a mutualistic relationship between the bryozoans and the crustaceans. Two classes are recognized here, Phylactolaemata and Gymnolaemata, and this is supported both by morphological and phylogenomic studies, but some authors treat the Stenolaemata as a third class. The fossil record suggests that the cheilostomes evolved from stem-group ctenostomes. About 6,300 living species are recognized, and there is a rich fossil record going back to the Early Ordovician.

CLASSIFICATION OF PHYLUM BRYOZOA

CLASS GYMNOLAEMATA Mainly marine bryozoans. Colonies with chitinous or calcified cystids; in calcified species, the cystid walls are primarily calcium carbonate, often with aragonite on the outer surface of the frontal walls; zooids rather small, monomorphic in some species, but especially the cheilostomes show several types of heterozooids; tentacle crowns circular or slightly oblique.

SUBCLASS EURYSTOMATA A highly diverse group of almost exclusively marine bryozoans. Colony form is extremely variable, soft or calcified, encrusting to arborescent; body wall lacks a continuous layer of muscles; zooids variably modified from basic cylindrical form; zooids joined by pores through which cords of tissue extend (the stolonal funiculus) and join with their neighbor's funiculus.

ORDER CTENOSTOMATA Colonies vary in shape from forms with hydroidlike individual zooids developing from free or creeping stolons to compact colonies; skeleton leathery, chitinous, or gelatinous, not calcified; openings through which tentacle crowns protrude lack operculum; zooids generally monomorphic. (e.g., *Aethozoon, Alcyonidium, Amathia, Bowerbankia, Flustrellidra, Nolella, Victorella*)

ORDER CHEILOSTOMATA Colony form varies, but generally of box-shaped zooids with calcareous walls; orifice with operculum; zooids often polymorphic; embryos usually develop in various types of brooding structures. (e.g., *Bugula, Callopora, Carbasea, Cellaria, Conopeum, Cornucopina, Cribrilaria, Cryptosula, Cupuladria, Electra, Eurystomella, Flustra, Hippothoa, Integripelta, Primavelans* (formerly *Hippodiplosia*), *Membranipora, Metrarabdotos, Microporella, Pentapora, Porella, Pyripora, Rhamphostomella, Schizoporella, Selenella, Thalamoporella, Tricellaria*)

SUBCLASS STENOLAEMATA Largely extinct; only surviving subgroup is Cyclostomata. Exclusively marine. Polypides housed in tubular, calcified skeletal compartments; zooids cylindrical or trumpet shaped, rarely polymorphic; each polypide surrounded by a coelomic sac, where the inner wall covers the gut, whereas the outer wall is free, forming the unique, so-called membranous sac, which consists of the coelomic epithelium, a series of tiny ring-shaped muscles, and a basal membrane; the body cavity outside the membranous sac, the exosaccal cavity, is continuous throughout the colony, either through small interzooidal pores or through larger common cavities; funiculus inside the coelomic cavity, not connecting neighboring zooids; reproduction involves specialized female zooids in which the fertilized egg develops through polyembryony, such that the embryos in a gonozooid are a clone. (e.g., *Actinopora, Crisia, Diaperoecia, Disporella, Hornera, Idmodronea, Tubulipora*)

CLASS PYLACTOLAEMATA Freshwater bryozoans. Colonies with chitinous or gelatinous cystids; zooids cylindrical, large, and monomorphic; tentacle crown large and usually horseshoe shaped; body wall muscles well developed; body cavity of the zooids in open connection throughout the colonies; a cord of tissue, the funiculus, extends from the gut to the body wall, but not between zooids; most produce asexual resting bodies called statoblasts. (e.g., *Cristatella, Hyalinella, Lophophus, Lophopodella, Pectinatella, Plumatella*)

The Bryozoan Body Plan

Bryozoan specialists have developed a complicated terminology, especially concerning the morphology of the cystids, and some terms have, quite confusingly, been given various definitions. Early workers mistakenly thought that bryozoan zooids were actually

composed of two organisms, the skeletal outer wall and the internal soft parts, which they named the cystid and polypide, respectively. These terms were redefined by Hyman (1959) and now have good meaning relative to the functional morphology of bryozoans. The **cystid** comprises the outer body wall—that is, the nonliving and living housing of each zooid. The **polypide** includes the **tentacle crown** (the lophophore) and soft viscera that can be protruded and retracted from the cystid (Figure 16.6). The opening in the cystid through which the tentacle crown extends is termed the **orifice** and bears a flaplike, chitinous covering, or operculum, in the cheilostomes.

The nature of the body wall differs among bryozoans, as does the form of the colony. It is entirely gelatinous or chitinous in the Ctenostomata and Phylactolaemata, but it has an inner calcified layer called the **zoecium** in the Cheilostomata and Cyclostomata (Figure 16.7). Many studies are based on colonies that have been cleaned of all organic material so that the specific characters of the calcified and often highly ornamented zoecia can be studied.

The Gymnolaemata include a bewildering array of colonial forms (Figure 16.5A–I). Some of the ctenostomes have colonies in which the zooids arise from runners or stolons on the substratum (e.g., *Triticella*, *Bowerbankia*). This apparently represents the ancestral gymnolaemate pattern as suggested by the fossil record. In the other forms, the zooids are more or less closely packed, with pores between neighboring zooids. These colonies may be sheet shaped and encrusting on stones or algae, erect and leaf shaped or arborescent, or in a few cases discoidal and free-living.

In addition to the variation in overall form among the colonies, zooids of many cheilostomes and some cyclostomes are polymorphic within a colony. Typical tentacle-crown-bearing, feeding zooids are called **autozooids**. The widespread *Membranipora* normally consists only of autozooids. Most other colony types have both the normal autozooids and various types of nonfeeding zooids, called **heterozooids**. Among these, **kenozooids** are reduced individuals modified, for example, for attachment to a substratum; various types of attachment discs, "holdfasts," and stolons are in this category. Many cheilostomes possess heterozooids called **avicularia**, each of which bears an operculum modified as a movable mandible (or jaw), which articulates against a rigid extension of the body wall called the **rostrum** (Figure 16.8). Some avicularia occur in the general layer of zooids, while others are large and situated at the side of the branched colonies (Figure 16.8D), but a much more common type is smaller and situated on the frontal wall or on the ovicells. A special type of avicularium is the pedunculate or bird's-head avicularium, which looks like the head of a parrot; it is attached to the colony through a stalk and able to perform nodding movements (Figure 16.8B,C). Avicularia, which were first described by Charles Darwin in 1845 based on observations of a bugulid made aboard the *Beagle*, probably function primarily to defend the colony against small organisms and keep the surface clean of debris.

Another type of heterozooid is the **vibraculum** (Figure 16.8A,E), which is thought to be a modified avicularium, with a flagellum-like operculum that sweeps over the colony surface. Vibracula may help remove sediment particles and other material, but convincing evidence for this function is wanting. In the free-living, discoidal cheilostomes, such as *Selenella* and *Cupuladria*, the vibracula are used in locomotion (Figure 16.8E).

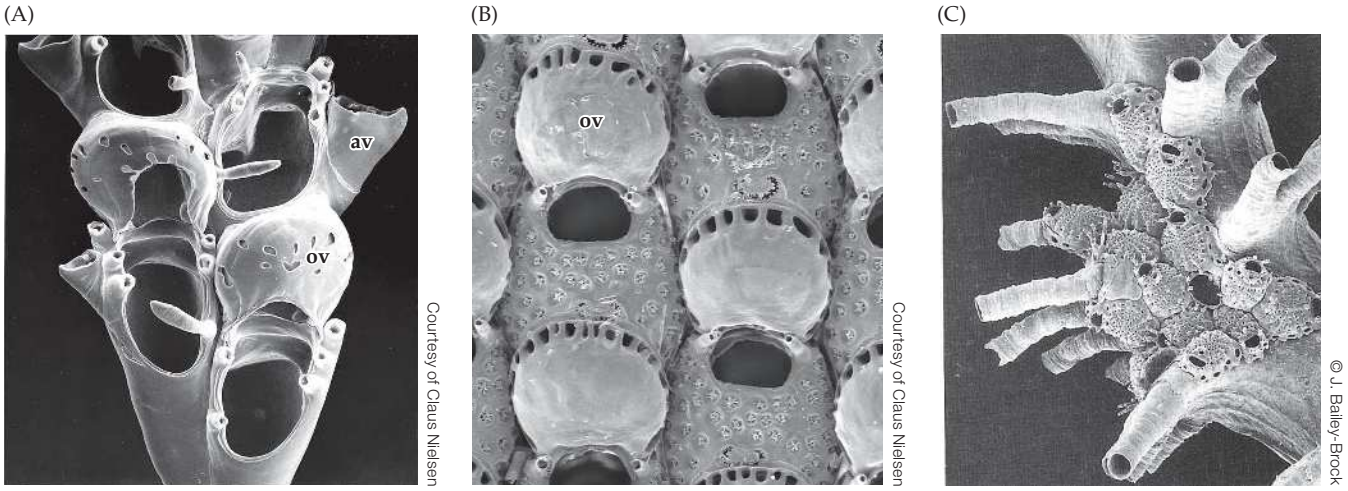

FIGURE 16.7 Zoecia of cheilostomes and cyclostomes (SEMs). (A) The cheilostome *Tricellaria occidentalis*; two zooids with ovicells (ov) and a lateral avicularium (av). (B) The cheilostome *Fenestrulina malusii*; rows of zooids with ovicells (ov). (C) Part of a colony of the cyclostome *Idmidronea* (the large tubular structures) with the small cheilostome *Cribrilaria* growing between the large tubes. (Note the small ancestrula in the lower middle of the colony, of a completely different structure with a large frontal membrane and small spines along the edge.)

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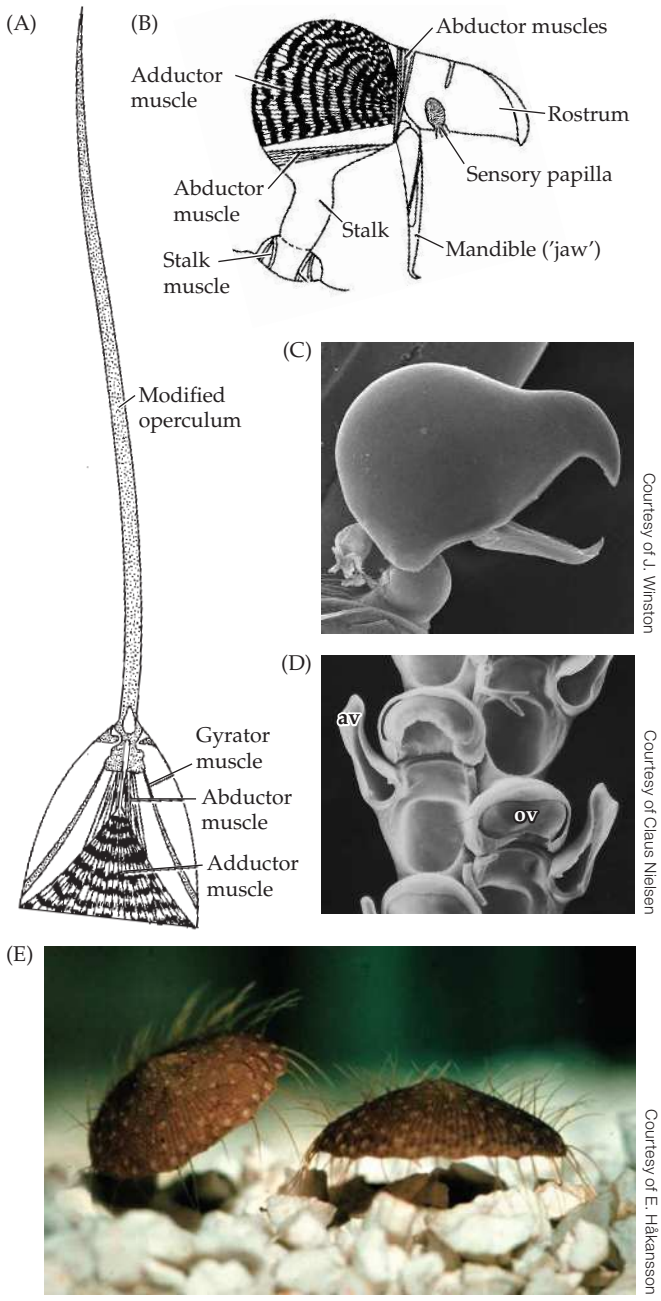

FIGURE 16.8 Heterozooids. (A) Diagram of a vibraculum. (B) Diagram of an avicularium. (C) SEM of an avicularium of *Bugula*. (D) Zoecia of *Tricellaria*; avicularia (av) and ovicell (ov). (E) Two colonies of *Selenella* walking with vibracula.

Most members of the Phylactolaemata display either plumatellid or lophopodid colony forms (Figure 16.5K,L). **Plumatellid** colonies are erect or prostrate and often highly branched, like *Plumatella*. In **lophopodid** colonies, the gelatinous body wall forms the surface of irregular clumps from which the tentacle crowns protrude, as seen in *Pectinatella* and *Lophophus*. The colonies of the remarkable *Cristatella* are gelatinous, sluglike, and capable of locomotion, gliding over the substratum powered by the action of the cilia of the tentacle crown.

The Body Wall, Coelom, Muscles, and Movement

The body wall comprises the outer secreted body wall, the underlying epidermis, and the peritoneum. The outer body wall may be uncalcified or have a strong calcified inner layer (the zoecium). Sheets of circular and longitudinal muscles are present between the epidermis and peritoneum in phylactolaemates, but these muscle sheets are specialized in the other groups to form various groups of separate muscles.

Many bryozoans possess ornate and species-specific surface sculpturing including spines, pits, and protuberances. Experiments indicate that the cheilostome *Membranipora membranacea* undergoes a rapid growth of new protective surface spines after being grazed by predatory nudibranchs. Some bryozoans also produce chemicals used as defense against would-be predators. These chemicals are probably all synthesized by symbiotic bacteria.

The mechanisms of polypide retraction and extension (protraction) differ among bryozoan species. The specific mechanism depends largely upon the arrangement of muscles, the degree of rigidity of the cystid, and the morphology of the coelomic compartments, which function as a hydrostatic skeleton (see Figure 16.6).

In all bryozoans, the main coelom provides a fluid-filled space with muscles acting directly or indirectly to increase hydraulic pressure for extension of the polypide. Thus, when the coelom is compressed, the polypide is partially forced out of the cystid, thereby extending the tentacle crown. The retractor muscles, which originate at the basal part of the cystid wall and insert on the thickened basal membrane surrounding the mouth, serve to pull the polypide back within the cystid. Generally, the methods of polypide extension are common to all bryozoans, but the muscle groups involved differ considerably in their morphology. Here we describe a few examples of how these movements are accomplished and, at the same time, illustrate variations on the basic bryozoan body plan.

The phylactolaemates show the simplest mechanism. They extend their polypides by contracting the muscles of the flexible body wall around the common body cavity. This action imposes pressure directly on the coelomic fluid and is similar to the mechanism seen in many other coelomate animals. These bryozoans possess a ring-shaped, muscular diaphragm just internal to the orifice through which the tentacle crown protrudes. The diaphragm relaxes as the tentacle crown is protracted and serves to partially close off the orifice when the tentacle crown has been withdrawn by retractor muscles (Figure 16.6E).

Ctenostomes possess an uncalcified, flexible body wall composed of gelatinous, chitinous, or leathery material. Contraction of transverse parietal muscles pulls the cystid walls inward, thereby causing an increase in

coelomic pressure that then extends the tentacle crown (Figure 16.6B). Retraction of the tentacle crown is accomplished by the usual retractor muscle, which is aided by longitudinal parietal muscles that pull in the atrial chamber. When the tentacle crown is fully retracted, a sphincter contracts to close the orifice and, in some species, fold a pleated collar over the end of the zooid.

Cheilostomes and cyclostomes show many intricate variations in the method of polypide extension and retraction, but they all rely on the constant volume of the coelom, which functions as a hydrostatic skeleton.

Cheilostomes have cystids that are calcified to various degrees. A completely stiff body wall would make polypide movements impossible, so various areas of the cystids are uncalcified and can be moved in or out by groups of special muscles of the body wall. In most species, the zooids are more or less boxlike (rather than erect or tubular). The outer surface of the box that bears the orifice is called the frontal surface. It has a partly uncalcified and flexible part called the **frontal membrane**, and contraction of parietal protractor muscles pulls the frontal membrane inward, thus increasing coelomic pressure and pushing out the polypide (Figure 16.6C). There are, of course, variations on this general theme. An operculum closes over the orifice when the polypide is retracted, but the exposed frontal membrane presents a weakness in the defense against predation, and many species have evolved more or less complicated protective structures (Figure 16.9). Some forms, known as the **cribrimorphs**, bear hard spines that project over the membrane and in some cases actually meet and fuse to form a cage above the vulnerable area (Figure 16.7C). In others a calcified partition, called the frontal shield or **cryptocyst**, lies beneath the frontal membrane, separating it from the soft parts within. The cryptocyst bears pores through which the protractor muscles extend (Figure 16.9). The most drastic modifications are seen in the so-called **ascophoran** type (Figure 16.9), in which the frontal wall is heavily calcified except for a small pore below the orifice. This opening, the ascopore, leads into the invaginated sac-shaped frontal membrane, called the **ascus**. The parietal muscles insert on the ascus. Cheilostomes are the most diverse and species-rich group of bryozoans.

Cyclostomes have erect, tubular zooids surrounded by heavily calcified zoecia (Figure 16.6D). The inflexibility of the body wall and the absence of well-developed sheets of muscles preclude use of direct compression, so they have evolved a mechanism of polypide protraction unique among the bryozoans. The structural features associated with this mechanism comprise a synapomorphy on which this group was established as a separate subclass. The key structure is the membranous sac, which is the detached peritoneum of the cystid wall plus its basal membrane and a series of tiny ring muscles. It is attached by ligaments to the body wall and separates the coelom from the outer exosaccal cavity. Distally, the

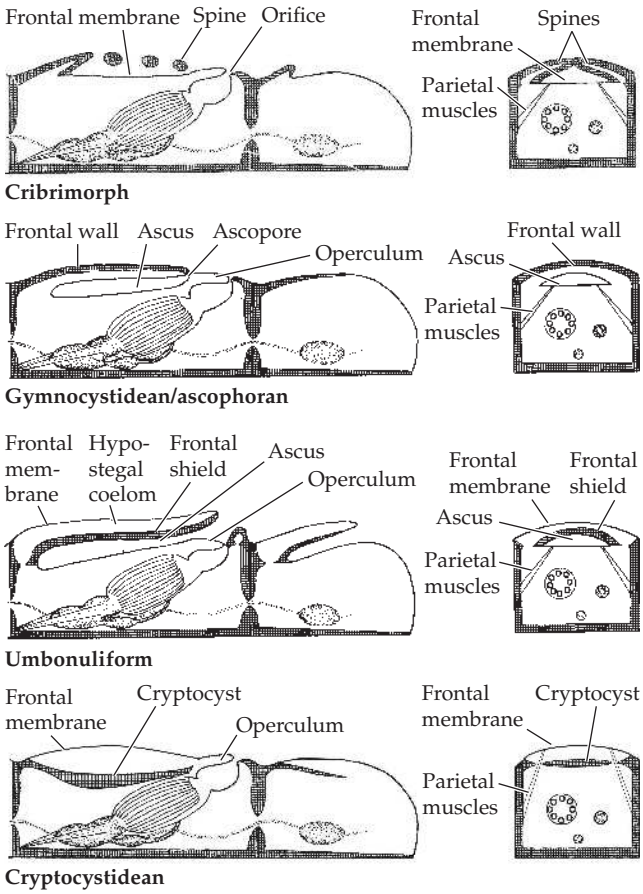

FIGURE 16.9 Frontal walls. Diagrams of four different types.

exosaccal space harbors a series of fine atrial dilator muscles. Protraction of the polypide involves relaxation of the retractor and atrial sphincter muscles and contraction of the atrial dilators and the ring muscles of the membranous sac. With the constant volumes of both the coelom and the exosaccal cavity, the polypide is squeezed out. When a zooid is retracted by the large retractor muscles, the atrial dilators are relaxed and a special atrial sphincter effectively closes the inner end of the atrium.

Zooid Interconnections

As discussed in Chapter 4, clear definitions of the term "colony" are sometimes elusive. This difficulty arises because it is not always easy to tell where one individual ends and another begins, or because the degree of structural and functional communication among individuals is uncertain or variable. Bryozoan zooids, at least autozooids, are clearly demarcated by the elements of the polypide (tentacle crown, gut, ganglion, and so on); however, the way in which the zooids are interconnected differs among groups.

In phylactolaemates the coelom is continuous among zooids, uninterrupted by septa (Figure 16.6E). Each zooid bears a tubular tissue cord called a **funiculus**

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that extends from the inner end of the curved gut to the body wall. All other bryozoans lack extensive coelomic connections, and the zooids are separated by various sorts of structural components.

Stoloniferous Eurystomata (e.g., *Bowerbankia*; Figure 16.6B) have septa spaced along the stolons between the zooids. A cord of tissue passes along the stolons and through pores in each septum. This cord, called a **stolonal funiculus**, connects with the funiculus of each zooid arising from the stolon. In most nonstoloniferous Eurystomata the cystid walls of adjacent zooids are penetrated by pores with tissue plugs, which, again, usually connect with the funiculus of associated zooids. In the cheilostomes the pores are covered by pore plates with a number of small openings.

The walls of adjacent zooids of cyclostomes bear interzooidal pores or common distal cavities that allow communication of exosaccal coelomic fluid (Figure 16.6D). The funiculus is contained within the coelom with the rest of the viscera and attaches the gut to the body wall. The exchange of nutrients between zooids, for example, between the feeding autozooids and the nonfeeding gonozooids, remains a mystery.

It is clear that bryozoan zooids are interconnected structurally, either by direct sharing of coelomic spaces or by funicular tissue, except for the enigmatic cyclostomes. Functionally, these connections provide a means of distributing materials through the colony, and perhaps they serve in other communal activities as well. Other special functions of the funiculus are discussed later in the chapter.

The Tentacle Crown, Feeding, and Digestion

The tentacle crown (which is a lophophore) is horseshoe shaped in the phylactolaemates (except for *Fredericella*) and circular in the gymnolaemates and cyclostomes. The tentacles are ciliated, with the cilia arranged in characteristic bands related to the feeding mechanism. Bryozoans are suspension feeders, although supplemental methods may also be used. They feed largely on protists, but some species are able to capture and ingest larger organisms.

Upon extension, the tentacles of the circular tentacle crowns of gymnolaemates and cyclostomes are erected in a funnel or bell-shaped arrangement around the mouth. Each tentacle bears four or five ciliary bands along its length, one frontal tract (lacking in the cyclostomes), and a pair of laterofrontal and lateral bands (Figure 16.10). During normal suspension feeding, the lateral cilia create a current that enters the open end of the funnel, flows toward the mouth, and then exits between the tentacles. Some food particles are carried directly to the area of the mouth by the central flow of water. Other potential food, however, moves peripherally with the current toward the intertentacular spaces. When a particle contacts the rather stiff laterofrontal cilia, a tentacle flick is initiated, moving the particle toward the central current (Figure 16.10E). Additional flicks may occur if particles have not reached the central current. A localized reversal of power stroke direction is initiated in the lateral cilia, and the particle may be tossed onto the frontal edge of the tentacle. The particle is repeatedly bounced in this fashion and is moved toward the mouth under the influence of a current generated by the frontal cilia.

Many bryozoans supplement suspension feeding by various means that allow them to capture relatively large food particles, including live zooplankton. Some species, such as *Bugula neritina*, are capable of trapping zooplankton or large algae by folding their tentacles over the prey and pulling it to the mouth. A number of bryozoans rock or rotate the entire tentacle crown, apparently sampling reachable water for food.

All the polypides in a colony transport water toward the surface of the colonies. This is no problem for branching, bushy types, but in colonies forming larger sheets the water must flow away again, and this has led to the formation of various types of **excurrent chimneys**. Polypides may simply bend away from a small area, which then creates a chimney. Large colonies of *Membranipora* show regularly spaced areas without polypides, which function as excurrent chimneys (Figure 16.11A). Other chimneys may be formed by small groups of nonfeeding male zooids or pregnant zooids with degenerated polypides. In leaf-shaped colonies (e.g., *Pentapora*), the leaf edges may function as excurrent areas (Figure 16.11B). The generation of strong excurrent water flow away from the colony surface helps to push nonfood material and feces far enough to reduce the possibility of recycling. Such currents, which move larger amounts of water over the tentacle crowns than could be moved by individual zooids, may be especially important to colonies inhabiting quiet water.

The digestive tract is U-shaped (Figures 16.6B,C and 16.12). The mouth lies within the tentacle ring, and in the Phylactolaemata it is overlain by an **epistome**. Cilia around the mouth keep the captured particles rotating in front of the mouth, and from time to time the mouth is opened, and in the gymnolaemates the particles are sucked into the triradiate pharynx by contraction of the radiating epitheliomuscular cells (Figure 16.6F). A valve separates the lower end of the pharynx from the descending portion of the stomach, which is called the **cardia** and in some species is modified as a grinding gizzard. The cardia leads to a central stomach from which a large cecum arises; the funiculus attaches to the bottom of the cecum. The ascending portion of the stomach, or **pylorus**, arises from the central stomach and leads to a proctodeal rectum and the anus, which lies outside the tentacle crown ring. A sphincter controls the flow of material from the pylorus to the rectum. The phylactolaemates have a flat, funnel-shaped, ciliated pharynx without radiating muscles, and the hindgut is elongated as an intestine.

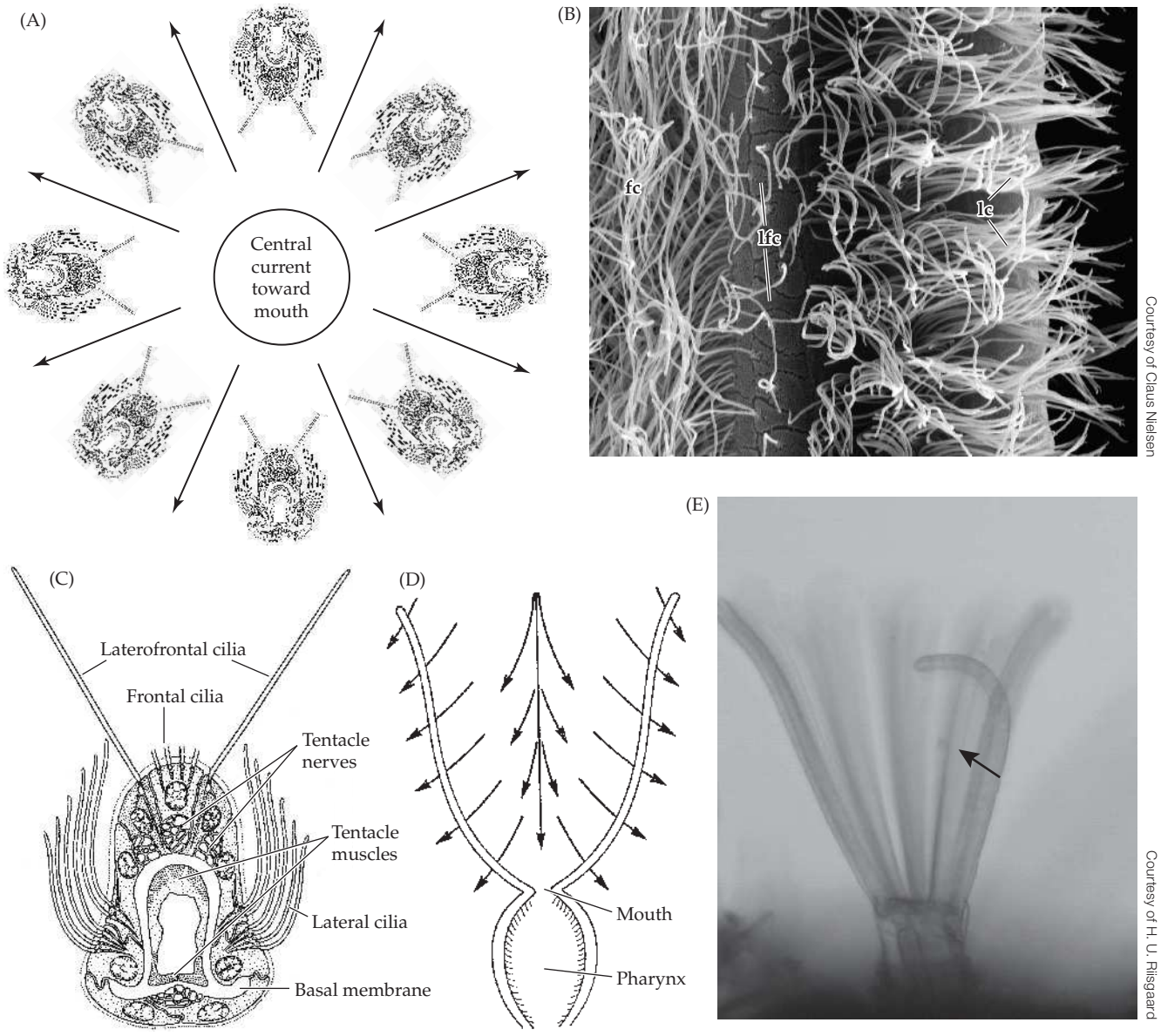

FIGURE 16.10 Tentacles and filter feeding. (A) Diagram of transverse section of a tentacle crown; the directions of the water currents set up by the lateral cilia are indicated. (B) SEM of one side of a tentacle of *Flustrellidra* with the three ciliary bands: frontal cilia (fc); lateral cilia (lc; note the metachronal waves); laterofrontal cilia (lfc, unnaturally curved due to fixation). (C) Transverse section of a tentacle of *Electra* (based on TEM). (D) Diagram of ciliary currents set up by the lateral cilia. (E) Tentacle flick. Note the small alga (arrow) that has just been pushed into the central current.

Digestion begins extracellularly in the cardia and central stomach, and it is completed intracellularly in all parts of the stomach. Food is moved through the gut by peristalsis and cilia. Undigested material is rotated and formed into a spindle-shaped mass by the cilia of the pylorus and then passed to the rectum for expulsion.

Circulation, Gas Exchange, and Excretion

There is no structural circulatory system in bryozoans, so movement of metabolites within single zooids is by diffusion. Given the small size of these animals, intrazooid diffusion distances are small, and the coelomic fluid provides a medium for passive transport. Interzooid circulation is facilitated by the common coelom in phylactolaemates, the cystid pores in cyclostomes, and the funicular cords of most Eurystomata. Gas exchange occurs across the walls of the extended parts of the polypide, particularly the tentacle crown. Bryozoans contain no respiratory pigments, and gases are carried in solution.

Nondigested particles and waste products accumulate in the cells of the stomach. The elimination of these wastes is not fully understood, but apparently it occurs at least in part by the cyclic degeneration of the polypides that form structures called **brown bodies**. New

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FIGURE 16.11 Excurrent chimneys. (A) *Membranipora*; the dark areas of empty cystids form the excurrent chimneys. (B) Diagram of a cross section of four leaves of a colony of *Primavelans* (formerly *Hippodiplosia*) showing the incoming currents set up by the tentacles (medium arrows), the currents along the colony surface below the tentacles (short arrows), and the excurrents (long arrows) at the edge of the leaves.

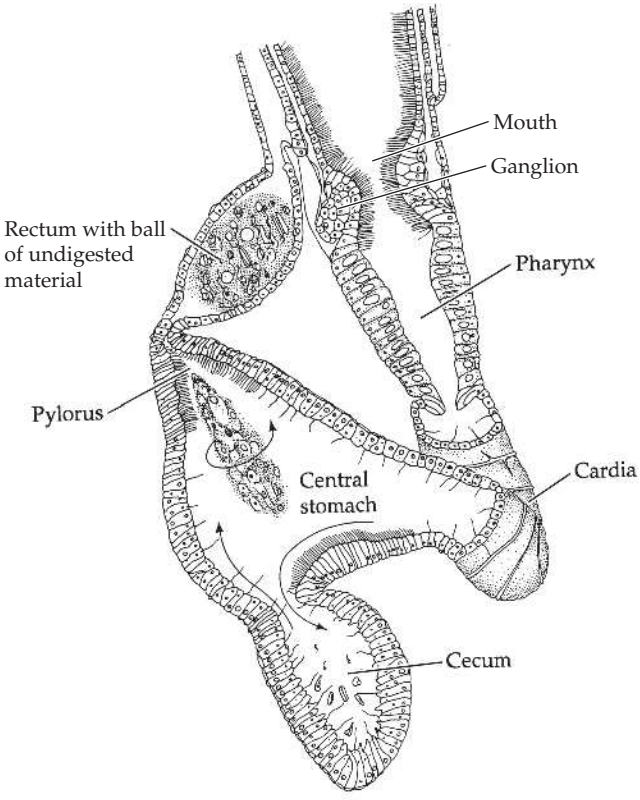
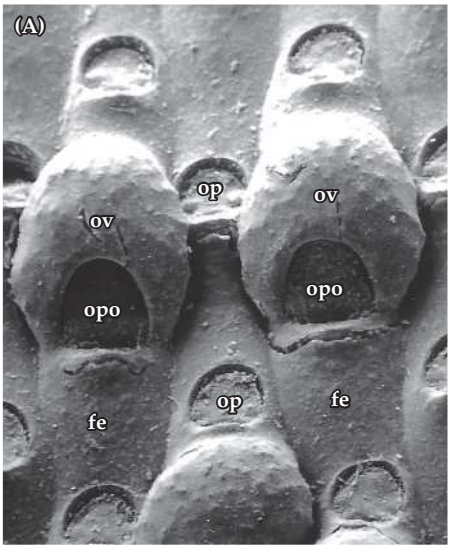


FIGURE 16.12 The gut of *Cryptosula*. The ingested particles rotate in the stomach and the rectum.

polypides are then formed through the usual budding process from the area of the orifice. In some Eurystomata the brown body is left within the basal part of the cystid, and the number of regenerated polypides can be assessed by the number of brown bodies. In other species, the brown body is taken up into the gut of the developing polypide and expelled as the first fecal pellet when the new polypide first protrudes from the cystid. In most stoloniferous ctenostomes, the old cystid with its brown body drops from the colony, and an entire new zooid regenerates from the stolon. In all cases, it is presumed that metabolic wastes are precipitated and concentrated in the brown bodies and thus eliminated or at least rendered inert.

Nervous System and Sense Organs

In concert with the sessile lifestyle and the lack of a discrete head in bryozoans, the adult nervous system and sense organs are predictably reduced. A neuronal mass, or cerebral ganglion, lies on the anal side of the pharynx (Figure 16.6B,C). Arising from this structure is a circumoral nerve ring. Nerves extend from the ring and ganglion to the viscera, and motor and sensory nerves extend into each tentacle. Interzooidal nerve fibers have been reported in some species, but their function remains unclear. The only known receptors are tactile cells on the tentacles (the laterofrontal ciliary cells [Figure 16.10B,C] and single cells on the abfrontal side) and on the sensory papilla of the avicularia (Figure 16.8B). The Eurystomata larvae have an apical organ, which supposedly is sensory, and a ciliated **pyriform organ** that is used in testing the substratum before settling. At least some bryozoans exhibit a marked negative geotaxis prior to settling. Experiments suggest that this geotaxis is a direct response to gravity, but the mechanism mediating this phenomenon is unknown. Many of the coronate



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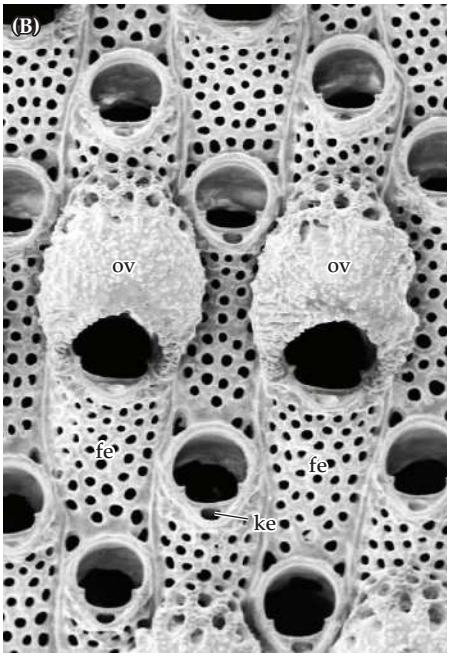

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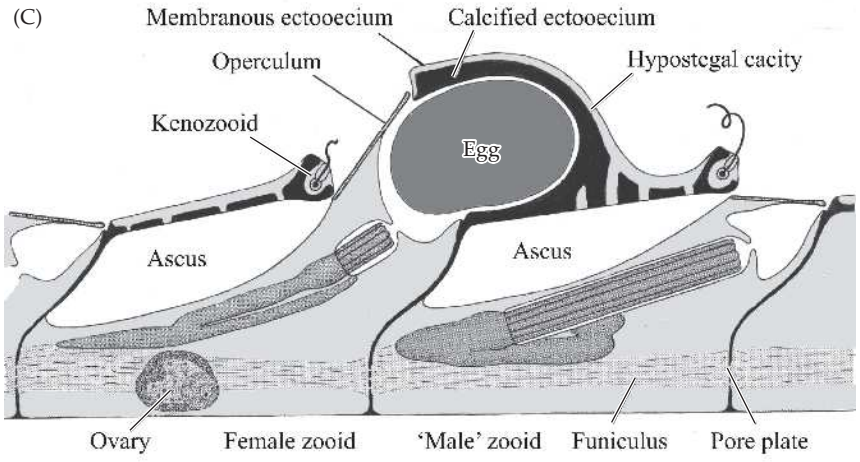

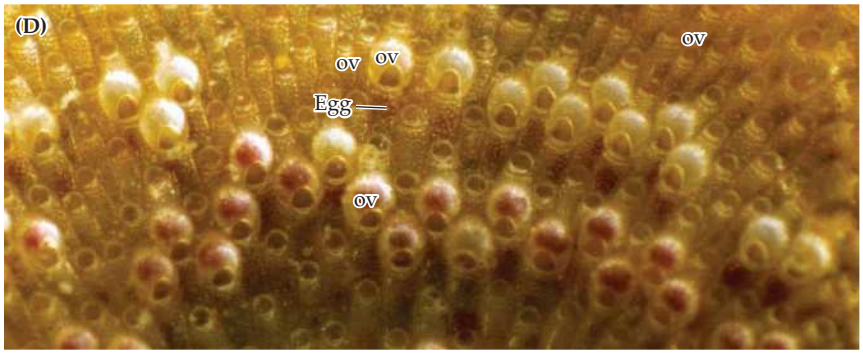

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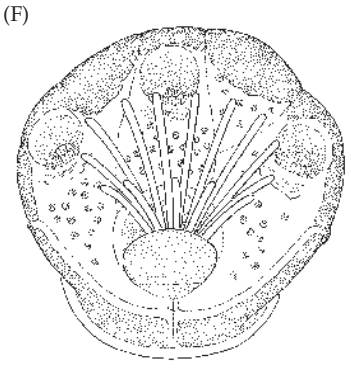

FIGURE 16.13 Reproduction of *Primavelans insculpta* (formerly *Hippodiplosia*). (A,B) SEM of two female zooids (fe), which have induced their distal neighbors to form an ovicell (ov); the operculum of a "male" zooid (op); the operculum of the ovicell (opo; the cracks at the kenozooids are artifacts). (A) Uncleaned with the outer periostracum and the opercula retained. (B) Cleaned zoecium of a similar part of the colony; kenozooid (ke). (C) Diagram of a median section of a female and a "male" zooid. (D) Part of a colony with rows of female and "male" zooids; the upper labeled ovicell (ov) is newly formed and still empty, and large cherry-red eggs can be distinguished in the body cavity of the females; the lower ovicell contains a newly deposited egg. (E) SEM of newly released larva (note heavy ciliation). (F) The composite ancestrula with one zooid with protruded tentacles and three developing zooids.

larvae have well-developed ocelli and are positively phototactic while free swimming. Settlement is often accompanied by a shift to a negative phototaxis.

Reproduction and Development

Sexual reproduction Bryozoan colonies are hermaphroditic. Some species may produce sperm and eggs in the same zooid (e.g., *Membranipora*), whereas other species (e.g., cyclostomes) have colonies with separate male and female zooids of very different shapes. Rather diffuse ovaries usually arise from transient patches of the peritoneum on the cystid wall. Testes usually develop on the funiculus (Figure 16.6C). Sperm differentiates in the body cavity, and the ripe sperm move to the coelom at the base of the tentacles and are eventually shed through small temporal pores at the tips of the abfrontal tentacles. The sperm enter the body cavity of a zooid with a ripe egg, probably through the supraneural pore located between the bases of two abfrontal tentacles, or the intertentacular organ, to fertilize the eggs. The few cheilostomes and ctenostomes that spawn fertilized

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eggs into the water (e.g., *Electra*, *Membranipora*, *Hislopia*, and some species of *Alcyonidium*) have the supraneural pore elevated on a pedestal called the **intertentacular organ** (Figure 16.6A). However, most species brood the eggs in more or less elaborate structures.

Phylactolaemates brood their embryos in embryo sacs produced by invaginations of the body wall. The eggs may leave the supraneural pore and become implanted into the embryo sacs in a method like that observed in ctenostomes (e.g., *Victorella*), but the process has not been observed.

Some ctenostomes (e.g., *Triticella*) attach the eggs to the atrial wall so that they become freely exposed when the polypides protrude. Others (e.g., *Victorella*) deposit the fertilized egg into a brood pouch formed by the atrial wall, and a further specialization is that the fertilized eggs are retained in the retracted atrium where the whole development takes place while the polypide degenerates (e.g., *Bowerbankia* and species of *Alcyonidium*).

A variety of brooding methods occur among cheilostomes, usually involving the formation of an external brooding structure called an **ovicell** (Figures 16.6C, 16.7A,B, 16.13A–D, and 16.14A). In many genera (e.g., *Fenestrulina*, *Primavelans*, and *Tegella*), the developing female zooids induce the developing distal zooid (male or female) to produce an ovicell by a specialization of the proximal part of the frontal wall (Figure 16.13A–D). Some species deposit a very large egg into the ovicell, where the development to the free-swimming lecithotrophic larval stage takes place. The opening is usually covered by the operculum of the maternal zooid. Other species desposit a small egg into the ovicell, which is closed by an extension of the distal wall of the maternal polypide. This extension is called the **oecial vesicle** and functions as a placenta that nourishes the developing embryo (e.g., *Bugula*) (Figure 16.14A).

Bryozoans undergo radial, holoblastic, nearly equal cleavage to form a coeloblastula or a stereoblastula. Subsequent development differs greatly among groups, but in all cases it involves a free-swimming dispersal form. Very little solid information exists on the derivation and fates of germ layers in bryozoans. This is especially true for mesoderm and coelomic linings.

In phylactolaemates, the fertilized egg enters a brood sac formed from the cystid wall, and later stages receive nourishment from the maternal zooid through various types of placentas. The coeloblastula develops into a cystidlike stage lacking endoderm and then generates one or more polypides through a normal budding process. This "larva" is ciliated and escapes the embryo sac for a short swimming life before settling and metamorphosing.

The coeloblastulae of Eurystomata undergo a gastrulation where four cells divide and one of each pair of daughter cells is shunted to the blastocoel as presumptive endoderm and mesoderm. Free-swimming larvae are eventually produced. Most of the species that free spawn have a characteristic laterally compressed, triangular larva called a **cyphonautes**, which

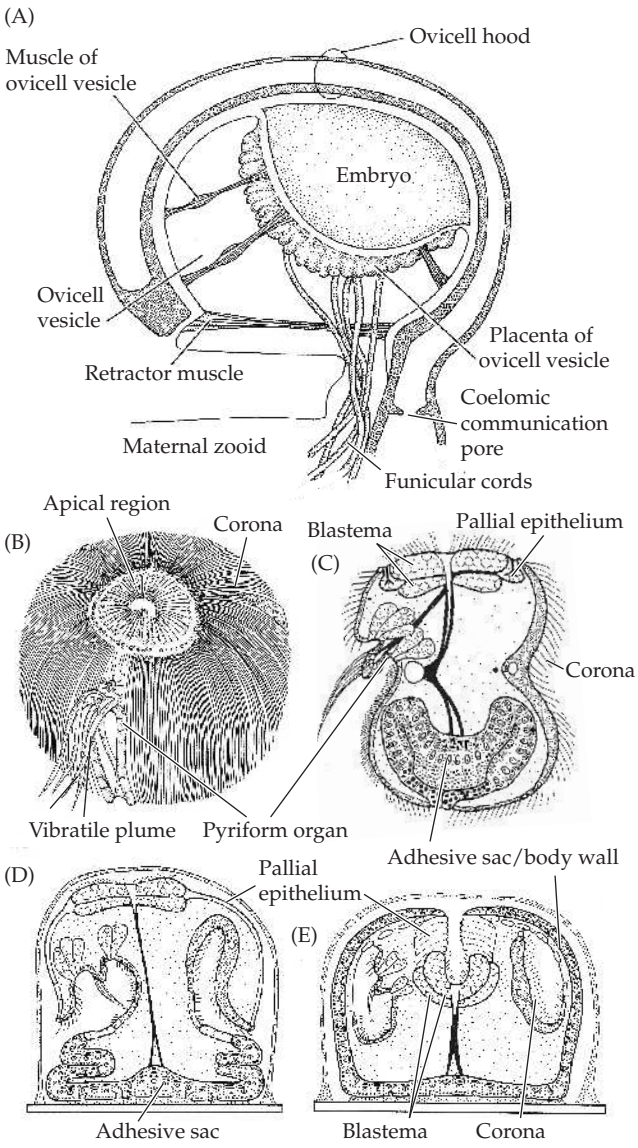

FIGURE 16.14 Brooding and larval metamorphosis of *Bugula neritina*. (A) Ovicell with an embryo that has grown large through nourishment from the placenta. (B) Drawing of a larva. (C–E) Larva, settling, and metamorphosis. (C) Median section of the larva. (D) The adhesive sac is everted in contact with the substratum, and a fine pellicle has been secreted; the everted pallial epithelium covers the upper side of the ancestrula, and the corona has become internalized. (E) The pallial epithelium has retracted again, and the epithelium of the adhesive sac now covers the whole ancestrula; the polypide will differentiate from the blastema.

swims by means of a ring of cilia at the "lower" edge of the triangular shells (Figure 16.15A,B). This larval type is found in both basal ctenostome and cheilostome groups. These larvae feed by means of the U-shaped ciliated ridge, which resembles and functions like one side of an adult feeding tentacle. They have a complete gut and may remain in the plankton for months, whereas the larvae of brooding species lack a digestive tract and lead very short, pelagic lives

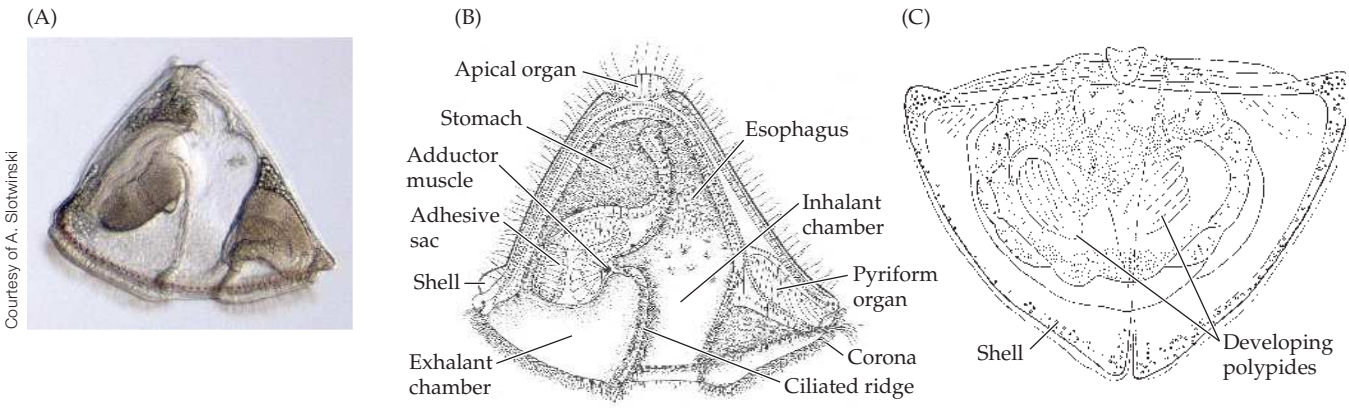

FIGURE 16.15 Larvae of *Membranipora*. (A) Cyphonautes larva. (B) Diagram of the morphology of the cyphonautes larva. (C) Newly settled larva; the shells are still covering the young ancestrula, which is developing a pair of polypides.

(Figures 16.13E and 16.14B). These more or less globular larvae are called **coronate larvae**, because the ciliation that covers almost the whole body is believed to be the extended ciliary ring of the cyphonautes larva. Despite these differences, Eurystomata larvae have some fundamental similarities. For example, they possess a complicated apical organ, a sensory pyriform organ complex, and a pouchlike **adhesive sac**, which are important in settling and metamorphosis (Figures 16.13E, 16.14B, and 16.15B).

In the cyclostomes, each colony contains only one or a few female zooids. When the small female zooid has become fertilized, its tentacles degenerate, and the zooid grows to a large, pear-shaped (Fig. 16.5G) or irregular **gonozooid**, nourished by the neighboring autozooids. The fertilized egg cleaves to form a ball of cells, which then undergoes a budding process, forming secondary embryos, which in turn bud tertiary embryos. Dozens of small, solid, asexually produced embryos may result from a single primary ball of cells. This phenomenon, called **polyembryony**, is very unusual in the animal kingdom. Each embryo develops cilia and escapes as a completely ciliated larva with an invagination at both poles, one representing the apical organ/pole and the other being the adhesive sac. The larva settles after a short free period and undergoes a metamorphosis similar to that described for the coronate Eurystomata larvae, with the frontal wall covered by the everted chitinous covering of the apical invagination.

Many bryozoan larvae are at first positively phototactic, and many possess pigment spots with a group of modified cilia that are thought to be light sensitive. Following a planktonic phase, the larvae usually become negatively phototactic and swim toward the bottom as they become competent (i.e., preparing to settle onto the substrate). Once in contact with the substratum, the pyriform organ complex is apparently used to test for chemical and tactile cues reflecting the suitability of the substratum for settling. Once a proper surface has been selected, the adhesive sac everts and secretes sticky material for attachment. After attachment, there is a thorough reorganization of tissue positions accompanied by histolysis of larval structures.

In gymnolaemates, the first zooid, the ancestrula, usually has one polypide, but two or more polypides are found in several species (Figures 16.13F and 16.15C). The settling cyphonautes larva everts the adhesive sac, which spreads out along the substratum and secretes the basal wall of the ancestrula. The shells open widely and become detached, while the underlying pallial epithelium secretes the frontal wall. The corona becomes enclosed in an inner ring-shaped cavity. Metamorphosis of the various types of coronate larvae shows considerable variation on this theme. In one type (e.g., *Bugula*; Figure 16.14C–E), the periphery of the everted adhesive sac extends along the sides of the settled larva finally to cover the whole outer wall of the larval body; thus, the whole cystid wall originates from the adhesive sac. In other types (e. g., *Bowerbankia*), the adhesive sac retracts again, and the pallial epithelium expands to cover the whole surface of the ancestrula.

Asexual reproduction As in all colonial animals, asexual reproduction is an integral part of the life history of bryozoans and is responsible for colony growth and regeneration of zooids. Each colony begins from the tissues of a metamorphosed larva, which develops one or a few zooids from the body wall, or in some Eurystomata from a mass of undifferentiated cells (called a **blastema**) connected with the apical organ. As in sexual reproduction, this first zooid or group of zooids that develops before feeding begins is called the ancestrula (Figures 16.7C and 16.13F). The ancestrula undergoes budding to produce daughter zooids, which subsequently form more buds, and so on. The initial group of daughter zooids may arise in a chain-like series, a plate, or a disc; the budding pattern determines the growth form of the colony and is highly variable among species. The ancestrula is usually of a shape different from that of the budded zooids (Figure

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FIGURE 16.16 Statoblasts of phylactolaemates.
(A) *Cristatella*. (B) Germinating statoblast of *Fredericella*.

16.7C), and in a few species, changes in zooid morphology along the growing colony have been observed.

Budding involves only elements of the body wall. In most Eurystomata, a partition forms that isolates a small chamber, the developing zooid, from the parent zooid. The bud initially includes only components of the cystid and an internal coelomic compartment. A new polypide is then generated from the living tissues of the bud (the epidermis and the peritoneum). The epidermis and peritoneum invaginate, the former producing the tentacle crown and the gut. The peritoneum produces all of the new coelomic linings and the funiculus. Budding in phylactolaemates is similar, except that the polypide develops first and only becomes isolated from the parent zooid in some species. Budding among cyclostomes is in need of further investigation.

In addition to budding, freshwater bryozoans (Phylactolaemata) reproduce asexually by the formation of **statoblasts** (Figures 16.6E and 16.16). These structures are extremely resistant to drying and freezing and are often produced in huge numbers during adverse environmental conditions. Statoblasts generally form on the funiculus and include peritoneal and epidermal cells plus a store of nutrient material. Each cellular mass secretes a pair of chitinous protective valves, differing among species in shape and ornamentation. The parent colony usually degenerates, freeing the statoblasts. Some statoblasts sink to the bottom, but others float by means of enclosed gas spaces and are thus called floatoblasts. Some bear surface hooks or spines and are dispersed by passive attachment to aquatic animals or vegetation (Figure 16.16A). With the return of favorable conditions, the cell mass generates a new zooid, which sheds its outer casing and attaches as a functional individual (Figure 16.16B).

Phylum Brachiopoda: The Lamp Shells

Members of the phylum Brachiopoda (Greek *brachium*, "arm"; *poda*, "feet") are called lamp shells because the shape of their exoskeleton resembles historical oil lamps (Box 16C; Figure 16.17). They have been known since at least the early Middle Ages, and their images were published in books in the late sixteenth century. All are solitary, marine, benthic creatures, although they often aggregate, forming clumps of individuals. The body, including the lophophore, is enclosed between a pair of dorsoventrally oriented valves. Unlike bivalve molluscs, with two lateral shells that hinge dorsally, brachiopod shells are arranged dorsal and ventral and hinge posteriorly. Most brachiopods are attached to the substratum

BOX 16C Characteristics of the Phylum Brachiopoda

1. Enterocoelic, coelomate lophophorates
2. Epistome present, with or without coelomic lumen
3. Body enclosed between two shells (valves), one dorsal and one ventral
4. Usually attached to the substratum by a stalk, the pedicle, or cemented by the ventral valve
5. Valves lined (and produced) by mantle lobes formed by outgrowths of the body wall and creating a water-filled mantle cavity
6. Lophophores circular to variably coiled, with or without internal skeletal support
7. Gut U-shaped; anus present (Linguliformea, Craniiformea) or absent (Rhynchonelliformea)
8. One or two (Rhynchonellida) pairs of metanephridia
9. Circulatory system rudimentary and open
10. Most gonochoristic with mixed or indirect life histories
11. Indirect developers with lecithotrophic larvae
12. Gametes developing from transient gonadal tissue on peritoneum of metacoel
13. Cleavage holoblastic, radial, and nearly equal; coeloblastulae usually with gastrulation by invagination; blastopore giving origin to mouth, or blastopore closing and mouth (and anus) forming secondarily
14. Solitary, benthic, marine

(A)

Courtesy of Verena Haeussermann

(B)

Courtesy of Dirk Schories

(C)

Courtesy of Nina Furchheim and Anne Kaufuss

(D)

Courtesy of Dave Meyer and Ben Datillo

(E)

Courtesy of Dirk Schories

(F)

Courtesy of Dirk Schories

FIGURE 16.17 Representative brachiopods. (A) *Magellania venosa* (Rhynchonelliformea). Reaching lengths of 9 cm, this is the largest living brachiopod; from Chilean fiords. (B) Close-up of *M. venosa*, showing the lophophore inside the shell and branched egg-carrying mantle canals shining through the dorsal valve. (C) At less than 1 mm in length, *Gwynia capsula* (Rhynchonelliformea) is the smallest living brachiopod; the gaping valves expose the lophophore, which is forming a small circle of single tentacles. (D) *Thecidellina meyeri* (Rhynchonelliformea), with fully opened shell. The orange lophophoral tentacles form an effective filter for microplankton. (E) The limpetlike *Novocrania lecointei* (Craniiformea), which directly attaches to hard substrates with its ventral valve. (F) The organophosphatic shelled *Discinisca lamellosa* (Linguliformea) with its fringing row of setae protruding from the mantle margin. (G) *Lingula* sp. (Linguliformea), removed from its burrow. (H) *Lingula* sp. (Linguliformea) in feeding posture. The arrows indicate the direction of water flow. (I) *Marginifera* sp., a spinose Permian brachiopod. (J) *Lingula* sp. for sale in a market in Southeast Asia, where it is locally consumed. (K) The articulate brachiopod *Frenulina sanguinolenta* (Rhynchonelliformea) from the tropical Pacific, showing the position of the lophophore. Attached to the shell is a purple bryozoan, *Disporella* sp.

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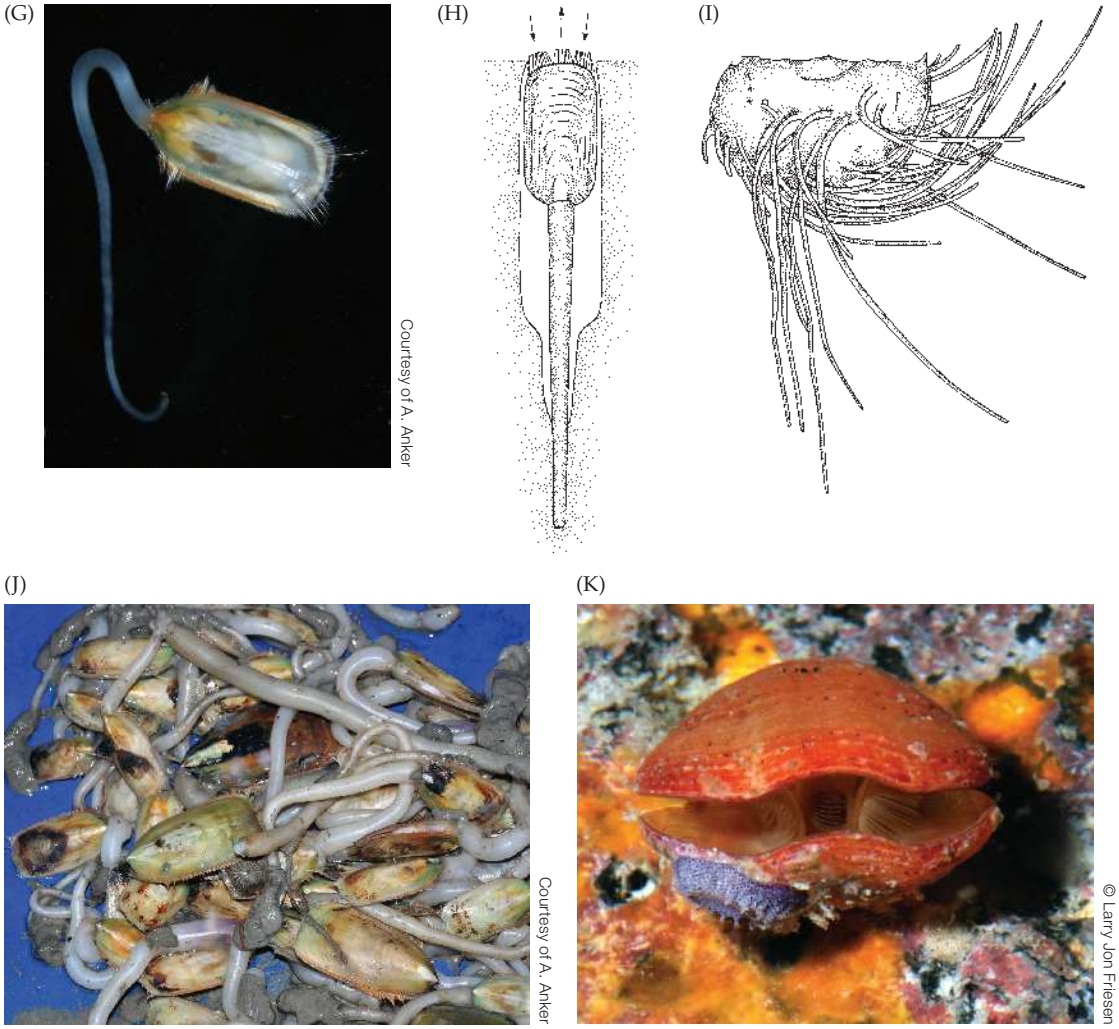

by a fleshy **pedicle** (Figure 16.18A,B), although some species lack a pedicle (e.g., *Novocrania*) and usually cement themselves directly to a hard substratum. On the other hand, some species that possess a pedicle do not form permanent attachments, such as *Anakinetica cumingi*, which lies free, and *Lingula* spp., which anchor in loose sand (Figures 16.17G,H,J and 16.18B). A few species possess both unattached and attached populations (e.g., *Neothyris lenticularis* and *Magasella sanguinea*).

The valves of the brachiopod shell are unequal and are attached to one another either posteriorly, by a tooth-and-socket hinge (Rhynchonelliformea), or simply by muscles (Linguliformea, Craniiformea). Rhynchonelliform brachiopods normally "sit" ventral side up, the pedicle usually arising from the ventral valve through a shell opening called the **foramen**. Most extant brachiopods measure 2 to 4 cm along the greatest shell dimension but range from less than 1 mm to over 9 cm in extreme cases. Although they are known from nearly all ocean depths, they are most abundant on the continental shelf.

The approximately 440 living species of brachiopods represent a small surviving fraction of the 12,000 to 15,000 extinct species that have been described. Their rich fossil record dates back at least 541 million years (earliest Cambrian), and possible stem-group brachiopods may be present even earlier in the fossil record. Brachiopods, especially rhynchonelliforms, were among the most abundant animals of the Paleozoic, but they declined in numbers and diversity after that time. Exceptionally preserved linguliforms are especially well known from the Cambrian Chengjiang biota, and there was a prolific radiation in the phylum during the Ordovician Period. It has been proposed that competition with epibenthic bivalve molluscs was at least partly responsible for the reduction in brachiopod diversity following their Paleozoic success. We recognize three living subphyla of Brachiopoda.

CLASSIFICATION OF THE BRACHIOPODA

SUBPHYLUM LINGULIFORMEA Valves not hinged, attached by muscles only; valves of organophosphatic composition, including apatite (calcium phosphate), chitin, collagen, and proteins; pedicle usually with intrinsic muscles and a coelomic lumen; lophophore without

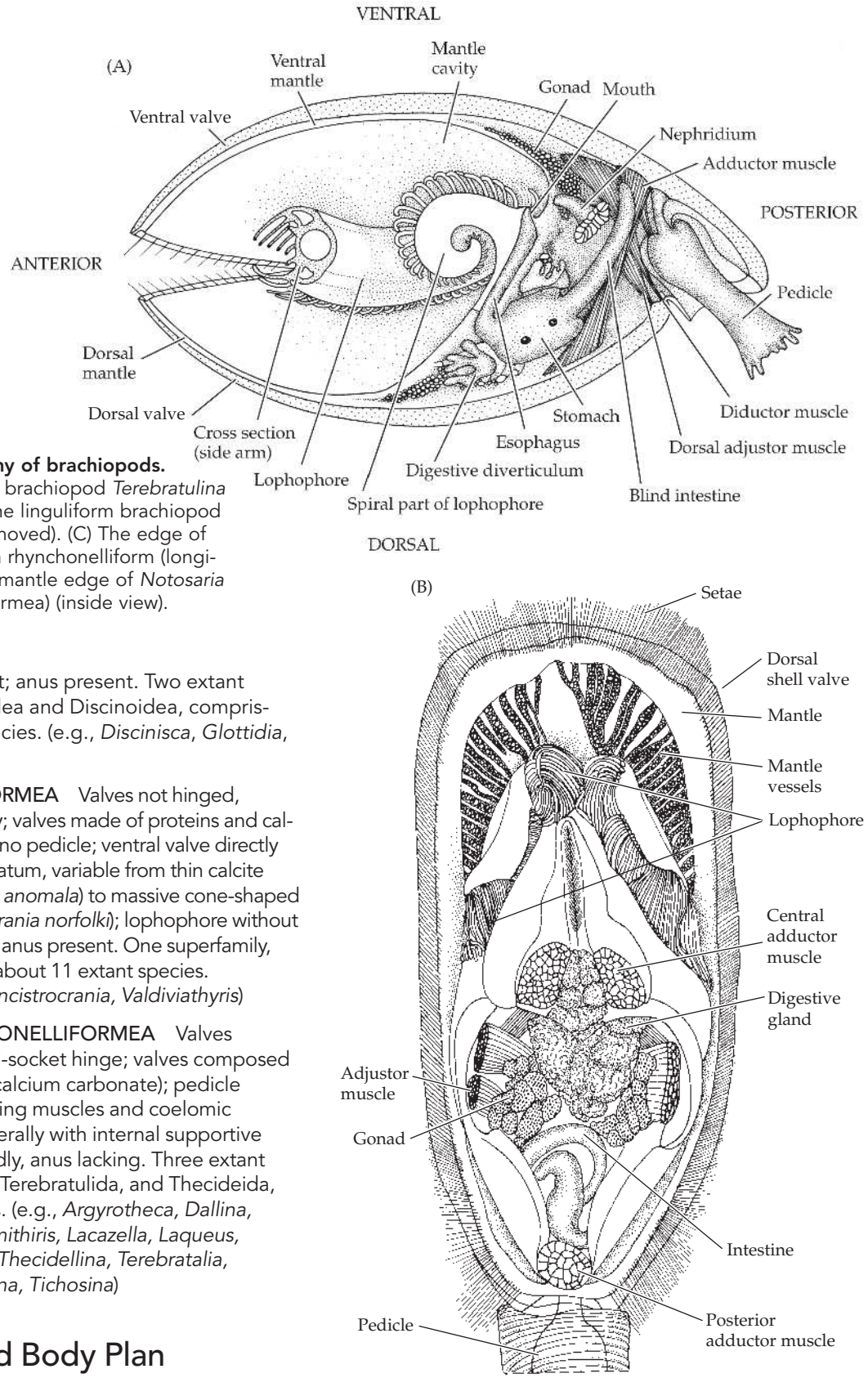

FIGURE 16.18 Anatomy of brachiopods. (A) The rhynchonelliform brachiopod *Terebratulina* sp. (cutaway view). (B) The linguliform brachiopod *Lingula* (ventral valve removed). (C) The edge of the shell and mantle of a rhynchonelliform (longitudinal section). (D) The mantle edge of *Notosaria nigricans* (Rhynchonelliformea) (inside view).

internal skeletal support; anus present. Two extant superfamilies, Linguloidea and Discinoidea, comprising about 25 extant species. (e.g., *Discinisca*, *Glottidia*, *Lingula*, *Pelagodiscus*)

SUBPHYLUM CRANIIFORMEA Valves not hinged, attached by muscles only; valves made of proteins and calcite (calcium carbonate); no pedicle; ventral valve directly cemented to hard substratum, variable from thin calcite lamella (e.g., *Novocrania anomala*) to massive cone-shaped valve (e.g., *Neoancistrocrania norfolki*); lophophore without internal skeletal support; anus present. One superfamily, Cranioidea, comprising about 11 extant species. (e.g., *Novocrania*, *Neoancistrocrania*, *Valdiviathyris*)

SUBPHYLUM RHYNCHONELLIFORMEA Valves articulated by tooth-and-socket hinge; valves composed of proteins and calcite (calcium carbonate); pedicle usually present, but lacking muscles and coelomic lumen; lophophore generally with internal supportive elements; gut ends blindly, anus lacking. Three extant orders: Rhynchonellida, Terebratulida, and Thecideida, with around 400 species. (e.g., *Argyrotheca*, *Dallina*, *Frenulina*, *Gryphus*, *Hemithiris*, *Lacazella*, *Laqueus*, *Liothyrella*, *Magellania*, *Thecidellina*, *Terebratalia*, *Terebratella*, *Terebratulina*, *Tichosina*)

The Brachiopod Body Plan

The Body Wall, Coelom, and Support

The shells of brachiopods comprise an outer organic **periostracum** and an inner structural layer or layers composed variably of calcium carbonate (calcite), calcium phosphate (apatite), proteins, chitin, and collagen. Extant discinids may have siliceous nanoparticles covering their periostracum. Various spines were also present in some fossil species in multiple lineages as outgrowths of the shell and served to anchor the animals in place (Figure 16.17I). In a fashion similar to that of molluscs, brachiopod shells are secreted by a **mantle**. This mantle is divided into a dorsal and a ventral mantle formed as an outgrowth of the body wall (Figure 16.18). The

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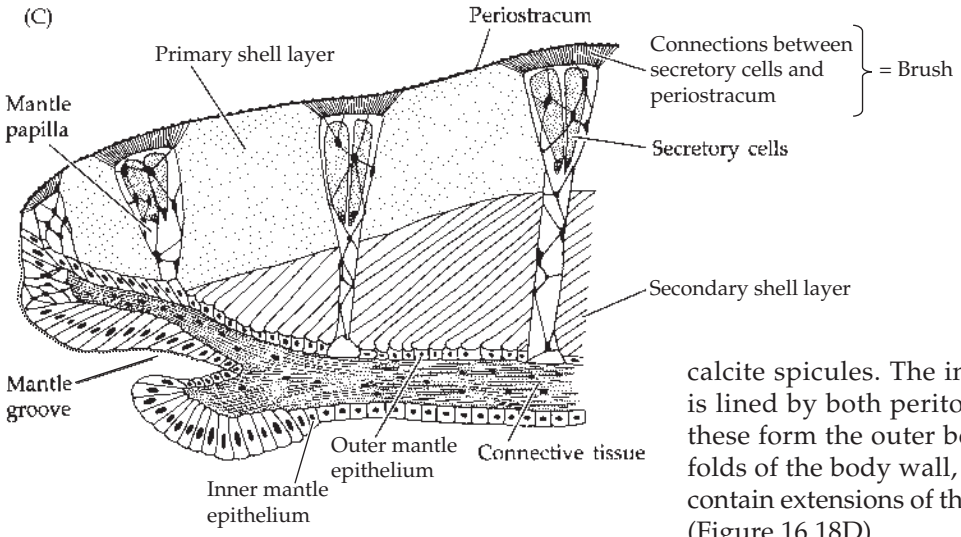
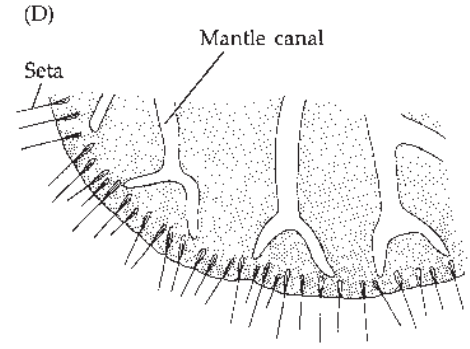




periostracum is secreted by the mantle edges in a periostracal slot, and the inner shell layer by the general mantle surface, the outer mantle epithelium. Shells of many brachiopods bear perforations, or punctae, extending from their inner surfaces nearly to the periostracum and containing tiny tissue extensions of the mantle (Figure 16.18), quite similar to the aesthetes found in chitons. The function of these mantle papillae is unknown, but some workers have suggested that they might serve as areas for food storage and gas exchange or in some way deter the activities of borers. Shells that lack perforations are termed impunctate.

The soft mantle lines and is attached to the dorsal and ventral valves of the shell and forms the water-filled mantle cavity, which houses the lophophore. The mantle edges often bear chitinous setae, which may protect the fleshy tissue and perhaps serve to prevent the entrance of large particles into the mantle cavity. Once thought to be a striking convergence with the annelid chaetae, the presence of chaetae/setae in both groups, with nearly identical ultrastructure and development, is used as a possible synapomorphy of lophotrochozoans. The mode of chaetogenesis has also been proposed to be related to spiculogenesis in molluscs.

The epidermal cells of the mantle and general body surface vary from cuboidal to columnar and are monociliated. Beneath the epidermis is a connective tissue layer of varying thickness, which in some species may house mesenchymal cells and can produce calcite spicules. The inner surface of the body wall is lined by both peritoneal and myoepithelial cells; these form the outer boundary of the coelom. Being folds of the body wall, the dorsal and ventral mantle contain extensions of the coelom, called **mantle canals** (Figure 16.18D).

The pedicle is an outgrowth of the body wall, arising from the posterior area of the ventral valve. In linguliforms it contains all the usual layers beneath the epidermis, including connective tissue, muscles, and a coelomic lumen. However, the pedicle of rhynchonelliforms lacks muscles and a coelomic cavity. In the latter case extrinsic muscle bands from the body wall itself operate the pedicle. In brachiopods that attach firmly, the tip of the pedicle bears papillae or fingerlike extensions that adhere tightly to the substratum.

The coelomic system of brachiopods includes the typical mesocoel and metacoel as the lophophoral and body coeloms, respectively. The epistome is solid in rhynchonelliforms, but in linguliforms it may contain coelomic cells that are continuous with the lophophoral mesocoel. The coelomic fluid includes various coelomocytes, some of which contain hemerythrin.

The Lophophore, Feeding, and Digestion

Like that of phoronids and bryozoans, the lophophore of brachiopods comprises a ring of tentacles surrounding the mouth. In brachiopods, however, the lophophore is produced as a pair of tentacle-bearing arms that extend anteriorly into the mantle cavity. The overall shape of the lophophore varies among taxa, from a simple circular or U shape to forms with highly coiled arms. The brachiopod lophophore also differs in that it is always contained within the protection of the valves and is essentially immovable. In most brachiopods, the lophophore and tentacles are held in position by coelomic pressure, whereas in most rhynchonelliforms the dorsal valve produces a lophophore-supporting structure, the brachidium. In some groups (e.g., Thecideida) the dorsal valve has ridges and grooves, instead of an erect lophophore skeleton, that help support and position the lophophore.

In order to pass a water current through the mantle cavity, the two valves must be opened slightly. The mechanisms of valve operation differ among members of the three subphyla. In hinge-bearing rhynchonelliforms, there are two pairs of muscles responsible for

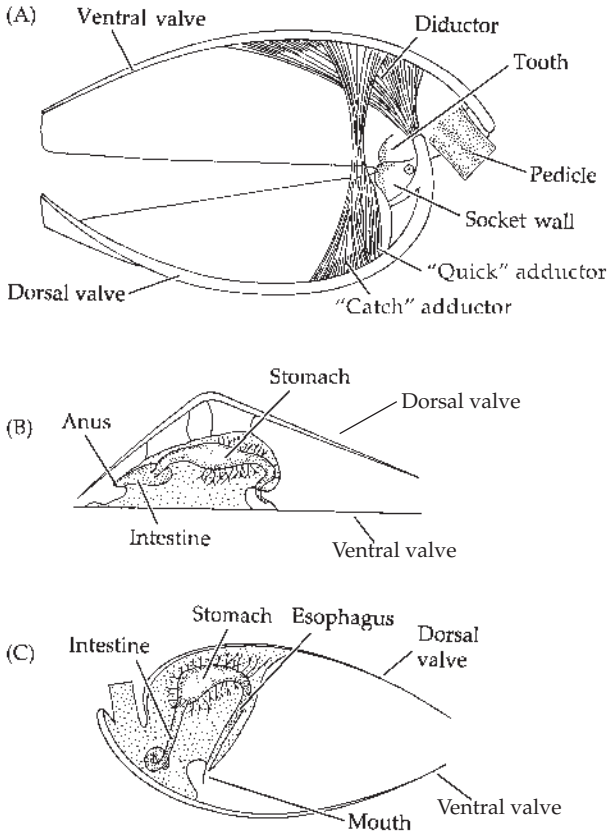
valve movements—whereas a pair of diductor muscles opens the valves (Figures 16.18A,B and 16.19A), the adductor muscle pair is responsible for shell closure. Linguliforms and craniiforms lack a hinge and do not possess diductor muscles. Instead, the gape is produced by contraction of the posterior adductor or the umbonal muscle and relaxation of different anterior muscle groups. Central adductor muscles are mainly used to close the valves. As both shell opening and closure depend on either rapid or long-lasting active muscle contraction, diductor and adductor muscles contain striated as well as smooth fibers.

Feeding currents are generated by the lophophoral cilia. Specific incurrent and excurrent flow patterns occur, varying with shell morphology and the shape and orientation of the lophophore. In any case, water is directed over and between the tentacles before it is passed out of the mantle cavity (Figure 16.20A). Each tentacle bears lateral and frontal ciliary tracts (Figure 16.20B). The lateral cilia of adjacent tentacles overlap and redirect food particles from the water to the frontal cilia by beat reversal. The frontal cilia beat toward the base of the tentacles, helping to direct trapped food. The lophophoral ridge, or brachial axis, bears a brachial food groove within which food material is moved to the mouth (Figure 16.20C). Brachiopods feed on nearly any appropriately small organic particles, especially phytoplankton.

The digestive system is U-shaped (Figures 16.18A and 16.19B,C). The mouth is followed by a short esophagus, which extends dorsally and then posteriorly to the stomach. A digestive gland covers most of the stomach and connects to it via paired ducts. The intestine extends posteriorly, where it ends blindly in rhynchonelliforms or recurves as a rectum terminating in an anal opening in inarticulated brachiopods. In the latter case the anus opens either medially (craniiforms) or on the right side of the animal (linguliforms). The absence of an anus is almost certainly a secondary loss in rhynchonelliforms and can be traced back to differences in the fate of the blastopore during early embryonic development, in comparison to craniiforms. Little is known about digestion in brachiopods, but some work on *Lingula* indicates that it occurs intracellularly in the digestive gland.

Circulation, Gas Exchange, and Excretion

The brachiopod circulatory system is open, much reduced, and largely unstudied. A contractile heart lies in the dorsal mesentery just above the gut (*Novocrania* possesses several "hearts"). Leading anteriorly and posteriorly from the heart, the blood vessels form channels within the connective tissue of the mesenteries, thus no true vessels are present. These channels branch to various parts of the body, but the pattern of circulation is not fully understood. It appears that the blood is separate



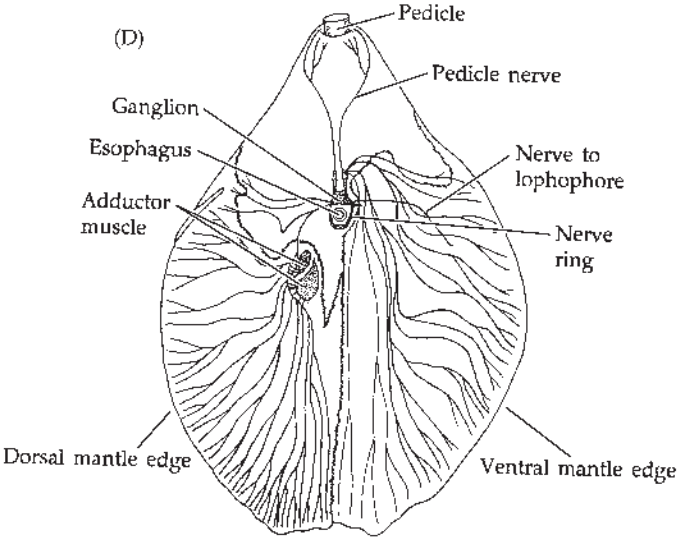


FIGURE 16.19 Anatomy of brachiopods. (A) The rhynchonelliform brachiopod *Calloria inconspicua* (Terebratelloidea) (ventral side up; cutaway view). Note the major muscles that operate the valves. (B) The complete gut of a craniiform. (C) The blind gut of a rhynchonelliform. (D) The nervous system of *Magellania flavescens* (Rhynchonelliformea). Note the dorsal and ventral aspects on the left and right sides of the drawing, respectively.

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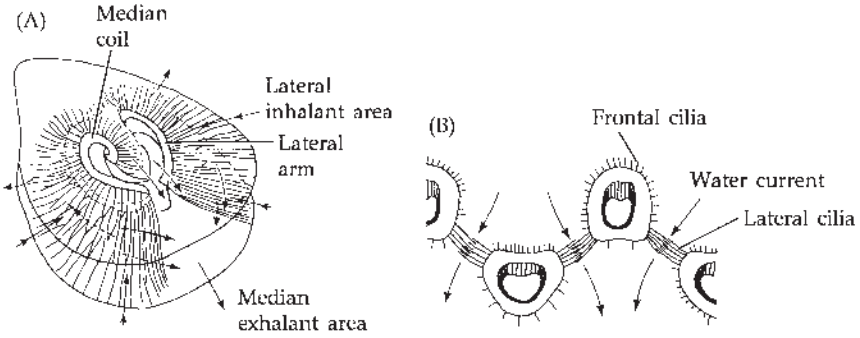

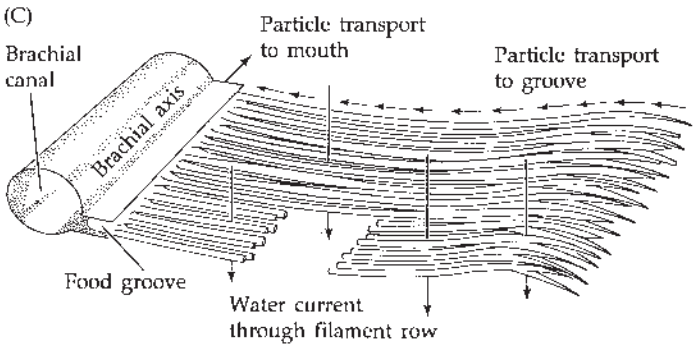

FIGURE 16.20 Feeding currents in brachiopods. (A) Feeding currents (arrows) of *Calloria inconspicua* (Rhynchonelliformea). (B) Lophophoral tentacles (section). The water (arrows) passes over lateral ciliary bands. (C) A portion of a lophophore. Food particles are transported along tentacles and the brachial food groove (arrows). (C after M. J. S. Rudwick. 1962. *Zool J Linn Soc* 44: 592–615.)

from the coelomic fluid, although both contain certain similar cells. The function of the circulatory system is thought to be largely restricted to nutrient distribution.

Gas exchange probably occurs across the general body surface, especially the lophophore tentacles and mantle. These structures not only provide large surface areas but also are sites over which water moves and is brought close to underlying coelomic fluid. This general arrangement and the presence of hemerythrin in certain coelomocytes suggest that the coelomic fluid, not the blood, is the medium for oxygen transport.

Brachiopods possess one or two pairs of metanephridia, with the nephrostomes opening to the metacoel. The nephridioducts exit through pores into the mantle cavity. The nephridia function as gonoducts as well as discharging phagocytic coelomocytes that have accumulated metabolic wastes. In the distal part of the metanephridia (nephridial canal), columnar cells absorb large quantities of coelomic fluid by endocytosis suggesting secondary urine formation as in other metanephridial systems. However, primary urine formation through a podocyte filter system from the blood vessel into the coelom has only been assumed for the periesophageal coelom in the rhynchonellid *Hemithiris psittacea*.

Nervous System and Sense Organs

The nervous system of brachiopods, as in many sessile invertebrates, is somewhat reduced. A dorsal ganglion and a ventral ganglion lie against the esophagus and are connected by a circumenteric nerve ring. Nerves emerge from the ganglia and nerve ring and extend to various parts of the body, especially the muscles, mantle, and lophophore (Figure 16.19D). As usual, the array of sense organs in these animals is compatible with their lifestyle. The mantle edges and setae are richly supplied with sensory neurons, probably tactile receptors. There is also evidence that brachiopods are sensitive to dissolved chemicals, perhaps through surface receptors on the tentacles or mantle edge. Members of at least one burrowing species of *Lingula* possess a pair of statocysts that are associated with orientation in the substratum. Larvae of some rhynchonelliform groups possess eyes composed of two photoreceptor cells almost certainly mediating their photonegative behavior prior to settlement and metamorphosis. Comparable to the vertebrate eye, brachiopod larval eyes contain a ciliary opsin as the photosensitive pigment. The larval nervous system in brachiopods has been shown to contain both serotonergic and histaminergic neurons.

Reproduction and Development

Asexual reproduction does not occur in brachiopods. Most species are gonochoristic, with gametes developing from patches of transient gonadal tissue derived from the coelomic epithelium in the metacoel. Gametes are released into the metacoel and escape through the metanephridia. In most cases both eggs and sperm are shed freely, and fertilization is external. A few species, however, brood their embryos until the larval stage is reached. In these cases sperm are picked up in the water currents of females, and the eggs are retained in a brooding area where they are fertilized. *Argyrotheca*, for example, broods its embryos in special caverns formed by the mantle epithelium. Species of Thecideida form brood pouches in either the dorsal or ventral valves as derivatives of the lophophore epithelium. Others retain their embryos on the arms

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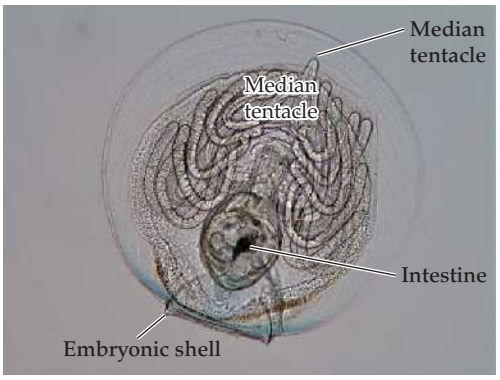

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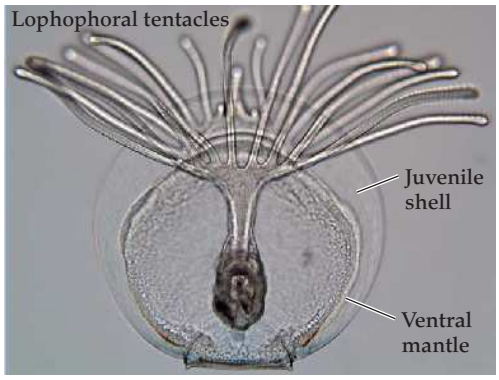

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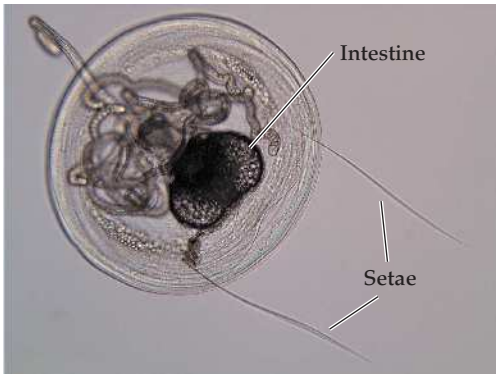

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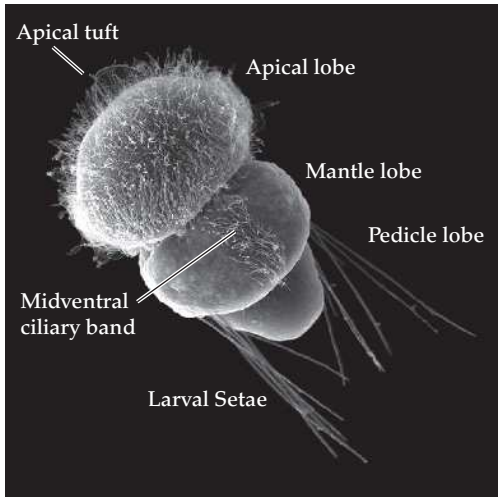

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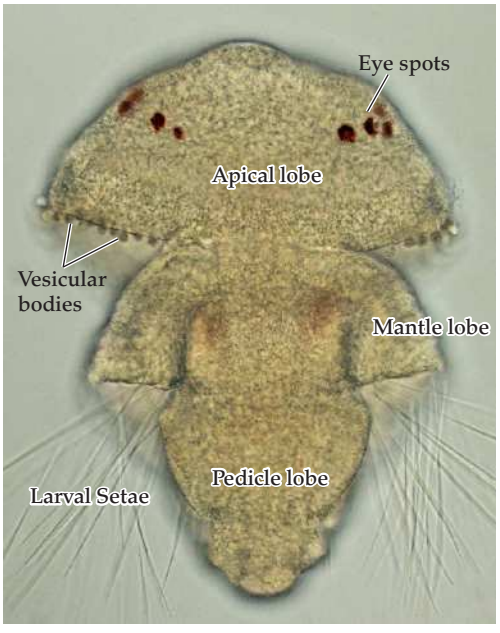

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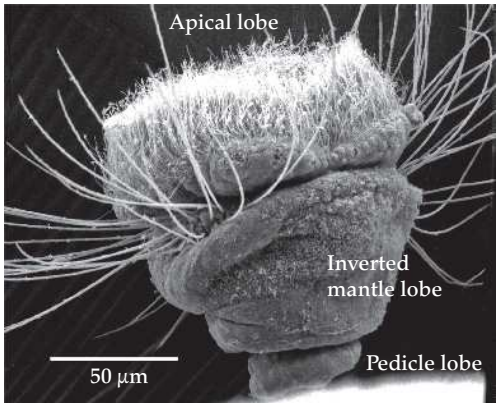

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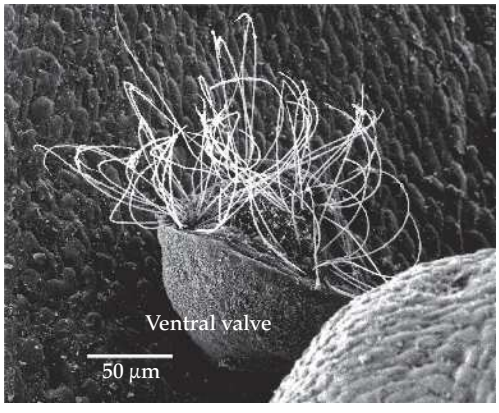

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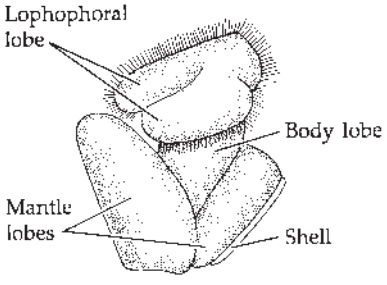

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◀ **FIGURE 16.21 Brachiopod lobate larvae and metamorphosis.** (A) Planktonic juvenile of *Glottidia* sp. (Linguliformea) with contracted lophophore. (B) The same *Glottidia* juvenile with expanded lophophore during active swimming. (C) The shelled planktonic juvenile of a discinid (Linguliformea). Note the pair of long posterior setae. (D) SEM photo of a three-lobed-stage larva of *Macandrevia cranium* (Rhynchonelliformea). Cilia are restricted to the apical lobe and a midventral band. (E) Three-lobed stage of *Terebratalia transversa* (Rhynchonelliformea) with two dorsolateral rows of red eyespots on the apical lobe. (F,G) Two subsequent metamorphic stages of *Laqueus erythraeus* (Rhynchonelliformea). Mantle lobe inversion starts immediately after attachment of the larva to the substrate. (H) Hatchling of *Lingula anatina* (Linguliformea) already equipped with two shelled mantle lobes and a ciliated lophophore rudiment.

of the lophophore, in special regions of the mantle cavity, or in modified depressions in a valve.

Cleavage is holoblastic, radial, and nearly equal; it leads to the formation of a coeloblastula. Gastrulation is by invagination, except in the brooding form *Lacazella mediterranea*, where it apparently occurs by delamination. The blastopore closes and the mouth forms secondarily (i.e., deuterostomy, in *Novocrania anomala*) or gives origin to the mouth (i.e., protostomy, in *Terebratalia transversa*). This transition from protostomy to deuterostomy is determined by the differential activity of Wnt signaling, together with the timing and location of mesoderm formation. The anus, when present, breaks through late as the gut grows and approaches the body wall. Mesoderm formation starts by proliferation of archenteral cells and subsequent separation from the larval gut anlage. Only during metamorphosis do the mesoderm cells diverge, thereby opening a lumen, the coelom. The origin of the prospective coelomic epithelium from archenteral cells can be interpreted as enterocoely.

Whether the developmental pattern is mixed or fully indirect, all brachiopods eventually enter a free-swimming stage (Figure 16.21). Although these planktonic forms differ morphologically, they have been compared to trochophore larvae, in which case the ciliary band around the apical lobe could be interpreted as homologue to the prototroch of a traditional trochophore, but this is controversial. Whereas lingulid brachiopods hatch as planktotrophic stages ("free-swimming juveniles") with a thorough and a first-formed ("embryonic") shell, all other groups hatch as nonfeeding stages. In discinids the hatchling has typical larval characters (e.g., larval setae) but quickly develops tentacles, a functional digestive system, and a first-formed shell while still in the planktonic stage. Craniiforms and rhynchonelliforms have a lecithotrophic larval stage that only develops tentacles and a shell and starts feeding upon settlement and metamorphosis.

In linguliforms, such as *Lingula*, the lophophore of the planktonic stage (Figure 16.21) can be protruded out from between the mantle lobes and can function to propel and feed the larva. As the mantle lobes and shell bear some weight, this developmental stage immediately sinks when the lophophoral tentacles are retracted into the mantle cavity. Extension of the growing pedicle while on the seafloor marks the start of the juvenile's benthic life. Thus, there is no drastic metamorphosis at the time of settling.

The free-swimming larvae of rhynchonelliforms are regionalized into an anterior (apical) lobe, a mantle lobe, and a pedicle lobe (Figure 16.21C–F). As craniiforms lack a pedicle throughout their life, their larval body has only an apical and a posterior lobe, the latter bearing three pairs of larval setal bundles. After a short larval life of a few days to weeks (depending on the ambient temperatures), the nonfeeding brachiopod larvae settle and metamorphose. As the pedicle lobe attaches to the substratum (only rhynchonelliforms), the mantle lobes flex forward over the anterior lobe. The now exterior surfaces of the mantle lobes commence secretion of the valves, while the anterior lobe differentiates into the body and the lophophore.

Chapter Summary

This chapter introduced you to the important clade Lophophorata—three phyla united by their possession of a unique, ciliated, tentacular feeding structure called the lophophore (and its associated epistome, which functions to move captured food particles form the lophophore to the mouth). The three lophophorate phyla (Phoronida, Bryozoa, Brachiopoda) are typically sessile, benthic suspension feeders (a few bryozoans have floating colonies) with U-shaped guts (which are advantageous for animals living encased in tubes, compartments, or shells). Phoronids are vermiform tube dwellers, usually living together in aggregations, and typically with a unique actinotroch larva. Bryozoans are colonial, with zooids that develop through budding and produce planktonic larvae. Brachiopods are solitary and shelled (with dorsal and ventral valves, as opposed to the right and left shells of bivalve molluscs), and they produce planktonic larvae. Major research areas important to our understanding of these three phyla are to resolve the nature of their "tripartite" body cavities, to find their exact phylogenetic placement with respect to other lophotrochozoans, and to determine the developmental mechanisms involved in producing the brachiopod shells and setae and the bryozoan housings, as well as whether these are related to modes of chaetogenesis, spiculogenesis, and shell formation in other lophotrochozoans.

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CHAPTER 17

Rouphozoa

The Phyla Platyhelminthes (Flatworms) and Gastrotricha (Hairy-Bellied Worms)

Since the eighteenth century, flatworms had generally been considered basal bilaterians because of their superficially simple-appearing and acoelomate body, their lack of a through gut (absence of an anus) or structural circulatory system, and other features. But during the late twentieth century molecular phylogenetic studies began to suggest otherwise, and by the 2010s phylogenomic analyses were indicating that platyhelminths and gastrotrichs were sister groups embedded well within the spiralian clade (and not placed near the base of Bilateria).

Introduction to Rouphozoa

Struck et al. (2014) introduced the name Rouphozoa for the Platyhelminthes-Gastrotricha clade; a derivative of the Greek word *rouphao*, for "ingestion by sucking," in reference to the common feeding mode of many of the free-living species. Although this mode of feeding is not uncommon among animals with strong sucking pharynxes, and the plesiomorphic state within Platyhelminthes is a pharynx simplex that engulfs instead of sucking prey, the name has stuck. In fact, few straightforward anatomical apomorphies seem to exist that define Rouphozoa, and both phyla seem to be characterized by features that are plesiomorphic for the Spiralia in general (dense body ciliation, protonephridia, etc.). One putative synapomorphy of Rouphozoa is the presence of duo-gland organs, described below, although similar organs also exist in other groups as well (e.g., annelids, nematodes). Both phyla are acoelomate, and their precise placement among the spiralian protostomes remains unresolved. Nevertheless, the clade Rouphozoa has continued to enjoy strong phylogenomic support since Struck and his colleagues first proposed it.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida

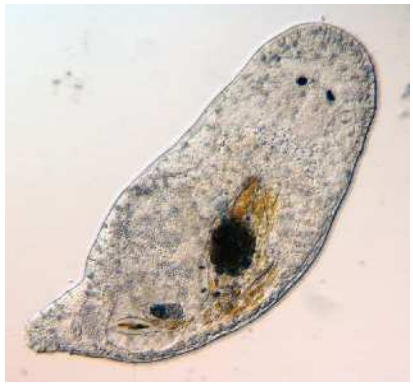
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent

*** Paraphyletic (excludes Hexapoda)

(A)

Courtesy of C. Laumer

(B)



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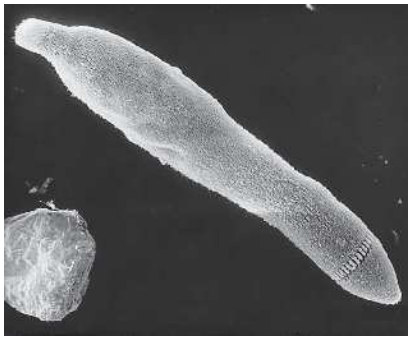

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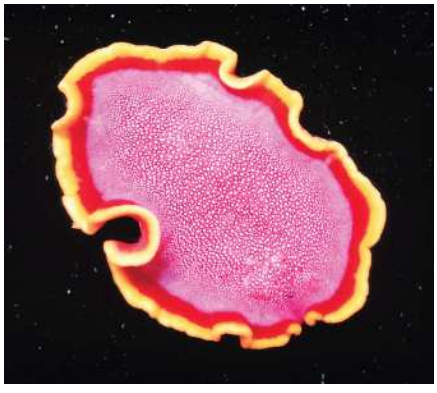

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The Phylum Platyhelminthes (Flatworms)

The phylum Platyhelminthes (Greek *platy*, "flat"; *helminth*, "worm") includes nearly 30,000 extant species of free-living and parasitic worms, and more than 100,000 undescribed species have been estimated to exist. Platyhelminths are triploblastic, nonsegmented, bilaterally symmetrical, acoelomate, soft-bodied, dorsoventrally flattened worms (Box 17A). They display a variety of body forms (Figure 17.1) and inhabit a wide range of environments. About 75% of all described species are parasitic, mostly belonging to the Monogenea and Trematoda (the flukes) and Cestoda (the tapeworms).

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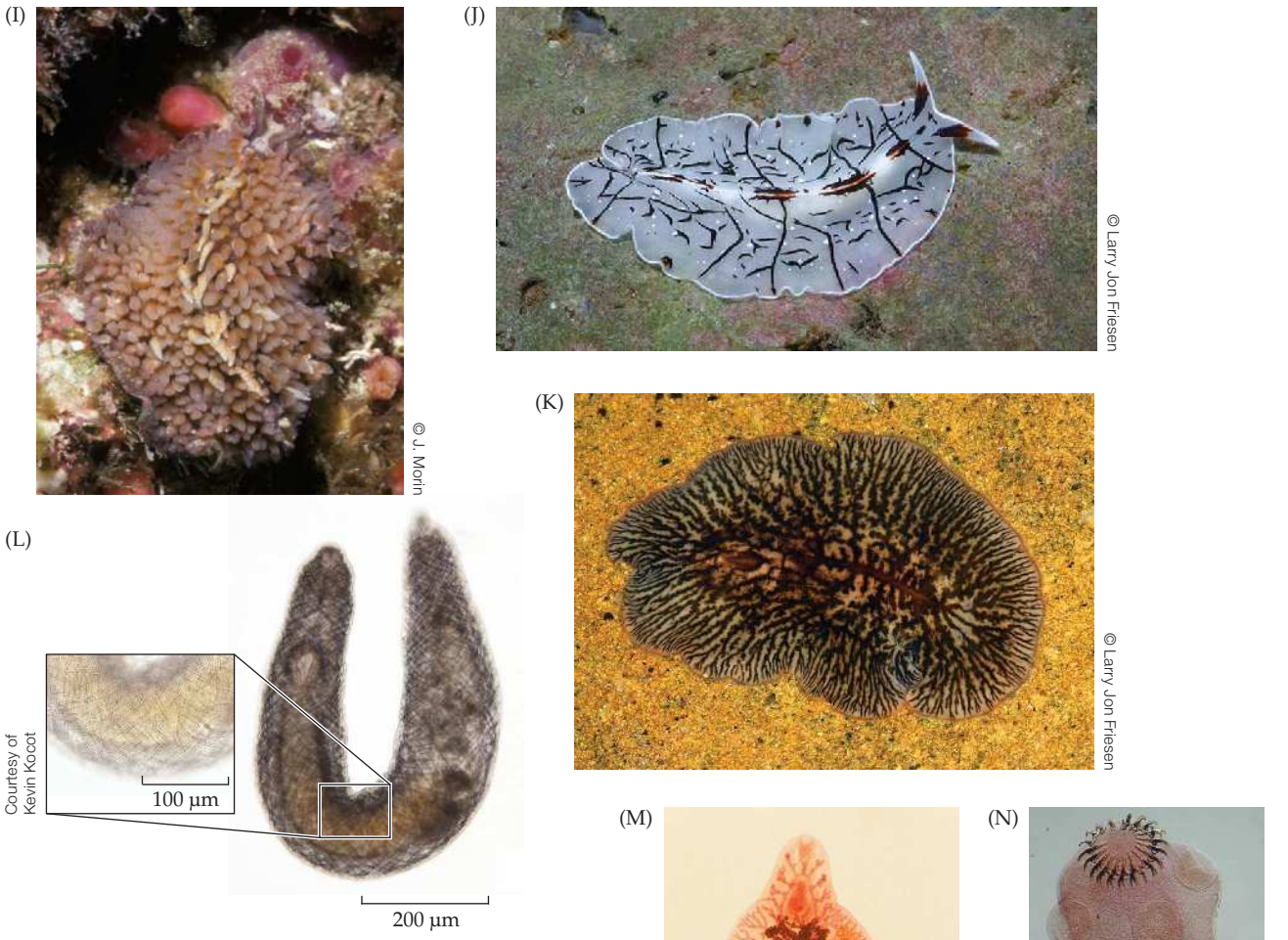

FIGURE 17.1 Representative flatworms. (A–K) Free-living flatworms. (A) *Catenula lemnae*, a catenulid. (B) *Macrostomum* sp. (a macrostomid). (C) The terrestrial triclad *Bipalium kewense*. (D) A colorful flatworm (*Bipalium* sp.) on a decayed leaf; Sarawak, Borneo, Malaysia. (E) SEM of *Cheliplana*, an interstitial rhabdocoel. (F) *Pseudobiceros bajae*, an intertidal polyclad flatworm from the Sea of Cortez, Mexico (also see chapter opener photo, *Pseudobiceros bedfordi*). (G) The strikingly colored polyclad *Pseudoceros ferrugineus*. (H) The familiar freshwater triclad *Girardia tigrina* (formerly *Dugesia tigrina*). (I) A polyclad flatworm in the genus *Thysanozoon*, a predator on small invertebrates, including barnacles. (J) A marine polyclad, *Eurylepta californica*. (K) *Hylocelis californica* (formerly *Alloioplana californica*), a common polyclad on the Pacific Coast of North America. (L) *Acanthomacrostomum* sp., a meiofaunal flatworm that has a layer of calcareous spicules just below the epidermis. This skeletal framework may provide protection and support in aiding in locomotion. (M) The liver fluke *Fasciola hepatica* (Digenea). (N) Anterior end of the tapeworm *Taenia* (Cestoda).

These parasites infect hundreds of millions of people around the globe, the most prominent being five species of human blood flukes in the genus *Schistosoma* that infect 200 million people worldwide with schistosomiasis (also known as bilharzia, or snail fever). Most of the free-living forms live in marine and freshwater benthic habitats and comprise a diverse, paraphyletic group formerly known as "turbellarians"; a few are terrestrial and some are commensal or parasitic in or on other invertebrates. Free-living marine flatworms are often some of the most colorful and graceful creatures found in shallow temperate to tropical waters and tide pools, and flatworms can be found down to the hadal zone of deep ocean trenches. As their name suggests, most flatworms are strikingly flattened dorsoventrally, although the body shape varies from cylindrical to flattened forms with broadly oval to elongate and ribbon-like shapes; a few bear short tentacles at the anterior

BOX 17A Characteristics of the Phylum Platyhelminthes

1. Free-living or parasitic, nonmetameric worms (Cestoda are strobilated)
2. Triploblastic, acoelomate, bilaterally symmetrical; often dorsoventrally flattened
3. Spiral cleavage (in some nonparasitic lineages) and 4d-derived mesoderm; many others with highly modified cleavage pattern
4. Complex, though incomplete, gut usually present; gut absent in some parasitic forms (Cestoda)
5. Cephalized, with a central nervous system comprising an anterior cerebral ganglion and (usually) longitudinal nerve cords connected by transverse commissures (ladderlike nervous system)
6. Multiciliated epidermal cells (few cilia per cell in Catenulida)
7. With protonephridia as excretory/osmoregulatory structures
8. Without discrete circulatory or gas exchange structures
9. With unique system of neoblast cells
10. Mucus typically produced by rhabdoids/rhabdites
11. Most hermaphroditic, with complex reproductive system and biflagellate sperm (aflagellate in Catenulida and Macrostomida)
12. Direct or indirect development, with distinct larvae in Polycladida (Götte's and Müller's larvae)

end or have other elaborations of the body surface. The free-living forms range from less than 1 mm to about 30 cm long (land planarians) or even 40 cm in some Lake Baikal flatworms of the genus *Baikalobia*; although most familiar species are 1–4 cm long, the vast majority of free-living flatworms are "microturbellarians." The largest of all platyhelminths are certain tapeworms that attain lengths of several meters (a tapeworm that infests blue whales grows to 10 m in length!).

Platyhelminths are triploblastic (i.e., they have true endomesoderm) and bilaterally symmetrical, show clear cephalization, and possess sophisticated excretory and reproductive organ systems. The solid (acoelomate) body plan usually includes a relatively dense mesenchyme (often called "parenchyme") between the gut and the body wall. The mesenchyme is not homogeneous, but comprises a multitude of differentiated cell types and small open spaces or **lacunae**. Within the mesenchyme of most flatworms are discrete excretory–osmoregulatory structures, the protonephridia, which are found in many invertebrate taxa, especially among protostomes. Most flatworms possess complex reproductive systems and an incomplete yet complex gut with a single opening serving for both ingestion and egestion. The mouth leads to a pharynx of varying complexity and then to a blind intestine. The gut is entirely lacking in tapeworms, as well as in a few other symbiotic species.

Taxonomic History and Classification

In his first edition of *Systema Naturae* (1735), Linnaeus established two phyla to encompass all of the known invertebrates. To one he assigned the insects and to the other the rest of the invertebrates. Linnaeus called this latter taxon Vermes (Greek, "worms"). By the thirteenth edition of *Systema Naturae* (1788), the various groups of flatworms had been placed together in the order Intestina. During the early 1800s, several biologists, including Lamarck and Cuvier, questioned and rejected the concept of the taxon Vermes, although the name continued to surface from time to time and actually persisted into the twentieth century as a dumping ground for almost any creatures with wormlike bodies (and many that were not so wormlike).

During the nineteenth century, the flatworms were eventually separated from most other groups of wormlike creatures. In 1851, C. Vogt isolated the flatworms and the nemerteans as a single taxon, which he called the Platyelmia, a name changed to Platyelminthes by Karl Gegenbaur in 1859. (Unfortunately, Gegenbaur also resurrected the phylum Vermes.) Gegenbaur's Platyelminthes (now Platyhelminthes) was eventually raised to the rank of phylum, comprising four classes: Turbellaria, Nemertea, Trematoda, and Cestoda. In 1876 Charles Minot dropped the nemerteans from this assemblage, although many workers did not accept this change for several decades. The legendary zoologist Libbie Hyman (1951) asserted the monophyly of Platyhelminthes, a view shared by Tor Karling (1974), Peter Ax (1985), and Ulrich Ehlers (1985), who recognized three clades (Acoelomorpha, Catenulida, and Rhabditophora) that have since each been supported by molecular phylogenetic studies. Later analyses of morphology and the advent of molecular gene sequence analyses have supported the monophyly of Catenulida + Rhabditophora (although these two major flatworm clades still lack unambiguous morphological synapomorphies) but suggested acoelomorphs were basal bilaterians rather than flatworms (see Chapter 9). With the removal of Acoelomorpha (which includes Acoela and Nemertodermatida), Platyhelminthes is now viewed as a monophyletic phylum.

The internal classification of flatworms has been subjected to frequent revisions. However, two recent studies by independent groups of researchers targeted platyhelminth phylogeny by analyzing different sets of thousands of genes (Egger et al. 2015, Laumer et al. 2015). These genomic studies, published at nearly the same time, resulted in nearly the same phylogeny. Our summary tree (see Figure 17.34) and classification are based primarily on this recent work. However, students can expect continued reorganization of the flatworms in the near future. There are over 6,500 species of free-living flatworms, over 12,000 species of flukes, and over 8,000 species of tapeworms.

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The free-living flatworms (formerly classified as "turbellarians," a category now known to be a paraphyletic group, although the name is still sometimes loosely used for the non-neodermatan platyhelminths) were previously grouped into two taxa on the basis of whether yolk is deposited within the cytoplasm of the ova (**endolecithal ova**) or separately, in special cells outside the ova (**ectolecithal ova**). Those with endolecithal ova were placed in the Archoophora and those with ectolecithal ova in the Neoophora. These names have been abandoned (but Euneoophora is used in some classifications) as formal taxa because they are now known to define nonmonophyletic groups of species. However, the names are still descriptive because the placement of yolk, as well as the uterine structures that mediate this process, provide additional characters for describing the various flatworm orders. The patterns also have important implications in the early development of these animals.

PLATYHELMINTHES CLASSIFICATION

SUBPHYLUM CATENULIDEA Catenulids (Figure 17.1A). Simple anterior pharynx and saclike gut; mesenchyme sometimes reduced to a fluid matrix (making them effectively blastocoelomate); sometimes with statocyst bearing 1 to 3 statoliths; brain lies at base or middle of preoral lobe; with a ciliated ventrolateral groove between base of preoral lobe and the rest of the body; tubules of excretory system mediodorsal; with a single biflagellate protonephridium; male genital opening dorsal and anterior; female ducts and accessory organs are lacking; with endolecithal ova and spiral cleavage. Catenulids are elongate freshwater and marine forms. A single order, Catenulida. (e.g., *Catenula*, *Paracatenula*, *Stenostomum*)

SUBPHYLUM RHABDITOPHORA With lamellated rhabdites, a duo-gland adhesive system and multiflagellate terminal cell in the protonephridia; most taxa with biflagellate sperm.

INFRAPHYLUM MACROSTOMORPHA Rhabditophora with duo-gland adhesive organ consisting of viscid gland and releasing gland necks emerging in a common collar of anchor cell microvilli; with a postoral neural commissure, and a protrusible pharynx simplex; with aflagellate sperm, endolecithal ova, and spiral cleavage.

ORDER HAPLOPHARYNGIDA Minute worms (to 6 mm long) with a simple proboscis and pharynx; proboscis separate from pharynx and beneath the anterior tip of the body (reminiscent of nemerteans); anal pore weakly developed, but permanent; brain encapsulated by a unique membrane; oviduct posterior to male genital apparatus; male copulatory organ consists of a posterior prostatic vesicle and an anterior stylet apparatus. One genus (*Haplopharynx*) and at least three species.

ORDER MACROSTOMIDA Macrostomids (Figure 17.1B). Simple pharynx; simple, saclike gut; with endolecithal ova and a common oviduct anterior to the male genital apparatus; small and predominately interstitial forms; marine and freshwater. (e.g., *Acanthomacrostomum*, *Macrostomum*, *Microstomum*)

INFRAPHYLUM TREPAXONEMATA Rhabditophorans with biflagellate sperm bearing a 9 × 2 + "1" pattern of microtubules.

SUPERCLASS AMPLIMATRICATA With a tendency to express an ample extracellular matrix; with spiral cleavage.

ORDER POLYCLADIDA Polyclads (Figure 17.1F,G,I–K). A diverse group of relatively large free-living flatworms with endolecithal ova; nearly all are marine; common in littoral zones throughout the world, especially in the tropics; predominately benthic and free-living. Some are so large and colorful as to be easily mistaken for sea slugs; some cases of mimicry are known. Many swim by graceful undulations of the body margins. A few are pelagic or symbiotic. (e.g., *Eurylepta*, *Hoploplana*, *Leptoplana*, *Notoplana*, *Planocera*, *Prostheceraeus*, *Pseudobiceros*, *Pseudoceros*, *Stylochus*, *Thysanozoon*)

ORDER PRORHYNCHIDA Freshwater and terrestrial flatworms, often bearing prominent anterior auricles and an anteriorly situated, complex pharynx; ovaries lecithoepitheliate, consisting of two kinds of cells, vitellocytes embracing the growing oocytes, both types of cells produced by a common proximal germinal tissue. (e.g., *Geocentrophora*, *Prorhynchus*). Some classification schemes place the freshwater Prorhynchida and the marine Gnosonesimida within the Lecithoepitheliata, a taxon comprised of about 30 species united on the basis of an intermediate condition between endolecithal and ectolecithal ova, but recent research considers Lecithoepitheliata to be nonmonophyletic.

SUPERCLASS GNOSONESIMORA Marine forms with apparent lecithoepithelial development of ova but closer structural and molecular affinities to Euneoophora; with ectolecithal ova (cleavage not yet described).

ORDER GNOSONESIMIDA A single marine genus is known (*Gnosonesima*), bearing a coniform bulbous pharynx.

SUPERCLASS EUNEOOPHORA Rhabditophorans whose ovary is divided into germinal and vitelline cell producing parts; with ectolecithal ova.

CLASS RHABDOCOELA Rhabdocoels. Bulbous or sometimes plicate pharynx; simple saclike gut

without diverticula; ectolecithal ova produced by ovaries that are usually fully separate from the yolk glands; spiral cleavage.

ORDER DALYTYPHLOPLANIDA A diverse group of free-living or ecto- or endosymbionts of marine and freshwater invertebrates (Figures 17.6B and 17.10). Molecular data suggest three main groups: neodalyellids, with an anterior mouth (e.g., *Anoplodium*, *Graffilla*, *Pterastericola*); thalassotyphloplanids, mostly marine species with the mouth not anterior (e.g., *Kytorhynchus*, *Mesostoma*, *Typhlorhynchus*); and limnotyphloplanids, mostly freshwater species (e.g., *Castrella*, *Dalyellia*, *Microdalyellia*). Limnotyphloplanids are small symbionts on freshwater decapod crustaceans, although a few live on other invertebrates or on turtles. (i.e., *Temnocephala*)

ORDER KALYPTORHYNCHIA Kalyptorhynchs (Figures 17.1E and 17.11E). Mouth not terminal; with a complex eversible proboscis at anterior end that is separate from the mouth and pharynx; free-living marine and freshwater species. (e.g., *Cheliplana*, *Cystiplex*, *Gnathorhynchus*, *Gyratrix*)

CLASS PROSERIATA Freshwater and marine free-living flatworms lacking lamellate rhabdites; bearing a cylindrical plicate pharynx; simple gut; spiral cleavage.

ORDER UNGUIPHORA Proseriates with pigment in the mantle cells of rhabdomeric receptors, and usually without a statocyst; molecular studies suggest that this order is in need of revision, and also that the enigmatic genus *Ciliopharyngiella* may belong here. (e.g., *Nematoplana*, *Polystyliphora*)

ORDER LITHOPHORA Proseriates without pigment in the mantle cells and usually with a statocyst; recent molecular studies indicate that this order is monophyletic and suggest that the families Coelogynoporidae and Calviriidae as well as Otoplanidae, Archimonocelididae, and Monocelididae may belong in this group. (e.g., *Calviria*, *Coelogynopora*, *Otoplana, Otoplanella*, *Archimonocelis*, *Monocelis*)

CLASS ACENTROSOMATA Rhabditophorans lacking genes controlling formation of centrosomes, leading to loss of highly regulated spiral cleavage (and, in some lineages, blastomere anarchy) during early development.

SUBCLASS ADIAPHANIDA Although there are no clear synapomorphies for this clade, it is strongly supported by molecular analyses; the name is from the ancient Greek word for "opaque," referring to the fact that most species have opaque bodies.

ORDER TRICLADIDA Triclads (Figures 17.1C,H, 17.2, and 17.6A). Freshwater, marine, terrestrial, and symbiotic forms; cylindrical plicate pharynx; gut three-branched with numerous diverticula; two germinaria located at anterior end of germovitelloducts. Most are free-living, including the familiar planarians. This taxon is monophyletic and used to be grouped into 3 suborders based largely on their ecology (marine, freshwater, and land planarians), but now they divide into Maricola and Continenticola, as the former suborder Terricola nests within the former Paludicola. Notable triclad genera include *Bdellocephala*, *Bdelloura*, *Bipalium*, *Crenobia*, *Dugesia* [formerly *Planaria*], *Endeavouria*, *Geoplana*, *Obama*, *Polycelis*, *Procotyla,* and *Schmidtea*.

ORDER PROLECITHOPHORA Prolecithophorans. Pharynx plicate or bulbous; gut simple; sperm aflagellate, with extensive membranous folds. Reduction of duo-gland adhesive system complete; genitalia variable but male aperture often opens forward, female reproductive system often opens to a common pore; small, free-living, marine, and freshwater. (e.g., *Plagiostomum*, *Urastoma*)

ORDER FECAMPIIDA Fecampiidans. Endoparasites of various marine invertebrates and vertebrates; lacking a pharynx and intestine; with a ciliated epidermis but with vertical ciliary rootlets reduced. (e.g., *Fecampia*, *Glanduloderma*, *Ichthyophaga, Kronborgia*)

SUBCLASS BOTHRIONEODERMATA

INFRACLASS BOTHRIOPLANATA Freshwater / terrestrial flatworms bearing a three-branched, diverticulated gut, and medial-posteriorly directed plicate pharynx; multiple follicular vitellaria.

ORDER BOTHRIOPLANIDA Monospecific, *Bothrioplana semperi,* a freshwater/terrestrial scavenger and predator on small invertebrates.

INFRACLASS NEODERMATA Flukes and tapeworms. Ciliated larval epidermis shed and replaced by a syncytial neodermis with subepithelial nuclei (the tegument); locomotory epidermal cilia bearing a single rootlet; epithelial sensory receptors with collars.

COHORT TREMATODA Digenean and aspidogastrean flukes (Figures 17.1M and 17.3A,B,E,F). With one or more suckers; lacking prohaptor and opisthaptor; male copulatory organ is a cirrus; 1 to 3 hosts during the life cycle, often including a mollusc; most are endoparasitic.

SUPERORDER ASPIDOGASTREA Aspidogastrean flukes.

ORDER ASPIDOGASTRIDA With a complex ventral sucker formed by lateral growth and

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subdivision of posterior part of sucker. Most with a single host (a mollusc) in life cycle; second host, when present, a turtle or a teleost fish; oral sucker absent. (e.g., *Aspidogaster*, *Cotylaspis*)

ORDER STICHOCOTYLIDA With complex ventral sucker formed by linear growth and subdivision of anterior part of sucker. Most with single host (a lobster) in life cycle; second host, when present, is a chondrichthyan fish. (e.g., *Stichocotyle*, *Rugogaster*)

SUPERORDER DIGENEA Digenean flukes.

ORDER DIPLOSTOMIDA Endoparasites of tetrapods; adult genital pore posterior to the ventral sucker; some with blood-dwelling adult stages. Usually with complex 3-host life cycles but occasionally with 2; first intermediate host is a mollusc. Includes the schistosomes. (e.g., *Schistosoma, Sanguinicola, Trichobilharzia, Tylodelphys*)

ORDER PLAGIORCHIIDA An extraordinarily diverse order of vertebrate endoparasites with a wide range of life cycle characteristics and hosts. Usually with at least a 2-host life cycle; first intermediate host is a mollusc. Fasciolosis is a snail-borne disease causing serious public and veterinary health problems worldwide, caused by infection with *Fasciola hepatica* or *F. gigantica* through foods or water contaminated with metacercarial cysts. (Other notable genera include *Echinostoma, Opisthorchis* [= *Clonorchis*], *Microphallus*, *Parorchis*)

COHORT MONOGENEA Monogenean flukes (Figure 17.3C). Oral sucker (prohaptor) reduced or absent; posterior hook-bearing sucker (opisthaptor) present; ventral sucker (acetabulum) absent; gut bifurcate; 3 rows of cilia on oncomiracidium larva; life cycle involves only 1 host. Most are ectoparasitic, usually on fishes (some occur on turtles, frogs, hippos, copepods, or squid); a few are endoparasitic in ectothermic vertebrates. Although previously classified according to the relative complexity of the opisthaptor (Figure 17.8; simple, Monopisthocotylea; complex, Polyopisthocotylea), the evolutionary relationships within and among these taxa remain unclear. Nine orders are now recognized. Monogenea and Cestoda constitute a clade called Cercomeromorpha.

ORDER CAPSALIDEA Capsalids. Gill and skin ectoparasites of elasmobranch and teleost fishes; flattened, leaflike bodies with a simple aseptate or septate opisthaptor; with 3 pairs of median sclerites and 14 small hooklets at the periphery of the opisthaptor. (e.g., *Capsala*, *Benedeniella*, *Trochopus*)

ORDER CHIMAERICOLIDEA Gill parasites of holocephalan fishes. (e.g., *Chimaericola*)

ORDER DICLYBOTHRIIDEA Gill parasites of acipenseriform fishes. Oral sucker absent; mouth ventral; lateral sclerites on opisthaptor absent. (e.g., *Diclybothrium*, *Paradiclybothrium*)

ORDER DACTYLOGYRIDEA Gill parasites of freshwater teleost fish; body with opisthaptor bearing 2–4 anchors with 14–16 marginal hooks, and 4 eyespots. (e.g., *Dactylogyrus*, *Ancyrocephalus*)

ORDER GYRODACTYLIDEA Skin and gill parasites of freshwater fish; body fusiform with terminal cephalic lobes; opisthaptor forms a half oval and is armed with 16 marginal hooks and a pair of median anchors (hamuli) stabilized with median bars. (e.g., *Gyrodactylus*, *Paragyrodactyloides*, *Acanthoplacatus*)

ORDER MAZOCRAEIDEA Gill parasites of clupeid and scombrid fishes; oncomiracidium with 1 pair of fused eyes; opisthaptor with 2 pairs of lateral sclerites. (e.g., *Clupeocotyle*, *Mazocraes*, *Grubea*)

ORDER MONOCOTYLIDEA Gill and ectodermal tissue parasites of mostly tropical elasmobranchs; opisthaptor with a single central and multiple peripheral suckers (loculi), often armed with hamuli and marginal hooks. (e.g., *Monocotyle*, *Potamotrygonocotyle*)

ORDER MONTCHADSKYELLIDEA Gill parasites of tropical reef fishes. (e.g., *Montchadskyella*)

ORDER POLYSTOMATIDEA Skin, gill, and urogenital parasites of aquatic and semiaquatic tetrapods; opisthaptor well developed with 3 pairs of suckers or 1 sucker pair. (e.g., *Polystoma*, *Oculotrema*, *Metapolystoma*)

COHORT CESTODA Tapeworms and their relatives (Figures 17.1N and 17.4). Exclusively endoparasitic; in most, the body consists of an anterior scolex, followed by a short neck, and then a strobila composed of a series of "segments" or proglottids, although basal taxa are monozoic (not strobilated); digestive tract absent. Previous classifications recognized several subclasses; until taxonomic uncertainty is resolved, we recognize 16 orders.

ORDER AMPHILINIDEA Endoparasites in the guts or coelomic cavities of cartilaginous and certain primitive bony fishes, less commonly in turtles; leaflike bodies, lacking scolex and monozoic (not strobilated); 10 minute hooks may be present at posterior of body if retained from decacanth larvae that may develop in crustaceans. (e.g., *Amphilina*, *Austramphilina, Gyrometra*)

ORDER GYROCOTYLIDEA Intestinal parasites of holocephalan fishes although also

reported in sharks; body stout, monozoic with a muscular anterior attachment organ; posterior body terminates in a rosettelike adhesive organ; lateral margins often ruffled; life cycles are unknown. (e.g., *Gyrocotyle, Gyrocotyloides*)

EUCESTODA

ORDER BOTHRIOCEPHALIDEA Gut parasites of teleost fishes and occasionally in acipenseriforms and amphibians; body strobilated with proglottids wider than long; scolex with a pair of bothria; occasionally with hooks; life cycle with 2–3 hosts, usually a crustacean first host and a teleost second host. (e.g., *Bothriocephalus*, *Triaenophorus*, *Polyonchobothrium*)

ORDER CARYOPHYLLIDEA Intestinal parasites of cypriniform and siluriform fishes; body monozoic (not strobilated); scolex often simple; with 2-host life cycles; oligochaetes as intermediate hosts. (e.g., *Archigetes*, *Paraglaridacris*)

ORDER CYCLOPHYLLIDEA Intestinal parasites of birds and mammals; body variable in size, scolex with 4 suckers, rostellum is present, may be armed or not; most species are hermaphrodites although the family Dioecocestidae is gonochoristic; highly diverse and possibly the most derived order of cestodes; life cycles with 2–3 hosts with diverse invertebrate and vertebrate species as intermediate and paratenic hosts. (e.g., *Dipylidium*, *Hymenolepis*, *Moniezia*, *Taenia*)

ORDER DIPHYLLIDEA Intestinal parasites of Chondrichthyes fishes; body strobilated with midventral genital pores; scolex with 2 bothria and a cephalic peduncle; life cycles are poorly known but larval stages occur in marine crustaceans and molluscs. (e.g., *Echinobothrium*, *Ditrachybothridium*)

ORDER DIPHYLLOBOTHRIIDEA Intestinal parasites of piscivorous vertebrates, usually mammals; body strobilated but with variable external differentiation; scolex always unarmed, usually with paired attachment grooves (bothria); with 2- to 3-host life cycles; copepod crustaceans as first intermediate hosts, second intermediate hosts within vertebrates. (e.g., *Diphyllobothrium*, *Ligula*, *Spirometra*)

ORDER LECANICEPHALIDEA Small intestinal parasites of rays and occasionally sharks; although probably paraphyletic, species are characterized by a scolex with 4 suckers or bothria and an apical structure that may have tentacles, cones, or additional suckers; life cycles are poorly known but may include molluscs, crustaceans, and teleosts as intermediate hosts. (e.g., *Polypocephalus*, *Quadcuspibothrium*, *Corrugatocephalum*)

ORDER LITOBOTHRIIDEA Intestinal parasites of lamniform sharks; scolex with apical sucker and several muscular, cruciform pseudosegments; life cycles are unknown. (e.g., *Litobothrium*)

ORDER ONCHOPROTEOCEPHALIDEA Small to medium-sized intestinal parasites of Chondrichthyes, as well as of freshwater fish, amphibians, reptiles, and occasionally mammals; strobila polyzoic, with proglottids, or with few anapolytic (nondetaching) proglottids; with lateral, irregularly alternating genital pores; scolex often with 4 muscular bothridia, unarmed or with 1 pair of hooks; occasionally with a rostellum-like apical structure; life cycles include 1 or 2 intermediate hosts (crustaceans or fish); this order has subsumed the former order Proteocephalidea and part of the Tetraphyllidea. (e.g., *Proteocephalus*, *Chambriella*, *Brachyplatysoma, Acanthobothrium*, *Platybothrium*)

ORDER PHYLLOBOTHRIIDEA Small to medium-sized intestinal parasites of sharks, batoids, and ratfish; strobili polyzoic and with proglottids, scolex often with 4 muscular bothridia. (e.g., *Calyptrobothrium*, *Chimaerocestos*, *Marsupiobothrium*)

ORDER RHINEBOTHRIIDEA Intestinal parasites of freshwater stingrays; scolex often with bothridial stalks. (e.g., *Spongiobothrium*)

ORDER SPATHEBOTHRIIDEA Intestinal parasites of Chondrichthyes and teleost fishes; body strobilated without external differentiation of proglottids; male and female genital pores close together and alternating dorsally and ventrally the length of the body; with 2-host life cycles; crustaceans as intermediate hosts; progenesis (early maturation) of larvae is widespread. (e.g., *Spathebothrium, Bothrimonus*)

ORDER TETRABOTHRIIDEA Intestinal parasites of marine homeotherms inhabiting pelagic ecosystems; body with well-defined strobilation; scolex with 4 muscular bothridia of variable form; rostellum lacking; eggs with 3 membranes; life cycles are unknown but are likely to involve crustaceans, cephalopods, and teleosts as intermediate hosts. (e.g., *Priapocephalus, Tetrabothrius, Trigonocotyle*)

ORDER TETRAPHYLLIDEA Intestinal parasites of elasmobranch fishes, rarely in holocephalan fishes; body strobilated with variable apolysis of proglottids; scolex often with 4 muscular bothridia that vary widely in form, often elongate, stalked and with hooks; life cycles are poorly known, but 3–5 hosts are likely and include molluscs, crustaceans, teleosts, and marine mammals; a recent molecular analysis has

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shown this order to be nonmonophyletic, and genera are being redistributed to other orders (Onchoproteocephalidea, Phyllobothriidea). (e.g., *Rhoptrobothrium*, *Dinobothrium*)

ORDER TRYPANORHYCHA Intestinal and stomach parasites of Chondrichthyes fishes; body strobilated with lateral genital pores; scolex with 4 eversible tentacles, each bearing a complex array of hooks; 2- to 3-host life cycles with crustaceans and teleosts and intermediate hosts. (e.g., *Dasyrhynchus*, *Halsiorhynchus*, *Otobothrium*)

The Platyhelminth Body Plan

The basics of a flatworm body plan can be appreciated by examining the rather complex structural features displayed by the free-living flatworms (Figure 17.2). The mesenchyme, derived from mesoderm, is fibrous and muscular, allowing for the formation of structural support and locomotion. Elaborate reproductive systems (male and female) provide for internal fertilization and enhance the production of yolky and encapsulated eggs. Most flatworms have abandoned free-swimming larval stages for mixed and direct life histories. Osmoregulatory structures in the form of protonephridia were most likely instrumental in the invasion of freshwater and later terrestrial environments.

The platyhelminth body plan has high energy demands for an active lifestyle. A major limiting factor for flatworms, functionally, is the absence of an efficient circulatory mechanism to move materials throughout the body. This problem is compounded by the lack of any special structures for gas exchange. These problems relate, of course, to the surface-to-volume dilemma discussed in Chapter 3. In the absence of circulatory and gas exchange structures, flatworms (particularly free-living ones) are constrained in terms of size and shape. They have remained relatively small and flat, with shapes that maintain short diffusion distances. The largest free-living flatworms have highly branched guts that assume much of the responsibility of internal transport.

Having a high surface-to-volume ratio and using the entire body surface for gas exchange create potential problems of ionic balance and osmoregulation in freshwater and terrestrial species, and of desiccation in intertidal and terrestrial habitats. The permeable body surface must be kept moist; thus, flatworms have invaded land rarely and mostly in very damp areas, although a few rhabdocoels and prorhynchids and several parasitic species have developed desiccation-resistant life stages. Flatworms have, however, exploited a variety of marine and freshwater habitats and are particularly successful as parasites and commensals, enjoying the benefits of living on or in their hosts.

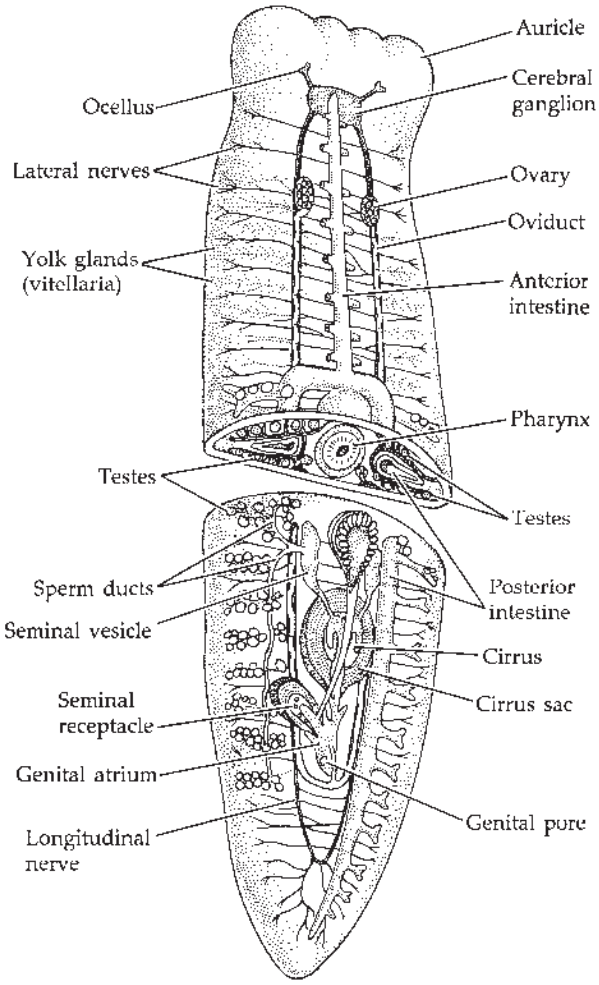

FIGURE 17.2 Anatomy of a generalized freshwater flatworm (order Tricladida).

The ancestral flatworm is thought to have been a free-living form, from which the present-day catenulids and rhabditophorans evolved and diversified. The flukes and tapeworms evolved from within the rhabditophoran assemblage (discussed in more detail later in this chapter). Thus, in each of the following sections we first examine the basic features of the free-living flatworms and set the stage for understanding not only the diversity within that body plan but the derivation of the specialized parasitic taxa as well.

Platyhelminths have become famous in biological lore for their unique totipotent stem cell system, the **neoblasts**, which can comprise around 20% or more of the cells in an adult animal. Neoblasts are thought to be competent for the renewal of all cell types, including germ cells, and they are presumed to be responsible for the maintenance of a healthy population of differentiated somatic cells. The power of neoblasts is what confers on flatworms their phenomenal regeneration powers.

The anatomy of free-living flatworms, flukes, and tapeworms is shown in Figures 17.2, 17.3, 17.4, and

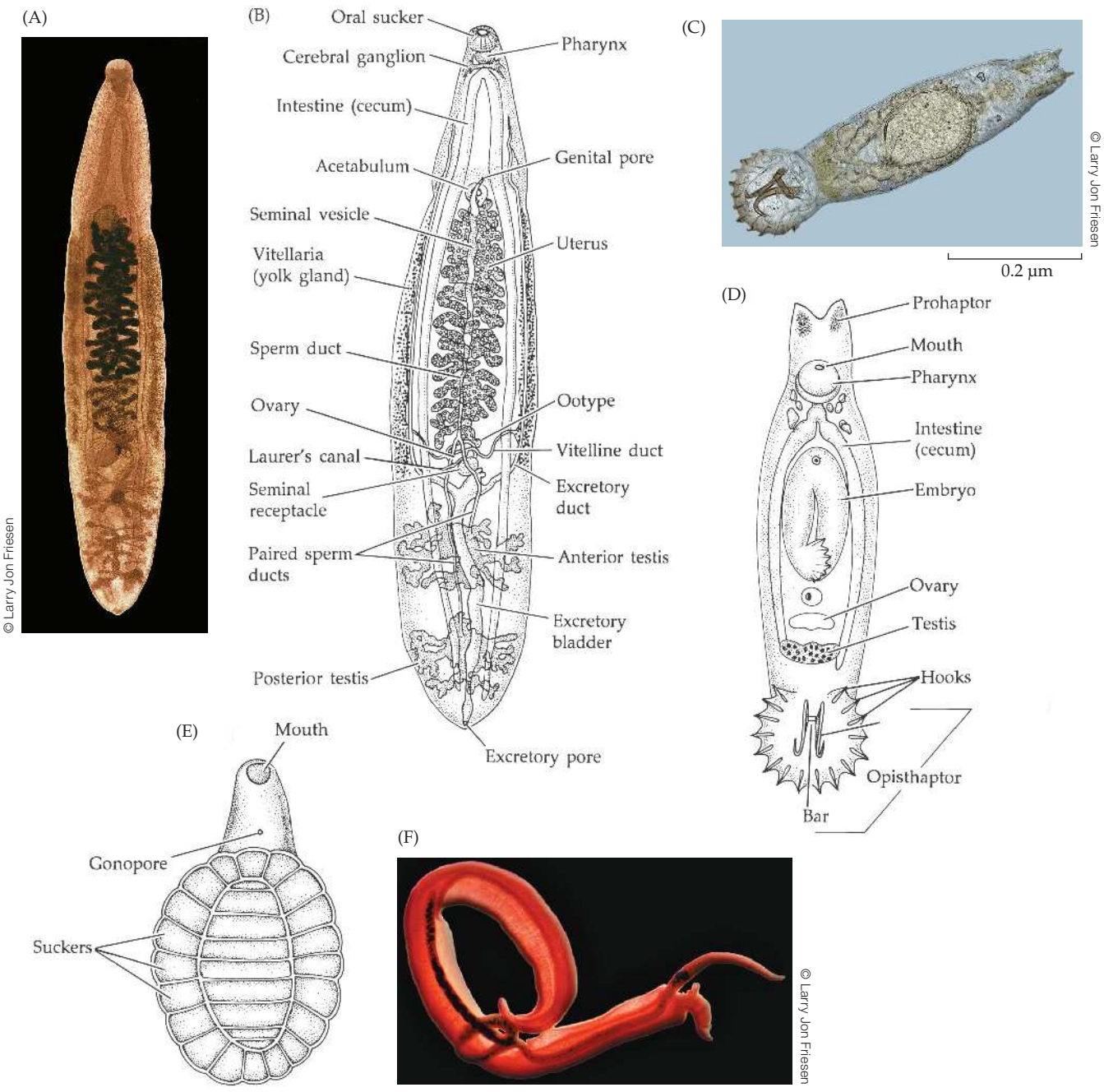

FIGURE 17.3 Representative flukes. (A,B) *Clonorchis sinensis*, a plagiorchiid trematode that inhabits human livers. (C,D) *Gyrodactylus* (Monogenea), an ectoparasite on fishes. (E) *Cotylaspis* (an aspidogastrid trematode). (F) The human blood fluke, *Schistosoma mansoni* (a copulating male and female), a diplostomidan fluke and one of the few gonochoristic flatworms.

17.6. Free-living flatworm species vary in shape from broadly oval to ribbonlike and are typically flattened dorsoventrally, although very small ones may be nearly cylindrical. The head is usually ill defined, except for the presence of sense organs. The mouth is often located ventrally, either near the middle of the body or more anteriorly, though again, there are exceptions (e.g., prorhynchids whose raptorial mouth is fully anterior; cestodes who have no mouth at all). Most flukes (Figure 17.3) are oval or leaf shaped and bear external attachment organs such as hooks and suckers. As their common name suggests, the tapeworms are typically elongate and ribbonlike (Figure 17.4). Their anterior end forms a tiny **scolex**, modified for attachment within the host; the rest of the body is essentially a reproductive machine.

Tapeworms live in the guts of vertebrates. Most species belong to the Cestoda and possess three distinguishable regions of the body. The **scolex** serves for attachment and is usually armed with hooks and suckers. Immediately behind the scolex is a short region called

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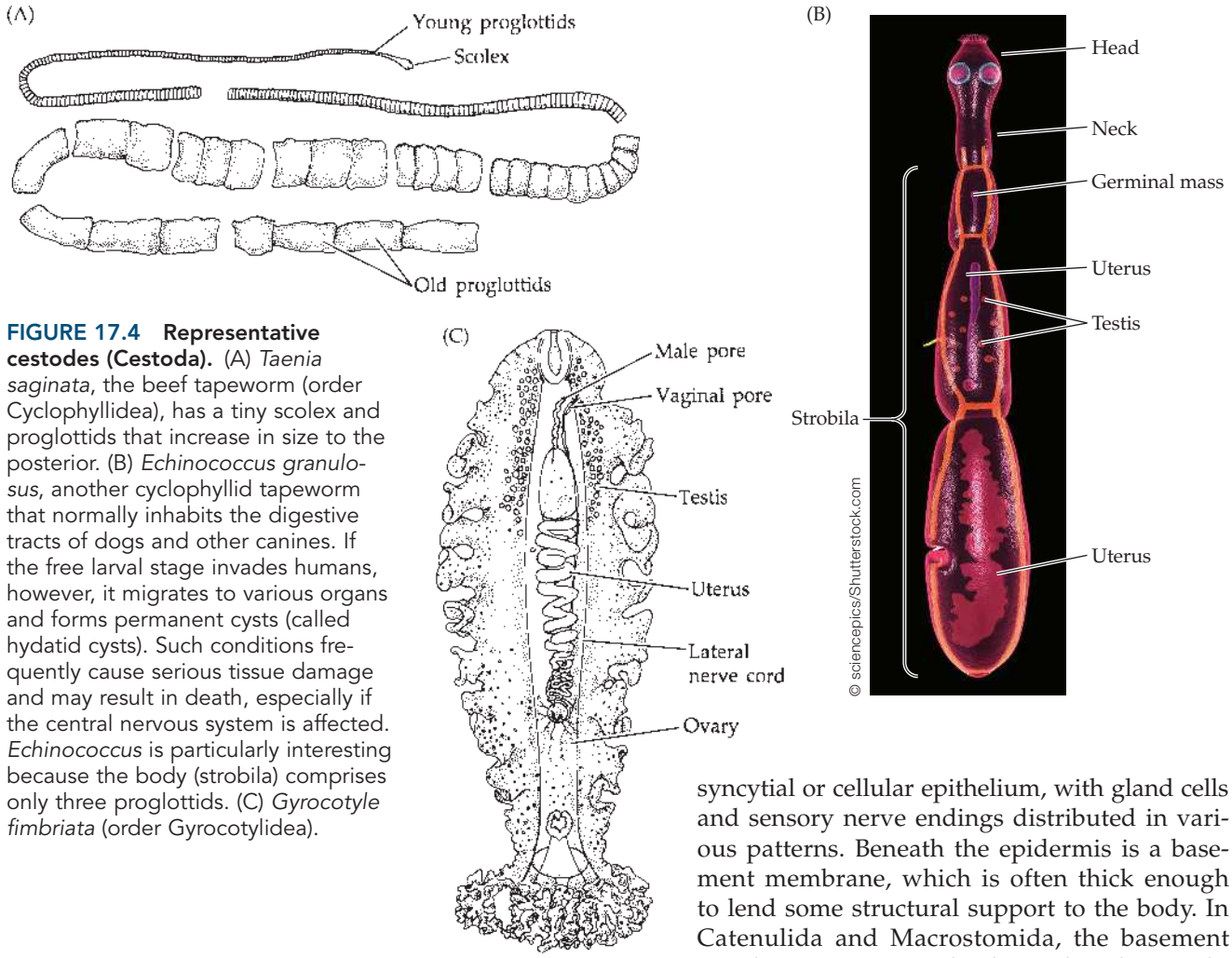

FIGURE 17.4 Representative cestodes (Cestoda). (A) *Taenia saginata*, the beef tapeworm (order Cyclophyllidea), has a tiny scolex and proglottids that increase in size to the posterior. (B) *Echinococcus granulosus*, another cyclophyllid tapeworm that normally inhabits the digestive tracts of dogs and other canines. If the free larval stage invades humans, however, it migrates to various organs and forms permanent cysts (called hydatid cysts). Such conditions frequently cause serious tissue damage and may result in death, especially if the central nervous system is affected. *Echinococcus* is particularly interesting because the body (strobila) comprises only three proglottids. (C) *Gyrocotyle fimbriata* (order Gyrocotylidea).

the **neck**, followed by an elongated, segmented trunk, or **strobila**, consisting of individual **proglottids**. The proglottids bud (strobilate) from a germinal zone in the neck (or at the base of the scolex when a neck is absent). As new proglottids arise at the base of the trunk, older ones mature, become inseminated, and fill with embryos. "Segmentation," or **strobilation**, in tapeworms is thus not by way of teloblastic growth (discussed in Chapters 15 and 20), and it is clearly not homologous to the segmentation seen in annelids and arthropods.

Tapeworms in the orders Amphilinidea and Gyrocotylidea are somewhat flukelike in appearance. They lack a scolex, and the body is not divided into proglottids. They are placed within the Cestoda because of the absence of a digestive tract and because of certain features of the life cycle. They may represent the primitive, prestrobilation body plan of the Cestoda.

Body Wall

Free-living flatworms The body wall of these species is multilayered and complex (Figure 17.5). The epidermis is composed of a wholly or partially ciliated, syncytial or cellular epithelium, with gland cells and sensory nerve endings distributed in various patterns. Beneath the epidermis is a basement membrane, which is often thick enough to lend some structural support to the body. In Catenulida and Macrostomida, the basement membrane is apparently absent, but this condition is viewed as secondarily derived. Internal to the basement membrane are smooth muscle cells, frequently arranged in rather loosely organized outer circular, middle diagonal, and inner longitudinal layers. The area between the body wall and the internal organs is usually filled with a mesenchyme (often called a parenchyme) that includes a variety of loose and fixed cells, muscle fibers, and connective tissue. Many macrostomorphans appear to lack a cellular mesenchyme.

The gland cells of the body wall are generally derived from ectoderm. When mature, many of these cells lie in the mesenchyme with a "neck" extending between epidermal cells to the body surface. These cells produce mucous secretions that serve a number of functions. In semiterrestrial and intertidal flatworms, the mucus forms a moist covering that provides protection from desiccation and aids in gas exchange. Most benthic flatworms possess a ventral concentration of mucous gland cells that secrete a slime that aids in locomotion. Mucous secretion around the mouth aids in prey capture and swallowing. Other gland cells or complexes of cells provide granules containing adhesives for temporary attachment, as well as granules that break the attachment, occurring several times per second. Such

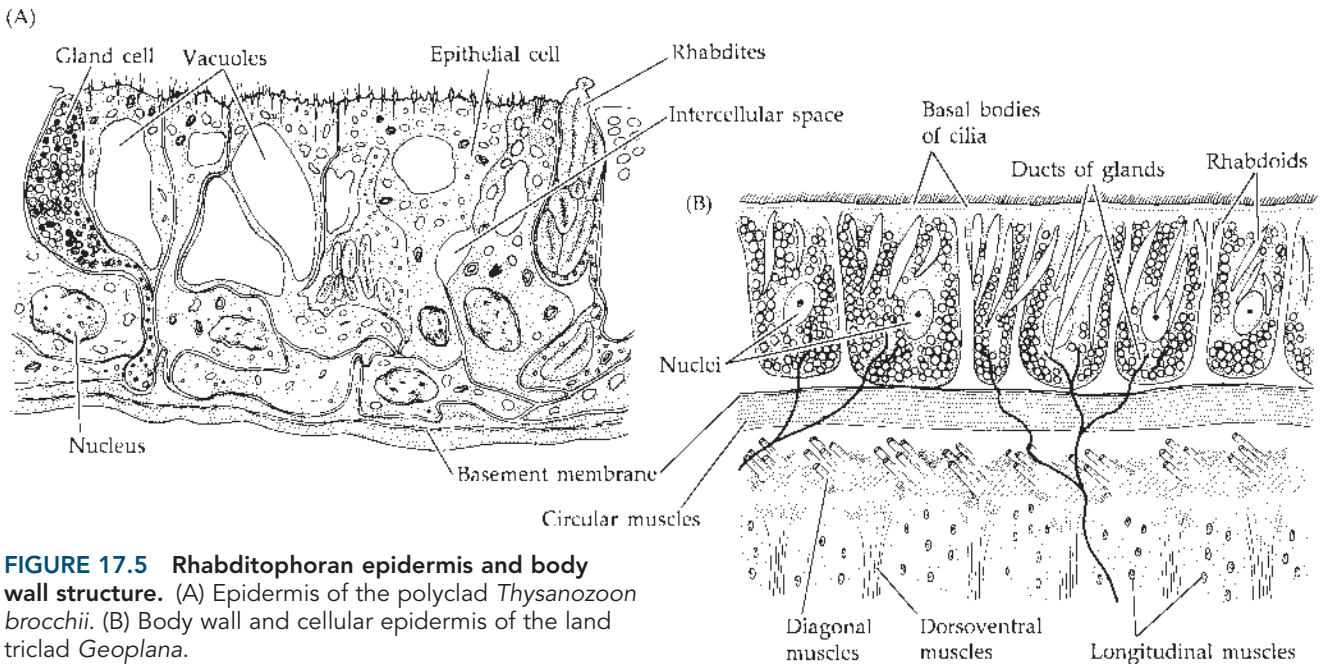

FIGURE 17.5 Rhabditophoran epidermis and body wall structure. (A) Epidermis of the polyclad *Thysanozoon brocchii*. (B) Body wall and cellular epidermis of the land triclad *Geoplana*.

duo-gland adhesion systems (often involving a third cell type that provides structural support) are widespread in free-living flatworms and other phyla with similar lifestyles. In some ectocommensal forms (e.g., *Bdelloura* triclads and various temnocephalid dalytyphloplanids; Figure 17.6) these adhesive glands are associated with special plates or suckers for attachment to the host.

In most free-living flatworms epidermal and subepidermal gland cells produce structures called **rhabdoids** (Figure 17.5B). These rod-shaped cellular inclusions produce mucus when moved to the surface of the epithelium. Some other phyla (e.g., Xenacoelomorpha, Gastrotricha, Nemertea, Annelida) have similar, but probably convergently evolved, secretory cellular bodies. The mucus aids in ciliary gliding and also may help protect animals from desiccation and from predators. Some rhabdoids that are produced by gland cells in the epidermis or mesenchyme have a distinct cortex (composed of concentrically arranged lamellae) and medulla, and these are called **rhabdites**. These structures

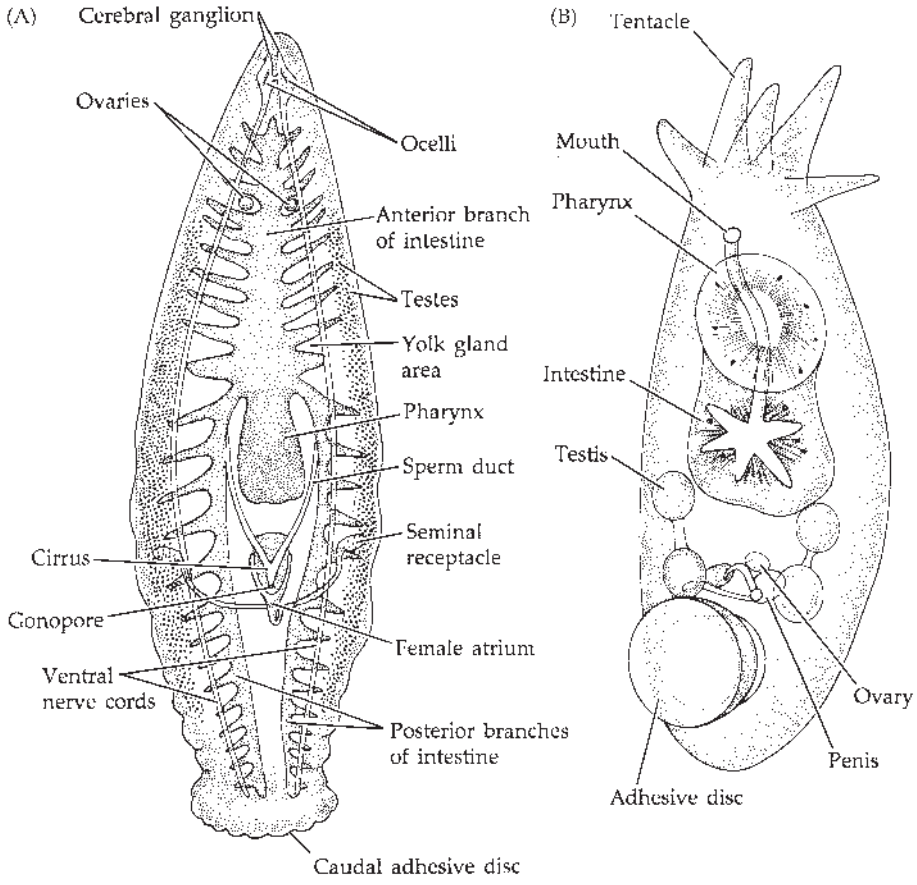

FIGURE 17.6 Two symbiotic euneoophoran flatworms with adhesive attachment organs. (A) *Bdelloura candida*, a triclad ectocommensal on horseshoe crabs (*Limulus polyphemus*). (B) *Temnosewella caeca* (formerly *Temnocephala caeca*), a rhabdocoel ectocommensal on *Phreatoicopsis terricola* (a freshwater isopod).

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can reach the body surface through intercellular spaces in the epidermis (Figure 17.5A). They also contribute to mucus production and, in some species, release noxious chemicals for defense. Rhabdites are diagnostic of the huge flatworm clade (subphylum) Rhabditophora. Somewhat similar structures, called "false rhabdites," have been described from the other main flatworm clade (subphylum) Catenulidea, but they may not be homologous to those of Rhabditophora.

Some species of free-living flatworms (e.g., macrostomids, proseriates, polyclads) have prominent tubercles covering the dorsal surface, and these probably also have a defensive role. In some species, unfired nematocysts from hydroid prey are transported to the tubercles. In others, such as species of *Thysanozoon*, the tubercles appear to release a powerful acid that may deter would-be predators.

Flukes and tapeworms Modifications of the outer body covering are common among parasites, and platyhelminths are no exception. Unlike the free-living flatworms, flukes and tapeworms possess an external covering called a **tegument**, formed of nonciliated cytoplasmic extensions of large cells whose cell bodies actually lie in the mesenchyme (Figure 17.7). The extensions fuse their margins such that the outer surface of the worm forms a functional syncytium. The tegument not only provides some protection, but also is an important site of exchange between the body and the environment. Gases and nitrogenous wastes move across this surface by diffusion, and some nutrients, especially amino acids, are taken in by pinocytosis. In tapeworms, the uptake of nutrients occurs solely across the body wall, and the surface area of the tegument is greatly increased by many tiny folds called **microtriches** (Figure 17.7B). As one of nature's more remarkable adaptations, these folds may interdigitate with the intestinal microvilli of the host organism and aid in the absorption of nutrients.

The nature of the tegument in flukes and tapeworms is viewed by some zoologists as unique and of major phylogenetic importance. The larvae of these parasitic worms have a "normal" ciliated epidermis over at least part of their bodies. However, this epidermis is shed, and postlarval stages develop a new, syncytial body covering—the **neodermis**. This phenomenon appears to be a unique synapomorphy uniting the Monogenea, Trematoda, and Cestoda as a monophyletic taxon that Ehlers named Neodermata (in reference to the "new skin" of these animals), a hypothesis that is now substantiated by all molecular phylogenetic analyses.

The tegument/neodermis is underlain by a basement membrane, beneath which is the mesenchyme. Most flukes and tapeworms have circular and longitudinal muscles within the mesenchyme, and sometimes diagonal, transverse, and dorsoventral muscles as well. The mesenchyme varies from masses of densely packed cells to syncytial and fibrous networks with fluid-filled spaces. In some digenean flukes (Trematoda: orders Diplostomida and Plagiorchiida), spaces form vessels

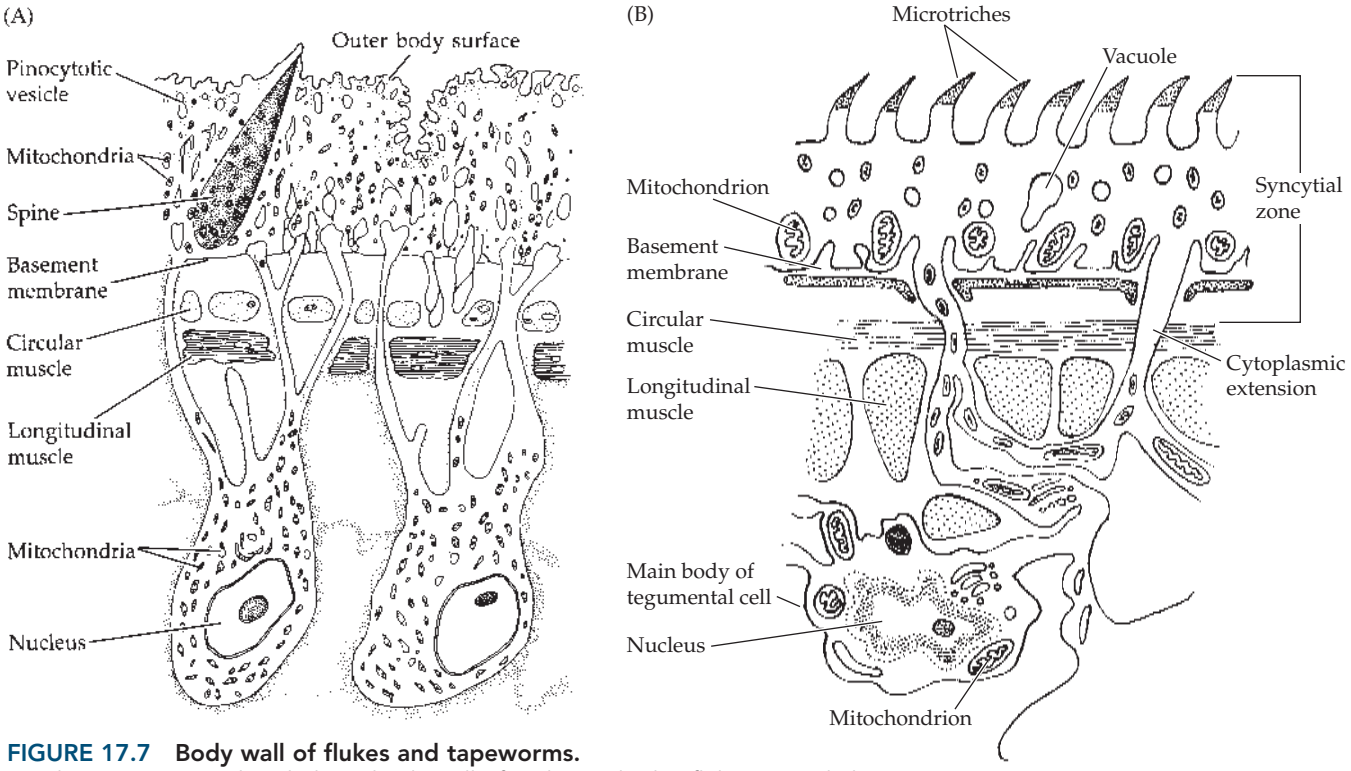


FIGURE 17.7 Body wall of flukes and tapeworms.
(A) The tegument and underlying body wall of a plagiorchiidan fluke (*Fasciola hepatica*; longitudinal section). (B) The tegument and body wall of a cestode (cross section).

through the mesenchyme called **lymphatic channels**, which contain free cells that have been likened to lymphocytes. The mesenchyme also contains gland cells with connections to the surface of the body through the tegument. These gland cells are few in number compared with those of free-living flatworms, and they are primarily adhesive in nature and associated with certain organs of attachment.

One of the least explored yet most interesting attributes of tapeworms, and indeed of all intestinal parasites, is their ability to thrive in an environment of hydrolytic enzymes without being digested. In addition to constant replacement of the outer tegument by underlying cells, one popular hypothesis is that gut parasites produce enzyme inhibitors (sometimes called "antienzymes"). One study showed that *Hymenolepis diminuta* (a common tapeworm in rats and mice) releases proteins that appear to inhibit trypsin activity. This tapeworm can also regulate the pH of its immediate environment to about 5.0 by excreting organic acids; this acidic output may also inhibit the activity of trypsin.

Support, Locomotion, and Attachment

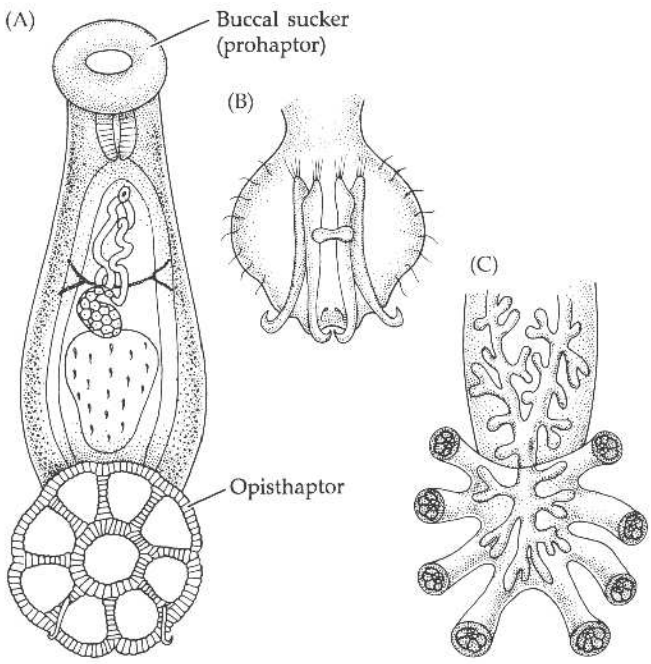
Only a very few flatworms possess any sort of special skeletal elements. In a few free-living species, tiny calcareous plates or spicules are embedded in the body wall (Figure 17.1L). Body support in all other flatworms is provided by the hydrostatic qualities of the mesenchyme, the elasticity of the body wall, and the general body musculature.

Most free-living, benthic species move on their ventral surface by cilia-powered gliding. Mucus provides lubrication as the animal moves and serves as a viscous medium against which the cilia act. Some of the larger or more elongate forms also use muscular contractions. The ventral surface of the body is thrown into a series of alternating transverse furrows and ridges that move as waves along the animal, propelling it forward. Muscular undulations of the lateral body margins allow some large polyclads to swim for brief periods of time. Muscular action allows the body to twist and turn, providing steerage. Some interstitial forms are highly elongate and use the body wall muscles to slither between sand grains. Many of these types of flatworms possess adhesive glands, the secretions of which provide temporary stickiness and enable the animals to gain purchase and leverage as they move.

Adult flukes lack external cilia, and their movement depends on their body wall muscles or on the body fluids of their host. Some move about slowly on or within their host by muscle action, and a few (e.g., blood flukes) are carried in the host's circulatory system. However, certain larval stages are highly motile and do swim using ciliary action. Once established within or on a host, it is usually advantageous for a fluke to stay more or less in one place. In that regard, nearly all of them are equipped with external organs for temporary or permanent attachment (Figures 17.3C and 17.8). Monogenean flukes typically have an anterior and a posterior adhesive organ called the **prohaptor** and the **opisthaptor**, respectively. The prohaptor consists of a pair of adhesive structures, one on each side of the mouth, bearing suckers or simple adhesive pads. The opisthaptor is usually the major organ of attachment and includes one or more well-developed suckers with hooks or claws.

The digenean flukes possess two hookless suckers. One, the **oral sucker**, surrounds the mouth, and the other, the **acetabulum**, is located elsewhere on the ventral surface (Figure 17.3B). These suckers are usually supplied with adhesive gland cells, although the well-developed ones operate mainly on suction produced by muscle action. The aspidogastrean flukes lack an oral sucker but have a large, subdivided ventral sucker (Figure 17.3E).

Adult tapeworms (Cestoda) do not move around much, but they are capable of muscular undulations of



Courtesy of J. DeMartini

FIGURE 17.8 Some attachment organs of monogenean flukes. (A) *Anoplocotyloides papillatus.* (B,C) Opisthaptors from monogenean flukes. (D) An unidentified fluke with suckered prohaptor and elaborate opisthaptor.

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the body. They remain fixed to the host's intestinal wall by the **scolex** (or, in the case of members of the cestode order Amphilinidea, by an anterior adhesive organ) and by the microtriches. The details of scolex anatomy (Figure 17.9) are extremely variable and have great importance in the taxonomy of tapeworms. The tip of the scolex in many cestodes (e.g., *Taenia*) is equipped with a movable hook-bearing **rostellum**, which is sometimes retractable into the scolex. In others (e.g., *Cephalobothrium*) the anterior end bears a protrusible sucker, or adhesive pad, called a **myzorhynchus**. The rest of the scolex bears various suckers or suckerlike structures and sometimes hooks or spines. There are three categories of adhesive suckers upon which ordinal and subordinal classification of cestodes is partially based. **Bothria** are elongate, longitudinal grooves on the scolex. They possess weak muscles but are capable of some sucking action. Bothria occur as a single pair and are typical of the orders Diphyllobothriidea (e.g., *Diphyllobothrium*) and Bothriocephalidea. Members of the nonmonophyletic order Tetraphyllidea (e.g., *Acanthobothrium*, *Phyllobothrium*) bear four symmetrically placed **bothridia** around the scolex. These foliose structures are often equipped with suckers at their anterior ends. The third and most familiar type of attachment structures on the scolex are true suckers, or **acetabula**. They are identical in structure and are probably homologous to the acetabula of digenean trematodes. There are usually four acetabula, placed symmetrically around the circumference of the scolex. They are characteristic of many members of the order Cyclophyllidea (e.g., *Dipylidium*, *Taenia*).

Feeding and Digestion

Free-living flatworms Most species are carnivorous predators or scavengers, feeding on nearly any available animal matter or, in the case of very small species, on bacteria or fungi in biofilms. A few are herbivorous on microalgae, and some species switch from herbivory to carnivory as they mature. Their prey include protists or almost any invertebrate small enough to be captured and ingested (e.g., small crustaceans, worms, tiny gastropods). Some species graze on sponges, ectoprocts,

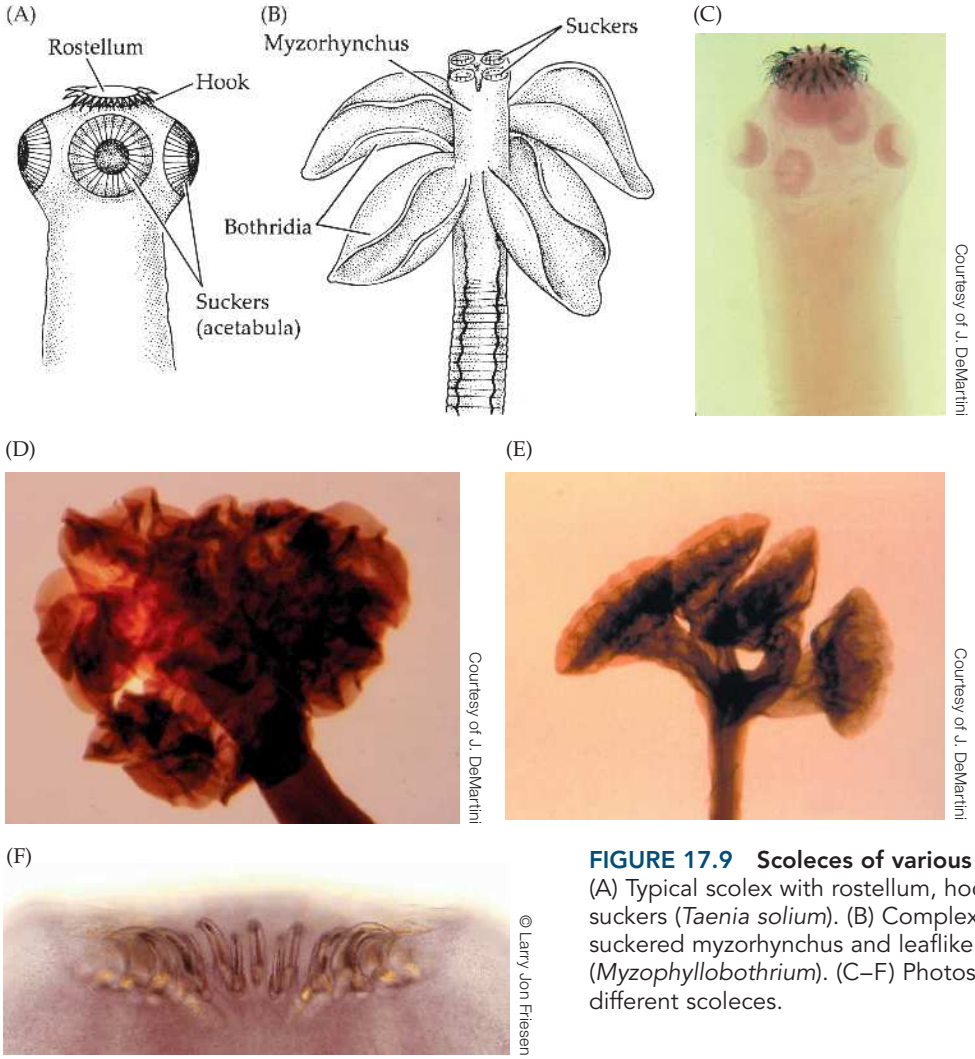

FIGURE 17.9 Scoleces of various cestodes. (A) Typical scolex with rostellum, hooks, and suckers (*Taenia solium*). (B) Complex scolex with suckered myzorhynchus and leaflike bothridia (*Myzophyllobothrium*). (C–F) Photos of four different scoleces.

and tunicates, and some consume the flesh of barnacles, leaving behind the empty shell. Most free-living flatworms locate food by chemoreception. Land planarians capture and consume earthworms, land snails, and insects. *Platydemus manokwari*, the 6.5 cm-long "New Guinea flatworm," is a highly invasive species that is a threat for endemic terrestrial molluscs; it has invaded throughout the Pacific, as well as in Europe, the Caribbean, and most recently Florida (USA). *Endeavouria septemlineata* is invasive in at least Hawaii and Brazil, where it feeds on a variety of invertebrates (e.g., isopods, millipedes, earwigs, gastropods). *Obama nungara*, a highly invasive South American species, has widely invaded Europe.

More than 100 species of free-living flatworms are known to be symbiotic with other invertebrates. Some of these are simply commensals that derive some protection from their associations, showing only physical modifications for temporary attachment. Others, however, feed upon their hosts, causing various degrees of damage and displaying true physiological dependency in the relationship. While we can devote space to mentioning only a few examples of symbiotic free-living flatworms, recognition of these situations is of considerable importance. First, it emphasizes the evolutionary adaptability of the flatworm body plan; second, it provides some essential foundation for our later discussion of the origins of the flukes and tapeworms.

Most of the symbiotic free-living flatworms belong to the class Rhabdocoela. Species in the family Temnocephalidae (Figure 17.6B) are ectocommensals within the branchial chambers of freshwater decapod crustaceans, where they feed on microorganisms in the host's gas exchange currents. Temnocephalids also occur on aquatic insects, molluscs, turtles, and a few other kinds of hosts. Several families of Dalytyphloplanida include symbiotic members. For example, *Syndesmis* live within the gut and coelomic fluid of echinoids, where they feed on protists and bacteria, and some may devour cells of their hosts (Figure 17.10). The genera *Graffilla* and *Paravortex* include several species of parasites in the digestive tracts of gastropod and bivalve molluscs, where they derive nutrients from the host tissues. Members of the family Fecampiidae (*Fecampia*, *Kronborgia*, *Glanduloderma*) are parasites in marine crustaceans and certain polychaete worms, where they reside in the host's body fluids and absorb soluble organic nutrients. Non-Rhabdocoela symbiotic species include the triclad *Bdelloura* (Figure 17.6A), an ectocommensal on the gills of *Limulus polyphemus*, the American horseshoe crab. At least two polyclads live and feed on coral (*Prosthiostomum montiporae* on Hawaiian *Montipora*; *Prosthiostomum acroporae* on Australian *Acropora*).

The digestive system of the free-living flatworms includes a mouth and a pharynx, which lead to an intestine, or **enteron**. Like that of cnidarians and Xenacoelomorpha, the free-living flatworm gut is incomplete, bearing a single opening, and thus may be called a **gastrovascular cavity**. The mouth varies in position from midventral to anterior. The pharynx is derived from embryonic ectoderm (i.e., it is stomodeal) and lined with epidermis. Epithelial **pharyngeal glands** are associated with the lumen of the pharynx; they produce mucus that aids in feeding and swallowing, and (in some species) they produce proteolytic enzymes that initiate digestion outside the body.

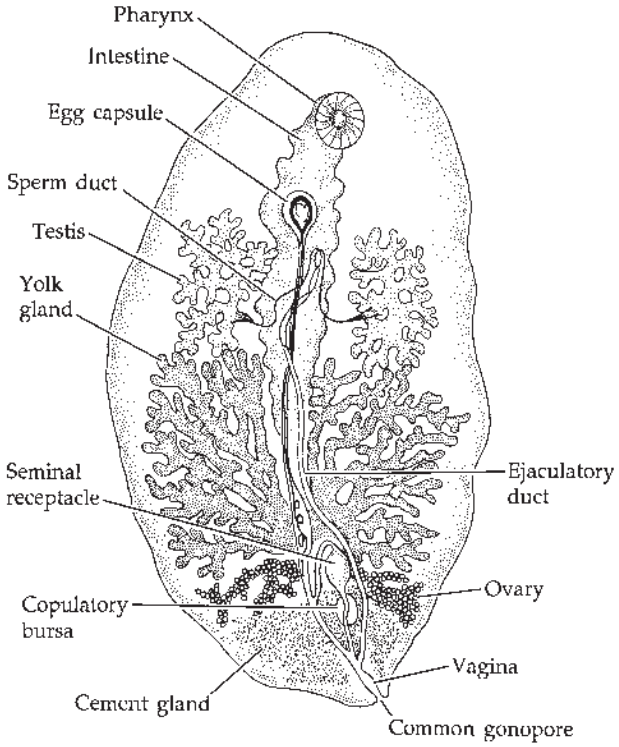

FIGURE 17.10 ***Syndesmis*, a symbiotic rhabdocoel from the gut of a sea urchin.**

The feeding methods of free-living flatworms vary with the size of the animal and the complexity of their food-gathering apparatus, especially the pharynx. As noted in the classification scheme, the nature of the pharynx varies greatly among taxa. There are three basic pharynx types among the free-living flatworms: simple, bulbous, and plicate (Figures 17.11 and 17.12).

A **pharynx simplex** (simple pharynx) is a short, ciliated tube connecting the mouth and intestine (Figure 17.12). This type of pharynx has been considered plesiomorphic within the phylum Platyhelminthes and is found in the orders Macrostomida and Catenulida. In all members of these orders, the pharynx leads to a simple saclike or elongate intestine generally lacking extensive diverticula. Free-living flatworms with a simple tubular pharynx are generally quite small, with the mouth located more or less midventrally. They usually feed by sweeping small organic particles and tiny prey into the pharynx by ciliary action.

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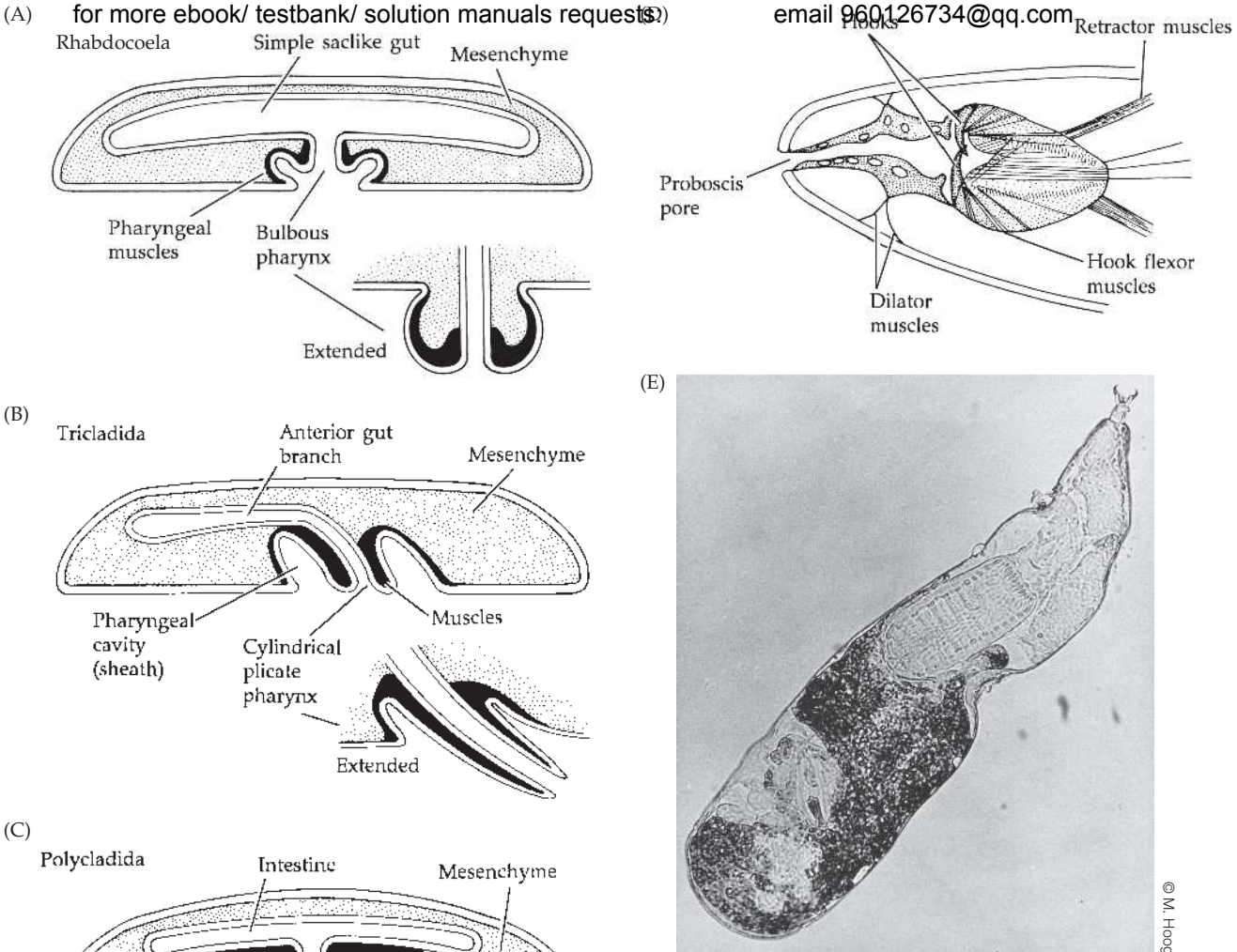

FIGURE 17.11 Pharynges of flatworms. (A–C) The pharynges of three free-living flatworms (sagittal sections). (D) The proboscis apparatus (sagittal section) of the rhabdocoel *Gnathorhynchus* (order Kalyptorhynchia). (E) *Cheliplana*, another rhabdocoel (order Kalyptorhynchia), with jawed proboscis extended (top right).

Those with an eversible pharynx usually fold their body around the prey or other food source and cover it with mucus from the epidermal glands. Then the pharynx is everted over or into the food item.

Some free-living flatworms, especially triclads, secrete digestive enzymes externally via special glands that empty through the pharyngeal lumen or from the tip of the pharynx. The food is partially digested and reduced to a soupy consistency prior to swallowing. Many other species swallow their food whole by the action of powerful pharyngeal muscles.

Rhabdocoels typically possess a slightly protractile, muscular, bulbous pharynx and a simple saclike gut (Figures 7.11A and 17.13A). Members of the Proseriata, Tricladida, and Polycladida have eversible plicate

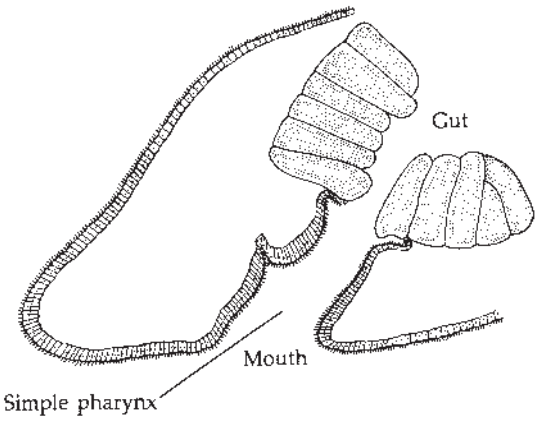

FIGURE 17.12 Sagittal section through anterior end of *Macrostomum* (Macrostomorpha), which has a simple tubular pharynx.

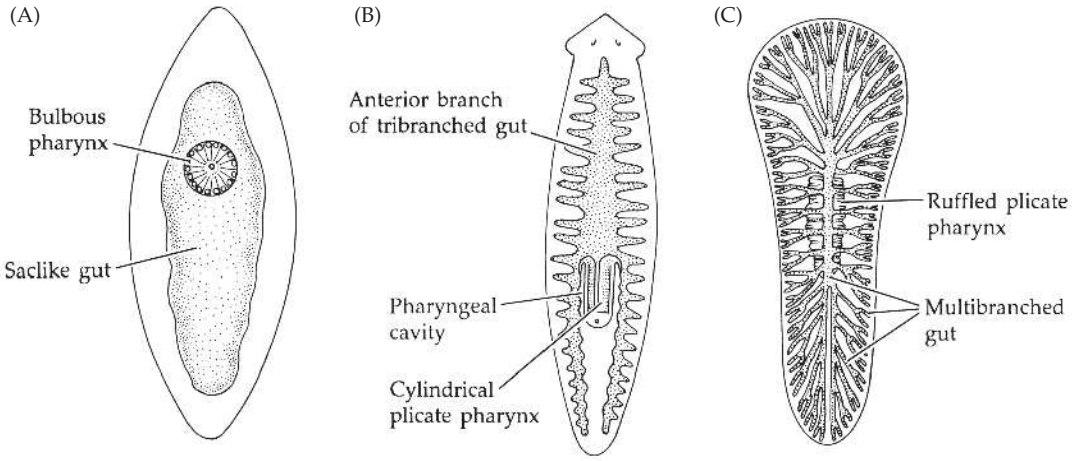

FIGURE 17.13 Pharynx type and gut shape combinations among free-living flatworms. (A) Rhabdocoela. (B) Tricladida. (C) Polycladida.

pharynges. The eversible portion of a plicate pharynx lies within a space called the pharyngeal cavity, which is produced by a muscular fold of the body wall (Figures 17.11 and 17.13).

Proseriates and triclads possess cylindrical plicate pharynges oriented along the body axis. Most polyclads have a ruffled, skirtlike plicate pharynx attached dorsally within the pharyngeal cavity. During feeding, a plicate pharynx is protruded by a squeezing action of extrinsic pharyngeal muscles. Once extended, the pharynx can be moved about by intrinsic muscles of its wall. Retractor muscles pull the pharynx back inside the cavity.

Active prey can be subdued in several ways. Some free-living flatworms produce mucus, which, in addition to entangling the prey, may contain narcotic or poisonous chemicals such as tetrodotoxin. A few flatworms use the sharp **stylet** of the copulatory organ to stab prey and even to introduce venom; one cannot help but concede the remarkable adaptive capacity of the flatworms. Members of the Kalyptorhynchia (Rhabdocoela) are unique among free-living flatworms in their possession of a muscular proboscis that is situated at the anterior end of the body and is separate from the mouth (Figure 17.11D,E); the proboscis, which in some species is armed with hooks, can be everted to grab prey.

Most of the free-living flatworms that possess a plicate pharynx are relatively large, especially the triclads and the polyclads. Associated with this large body size is an elaboration of the intestine. As the names imply, the triclad intestine comprises three main branches, one anterior and two posterior, each with numerous diverticula, whereas the intestine of polyclads is multibranched with diverticula (Figure 17.13B,C). These ramifications of the intestine not only provide an increased surface area for digestion and absorption, but also are a means of distributing the products of digestion through the relatively large body in the absence of a circulatory system. The lining of the intestine is a single cell layer of phagocytic nutritive cells and enzymatic gland cells (Figure 17.14). In some groups, the gastrodermis is ciliated.

In most free-living flatworms, initial digestion is extracellular, mediated by endopeptidases secreted from the pharyngeal glands or from enzymatic gland cells within the intestine. The partially digested material is distributed throughout the gut, then phagocytized by the intestinal cells, wherein final (intracellular) digestion occurs. There are, however, some notable exceptions to this sequence. Bowen (1980) described an interesting phagocytic process in the freshwater triclad *Polycelis tenuis*. Following the ingestion of tiny food particles or the preliminary extracellular digestion of larger food, the intestinal phagocytic cells extend processes into the gut lumen, nearly occluding the digestive cavity. These processes interdigitate to form

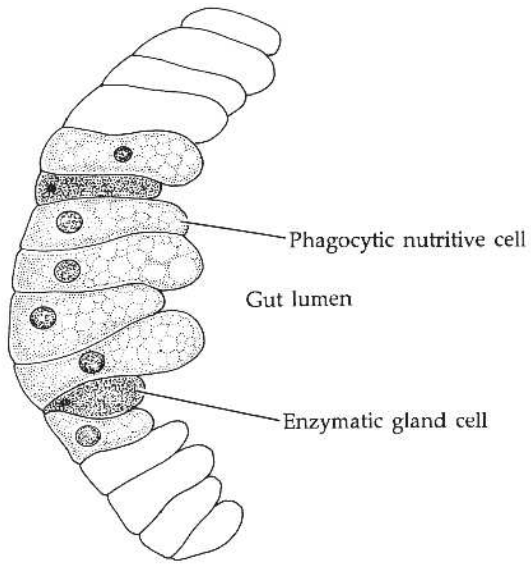

FIGURE 17.14 The gut lining (partial cross section) of a freshwater triclad contains enzymatic gland cells and phagocytic nutritive cells.

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a complex web, forcing food material into the phagocytes, where digestion is completed.

Since flatworms generally lack a through gut, any undigested material must be expelled through the mouth. As discussed in Chapter 3, a major limitation of single-opening guts is the restriction on regional specialization. However, an incipient anus occurs in several flatworms; but does this represent an "experiment" with through gut in this group, or does it represent vestiges of a through gut they once had and have lost? One macrostomorphan, *Haplopharynx rostratus*, possesses a minute anal pore, some polyclads have pores at the ends of gut branches, and some proseriates (e.g., *Tabaota*) may form a temporary anus.

Flukes and tapeworms Adult flukes feed on host tissues and fluids or, in some cases, material within the host's gut. Most of the food is taken in through the mouth by a pumping action of the muscular pharynx, but some organic molecules are picked up across the tegument by pinocytosis. The anterior part of the digestive system includes a mouth, a muscular pharynx, and a short esophagus. The esophagus leads to a pair of intestinal **ceca** (occasionally, a single cecum), which extend(s) posteriorly in the body (Figures 17.3 and 17.15). The lining of the ceca includes absorptive nutritive cells and enzymatic gland cells. Digestion is at least partly extracellular. Some flukes secrete enzymes from the gut out the mouth, or from the suckers, to partially digest host tissue prior to ingestion.

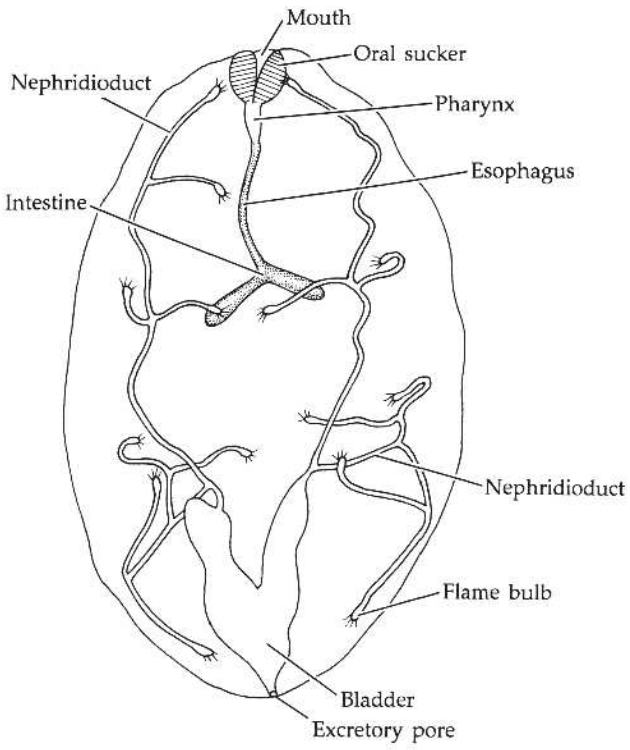

FIGURE 17.15 Gut and protonephridial system of *Microphallus* (order Plagiorchiida; see also Figure 17.3). In most monogenean flukes, the protonephridial ducts are separate and terminate anteriorly in separate pores.

Cestodes lack any vestige of a mouth or digestive tract. All nutrients must be taken into the body across the tegument. Uptake probably occurs by pinocytosis and by diffusion across the increased surface area of the microtriches. Some work suggests that tapeworms are unable to take in large molecules and thus rely to a considerable extent on the digestive processes of their hosts and the secretion of enzymes outside their bodies to chemically reduce the size of potential nutrient material. It has also been proposed that the surface of the scolex may absorb host tissue fluids through the site of attachment to the gut wall.

Many parasites, in numerous phyla, have been shown to alter the behavior of their hosts in ways that are beneficial to themselves, usually by causing the host to position itself such that the odds of success in the next stage in the parasite's life cycle are improved. Parasitic platyhelminths are no exception. For example, larvae of the digenean *Microphallus papillorobustus* encyst in the nervous systems of two species of amphipods (*Gammarus* spp.). There, they induce photophilia in animals that are usually photophobic. Consequently, infected amphipods are more likely than uninfected animals to be eaten by seagulls (a potential final host). When the cestode *Eubothrium salvelini* reaches the developmental stage where it is infective to the final host (brook trout, *Salvelinus fontinalis*), its intermediate host—the copepod *Acanthocyclops vernalis*—begins to swim more often than normal, making it more likely to be eaten by the fish. The beetle *Tribolium confusum* is an intermediate host to the tapeworm *Hymenolepis diminuta*. Evidence suggests the beetle might be more attracted to rat feces that contain the cestode's eggs than to uninfected feces. The same may be true of cockroaches (*Periplaneta americana*) confronted with the feces of rats parasitized by the acanthocephalan *Moniliformis moniliformis*. Infection by the digenetic trematode *Parorchis acanthus* reduces feeding by more than 80% in marsh snails (*Littoraria irrorata*).

Circulation and Gas Exchange

As mentioned earlier, except for the lymphatic channels in some flukes, flatworms lack special circulatory or gas exchange structures. This condition imposes restrictions on size and shape. The key to survival with such limitations and a generally solid mesenchyme is the maintenance of small diffusion distances. Thus, the flatness of their bodies facilitates gas exchange across the body wall, between the tissues and the environment; nutrients are distributed internally by the digestive system and by diffusion, which is aided by general body movements.

The endoparasitic flatworms are capable of surviving in areas of their host where oxygen is absent. In such cases, they rely on anaerobic metabolism, producing a variety of reduced end products (e.g., lactate,

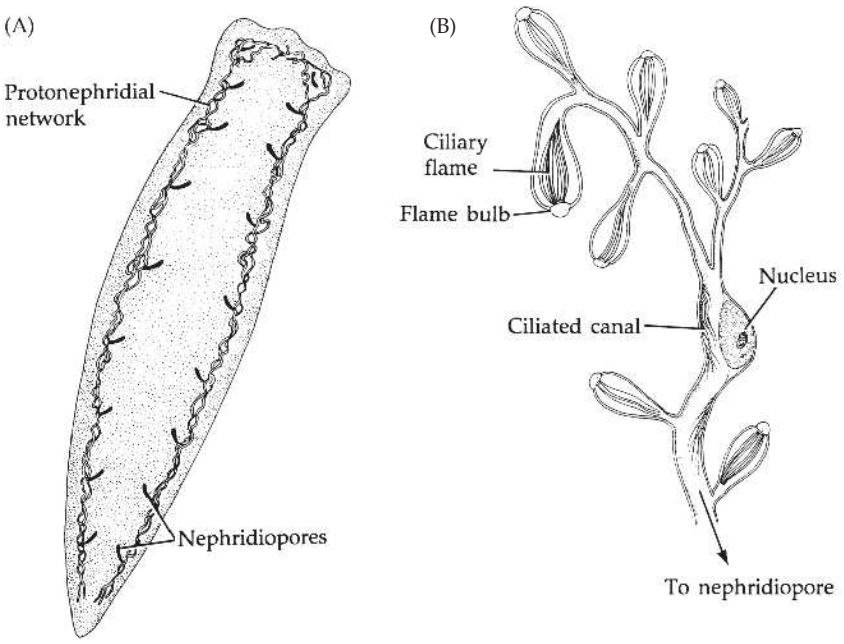

FIGURE 17.16 Nephridia of euneoophoran flatworms. (A) The protonephridial system in a freshwater triclad. (B) The nephridial arrangement in a rhabdocoel that has anucleate flame bulbs attached to collecting tubules.

succinate, alanine, and long-chain fatty acids). Most of these adaptable animals also possess the appropriate enzymes for and are capable of aerobic respiration in the presence of oxygen.

Excretion and Osmoregulation

Protonephridia seem to occur in all free-living flatworms (except some marine catenulids) and consist of flame bulbs that may occur singly (as they do in some catenulids) or in pairs (from one to many pairs in different taxa). The protonephridia connect to networks of collecting tubules that coalesce as nephridioducts (sometimes called excretory ducts), and then to one or more nephridiopores (Figure 17.3B, 17.15, and 17.16). Protonephridia in free-living flatworms function primarily as osmoregulatory structures. Freshwater species tend to have more protonephridia and more complex tubule systems than do their marine counterparts. Although some ammonia is released via the protonephridia, most metabolic wastes (including ammonia) are lost by diffusion across the body wall. Typically, two nephridioducts drain the nephridia. In some cases there is a storage area, or bladder, that connects with a posterior nephridiopore, such as in digenean flukes, or to a pair of anterior pores in the monogenean types (Figure 17.15). As in free-living flatworms, the protonephridia of flukes are primarily osmoregulatory.

Tapeworms possess numerous flame bulb protonephridia throughout the body. The flame bulbs drain to pairs of dorsolateral and ventrolateral nephridioducts that run the length of the body (Figure 17.17). Although some variation in plumbing occurs, the ventral ducts are typically connected to one another by transverse tubules near the posterior end of each proglottid. In relatively young worms that have not lost any proglottids (see the section on Reproduction and Development), the excretory ducts lead to a collecting bladder in the most posterior proglottid. Once this terminal proglottid is lost, the nephridioducts open separately to the outside on the posterior margin of the remaining hindmost proglottid. There is still much to be learned about the protonephridia of cestodes. They probably function both in excretion and osmoregulation. They may also serve to eliminate certain organic acid products of anaerobic cellular

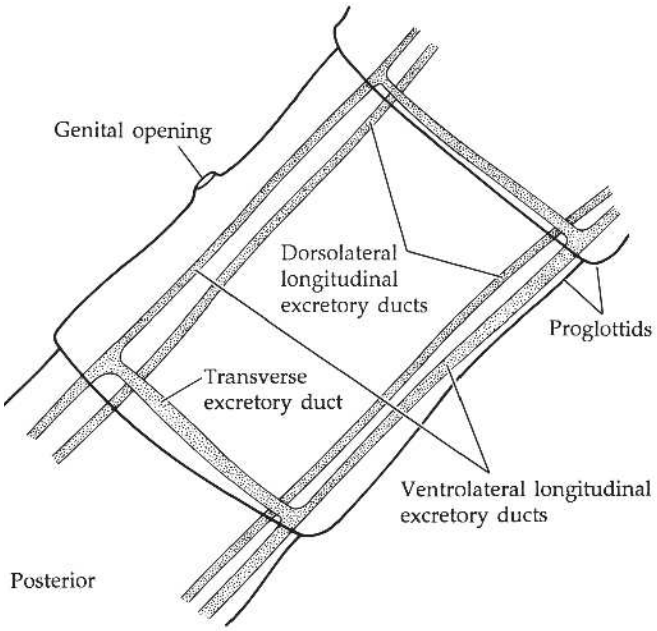

FIGURE 17.17 The arrangement of major protonephridial ducts in a cestode proglottid (ventral view).

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metabolism. Some experimental work indicates that tapeworms are capable of precipitating and storing some waste products within their proglottids.

Nervous System and Sense Organs

Free-living flatworms The nervous systems of these species vary from a simple netlike nerve plexus with only a minor concentration of neurons in the head (similar to that seen in the phylum Xenacoelomorpha), to a distinctly bilateral arrangement with a well-developed cerebral ganglion and longitudinal nerve cords connected by transverse commissures (Figure 17.18). The more advanced condition is referred to as a ladderlike nervous system. Even many of those species that possess distinctly centralized nervous systems have a plexus formed by the repeated branching of nerve endings (e.g., polyclads). In general, larger flatworms show an increasing concentration of the peripheral nerves into fewer and fewer longitudinal cords and an accumulation of neurons in the head as an associative center or cerebral ganglion. Furthermore, they show a tendency to separate the elements of the nervous system into distinct sensory and motor pathways and to develop a circuitry that operates primarily on unidirectional impulse transmission.

Free-living flatworms have a general concentration of sense organs at the anterior end of the body and an elaboration of receptor types that are compatible with their lifestyle. Tactile receptors are abundant over much of the body surface as sensory bristles projecting from the epidermis, but they tend to concentrate at the anterior end and around the pharynx. Benthic free-living flatworms orient to the substratum by touch; they are positively thigmotactic ventrally and negatively thigmotactic dorsally.

Most free-living flatworms are equipped with chemoreceptors that aid in food location. Although sensitive over most of the body, free-living flatworms have distinct concentrations of chemoreceptors anteriorly, particularly on the sides of the head. Some forms, such as the familiar freshwater planarians and the prorhynchidans, have the chemoreceptors located in flaplike processes called **auricles** on the head (Figures 17.2 and 17.18C), whereas others have these sense organs in ciliated pits, on tentacles, or distributed over much of the anterior end of the body. The epithelium bearing the chemoreceptors is usually ciliated and frequently forms depressions or grooves. The cilia are the receptor organelles, but they also circulate water, thus facilitating sensory input from the environment.

The utilization of chemoreception in locating food has been demonstrated in many free-living flatworms. Some are known to home in on concentrations of dissolved chemicals associated with potential food. Others, such as *Dugesia*, hunt by waving the head back and forth as they crawl forward, exposing the auricles to any chemical stimulus in their path. When exposed to diffuse chemical attractants, some free-living flatworms begin a trial-and-error behavior pattern. If unable to determine the direction of the attractant, the worm begins moving in a straight line. If the stimulus weakens, the animal makes apparently random turns until it encounters sufficient stimulus, then moves toward it. This behavior can eventually bring the animal near enough to the food source to home in on it directly. Some species orient to water movements by rheoreceptors located on the sides of the head (Figure 17.18D).

Statocysts are common in certain flatworms, notably in members of the Catenulida and Proseriata. These groups include mostly swimming and interstitial forms in which orientation to gravity cannot be accomplished by touch. When present, the statocyst is usually located on or near the cerebral ganglion. Ehlers (1991) presents details on the ultrastructure of some flatworm statocysts.

Most free-living flatworms possess photoreceptors in the form of inverted pigment-cup ocelli (Figure 17.18E). A few macrostomids possess simple pigment-spot ocelli, which are presumed to be primitive within the flatworms. Many species bear a single pair of ocelli on the head, but some, such as certain polyclads and terrestrial triclads, may have many pairs of eyes. In a few terrestrial forms (e.g., *Parakontikia ventrolineata*) and many of the large tropical polyclads, numerous eyes extend along the edges of the body. Most free-living species are negatively phototactic. The dorsal placement of the eyes and the orientation of the pigment cups facilitate the detection of light direction as well as intensity. Larvae of the polyclad flatworm *Pseudoceros canadensis* possess two dissimilar kinds of eyes. The right eye appears to be microvillar (i.e., rhabdomeric), but the left one has components of both microvillar and ciliary origin (Eakin and Brandenberger 1980). The nature of these two eye types was noted in Chapter 3.

Neurosecretory cells have been known in free-living flatworms for more than three decades, and work continues on exploring their functions. These special cells are generally located in the cerebral ganglion, but they also occur along major nerve cords in at least some species. Neurosecretions play important roles in regeneration, asexual reproduction, and gonad maturation in free-living species that could serve as models for understanding similar functions in parasitic species.

Flukes and tapeworms The nervous system of flukes is distinctly ladderlike and very similar to that in many free-living flatworms (Figure 17.19). The cerebral ganglion comprises two well-defined lobes connected by a dorsal transverse commissure. Nerves from the cerebral ganglion extend anteriorly to supply the area of the mouth, adhesive organs, and any cephalic sense organs.

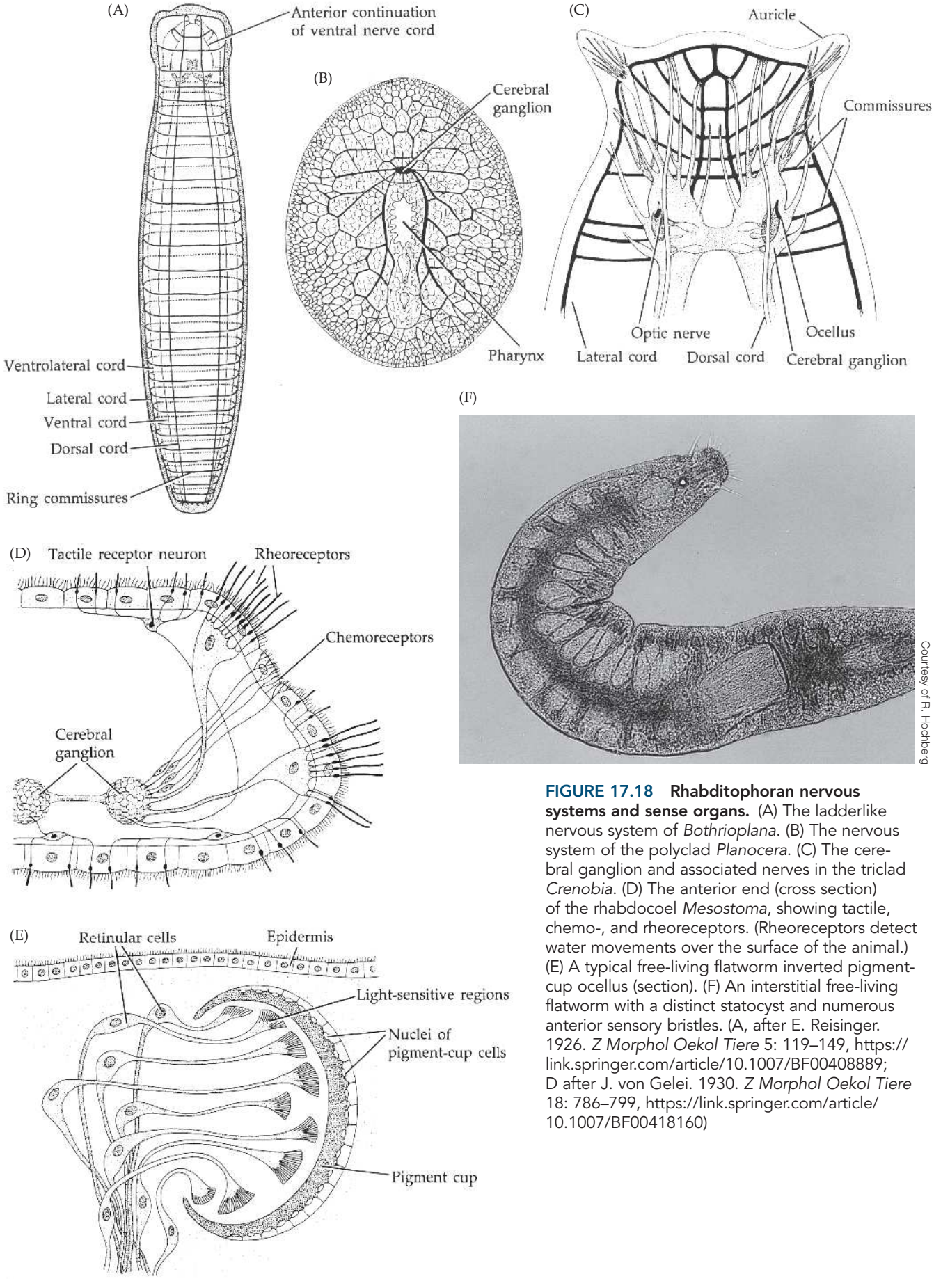

FIGURE 17.18 Rhabditophoran nervous systems and sense organs. (A) The ladderlike nervous system of *Bothrioplana*. (B) The nervous system of the polyclad *Planocera*. (C) The cerebral ganglion and associated nerves in the triclad *Crenobia*. (D) The anterior end (cross section) of the rhabdocoel *Mesostoma*, showing tactile, chemo-, and rheoreceptors. (Rheoreceptors detect water movements over the surface of the animal.) (E) A typical free-living flatworm inverted pigment-cup ocellus (section). (F) An interstitial free-living flatworm with a distinct statocyst and numerous anterior sensory bristles. (A, after E. Reisinger. 1926. *Z Morphol Oekol Tiere* 5: 119–149, https://link.springer.com/article/10.1007/BF00408889; D after J. von Gelei. 1930. *Z Morphol Oekol Tiere* 18: 786–799, https://link.springer.com/article/10.1007/BF00418160)

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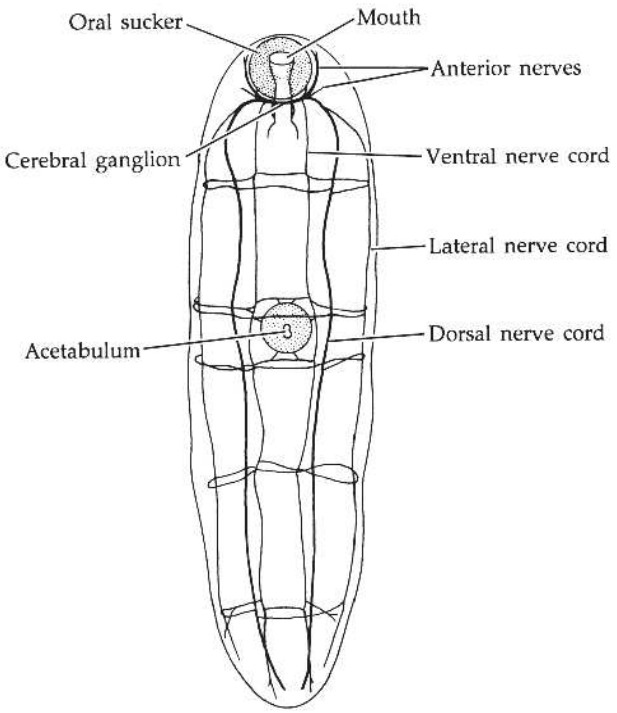

FIGURE 17.19 A generalized ladderlike nervous system of a trematode (ventral view).

Extending posteriorly from the cerebral ganglion are up to three pairs of longitudinal nerve cords with transverse connectives. A pair of ventral cords is usually most well developed, and dorsal cords are present in the digenean flukes. Most flukes also have a pair of lateral nerve cords. The suckers of flukes bear tactile receptors in the form of bristles and small spines. There is also some evidence of reduced chemoreceptors. Nearly all monogenean flukes possess a pair of rudimentary pigment-cup ocelli near the cerebral ganglion.

The cerebral ganglion of cestodes is usually a complex nerve ring located in the scolex (Figure 17.20). The ring bears ganglionic swellings and gives rise to a number of nerves. Anterior nerves, in the form of a ring or plexus, serve the rostellum (when present) and other attachment organs. Lateral cerebral ganglionic swellings give rise to a pair of major lateral longitudinal nerves, which extend the length of the animal. In each proglottid, these nerves bear additional ganglia from which transverse commissures arise and connect the two longitudinal cords. Additional longitudinal nerves are often present; the most typical pattern includes two pairs of accessory lateral cords—a pair of dorsal cords and a pair of ventral cords. As might be expected, sense organs are greatly reduced in cestodes and are limited to abundant tactile receptors in the scolex.

Reproduction and Development

Asexual processes Asexual reproduction is common among freshwater and terrestrial free-living flatworms, and it generally occurs by transverse fission. In the catenulids and macrostomorphans, an odd sort of multiple transverse fission occurs wherein the individuals thus produced remain attached to one another in a chain until they mature enough to survive alone (Figure 17.21A). Some freshwater triclads (e.g., *Dugesia*, *Schmidtea*) split in half behind the pharynx, and each half goes its own way, eventually regenerating the lost parts. A few (e.g., *Phagocata*) reproduce by fragmentation, each part encysting until the new worm forms.

The remarkable regenerative abilities of free-living flatworms have been studied intensely for many years. Much of this experimental work has been conducted on triclads. Underlying all of the bizarre results of various surgeries performed on these animals (Figure 17.21B,C) is the fact that the cells of organisms like *Dugesia* are not totipotent; an anterior–posterior body polarity exists in terms of the regenerative capabilities of the cells. However, the cells in the midbody region are less fixed in their potential to produce other parts of the body than are those toward the anterior or posterior ends. Thus, if the flatworm is cut through the middle of the body (as occurs in natural transverse fission), each half will regenerate the corresponding lost part. However, if the animal is cut transversely near one end—say, separating a small piece of the tail from the rest of the body—the larger piece will grow a new posterior end, but the piece of tail lacks the capability to produce an entire new anterior end. This gradient of cell potency has been of particular interest to cell biologists and medical researchers because of its relevance to healing and regeneration potential in higher animals.

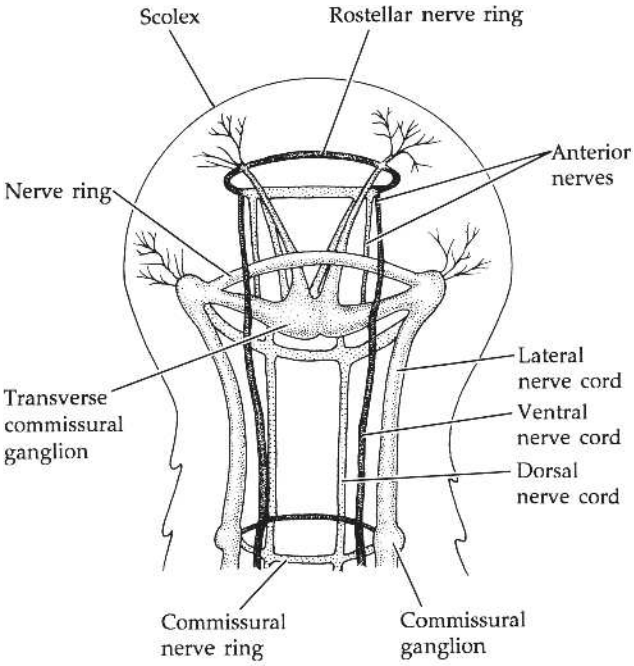

FIGURE 17.20 Cestode nervous system. The anterior end of *Moniezia*, a cyclophyllidean. The longitudinal cords extend the length of the animal.

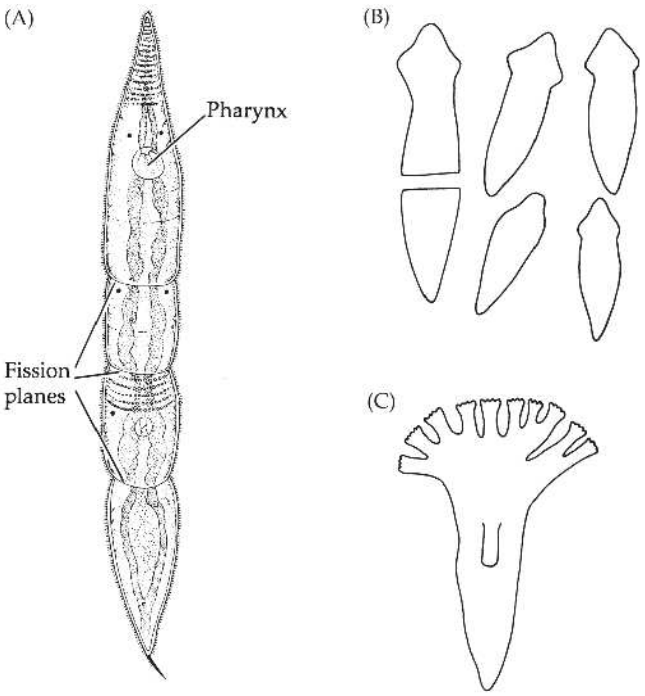

FIGURE 17.21 Asexual reproduction. (A) Asexual reproduction by transverse fission in a macrostomorphan flatworm, *Alaurina*. (B,C) Regeneration after experimental injuries in planarians.

Asexual reproduction is an important feature of the life cycle of flukes, where the ability to reproduce asexually helps ensure survival, particularly when potential mates may not be nearby.

Sexual reproduction: Free-living flatworms Most free-living flatworms are hermaphroditic and possess complex and highly diverse reproductive systems (Figure 17.22). The male system includes single (e.g., Macrostomorpha), paired (e.g., many Rhabdocoela), or multiple (e.g., Polycladida) testes. The testes are generally drained by collecting tubules that unite to form one or two sperm ducts, which often lead to a precopulatory storage area or seminal vesicle. Prostatic glands, which supply seminal fluid to the sperm, are often associated with and empty into the seminal vesicle. The seminal vesicle is typically part of a muscular chamber called the **male atrium**, which houses the copulatory organ. The actual organ of sperm transfer may be a papilla-like penis or an eversible cirrus, through which sperm are forced out by muscular action of the atrium.

The female reproductive system is more variable than that of the male. Much of the variation is related to whether the flatworm in question produces **endolecithal** or **ectolecithal** ova—that is, whether the worm is described as **archoöphoran** or **neoöphoran**. The archoöphorans (e.g., Macrostomida, Polycladida) typically possess an organ that produces both eggs and yolk. The final product is endolecithal ova. Such an organ is called a **germovitellarium,** and it may occur either singly or paired. In the neoöphorans (e.g., the order Prolecithophora and the entire superclass Euneoophora), the ovary (**germarium**) is separate from the yolk gland (**vitellarium**). Yolk-free eggs are produced by the ovary and then cellular yolk is transported through a vitelline duct and deposited alongside the ova inside the eggshell, a process resulting in ectolecithal ova.

In both cases, the eggs are typically moved via an oviduct toward the female atrium, which often bears special chambers for storage of sperm (i.e., seminal receptacle and copulatory bursa). Associated with this arrangement may be a variety of accessory glands, such as **cement glands**, for the production of shells and egg cases.

The male and female gonopores are often separate, the female opening usually located posterior to the male pore. In some species, however, the two systems share a common genital opening, and in a few the male atrium curiously opens just inside the mouth. In the latter case, the mouth is referred to as an **orogenital pore**.

Mating is usually by mutual cross-fertilization. The two mates align themselves so that the male gonopore of each is pressed against the female gonopore of the mate (Figure 17.23A). The male copulatory organ, or **stylet** (or penis or cirrus), is everted by hydrostatic pressure caused by the muscles surrounding the atrium and is inserted into the mate's female atrium, where sperm are deposited. The mates then separate, each going its own way and carrying foreign sperm. Fertilization usually occurs as the eggs pass into the female atrium or within the oviduct itself. The zygotes are frequently stored for a period of time in special parts of the female system or in enlarged oviducts; any such storage area is called a **uterus**.

Some macrostomorph and polyclad flatworms exhibit hypodermic insemination, whereby the male stylet is thrust through the body wall of the mate and sperm are forcibly injected into the mesenchyme. In other polyclads, individuals receive spermatophores from partners on their dorsal surface. Whereas most flatworms mate in pairs, such dermal impregnation may occur in groups. By a method not yet understood, after mating, the sperm find their way to the female system and fertilize the eggs.

In the genus *Macrostomum*, a close correspondence exists between the morphology of sperm, the morphology of the male stylet, and whether insemination is hypodermic or occurs by copulation (Figure 17.23C,D). Sperm in all *Macrostomum* have "feelers," anterior projections that embed themselves into the wall of the female reproductive tract in position to allow fertilization. However, depending on the species, sperm may also possess backwardly directed bristles. Species in which the stylet is hooked engage

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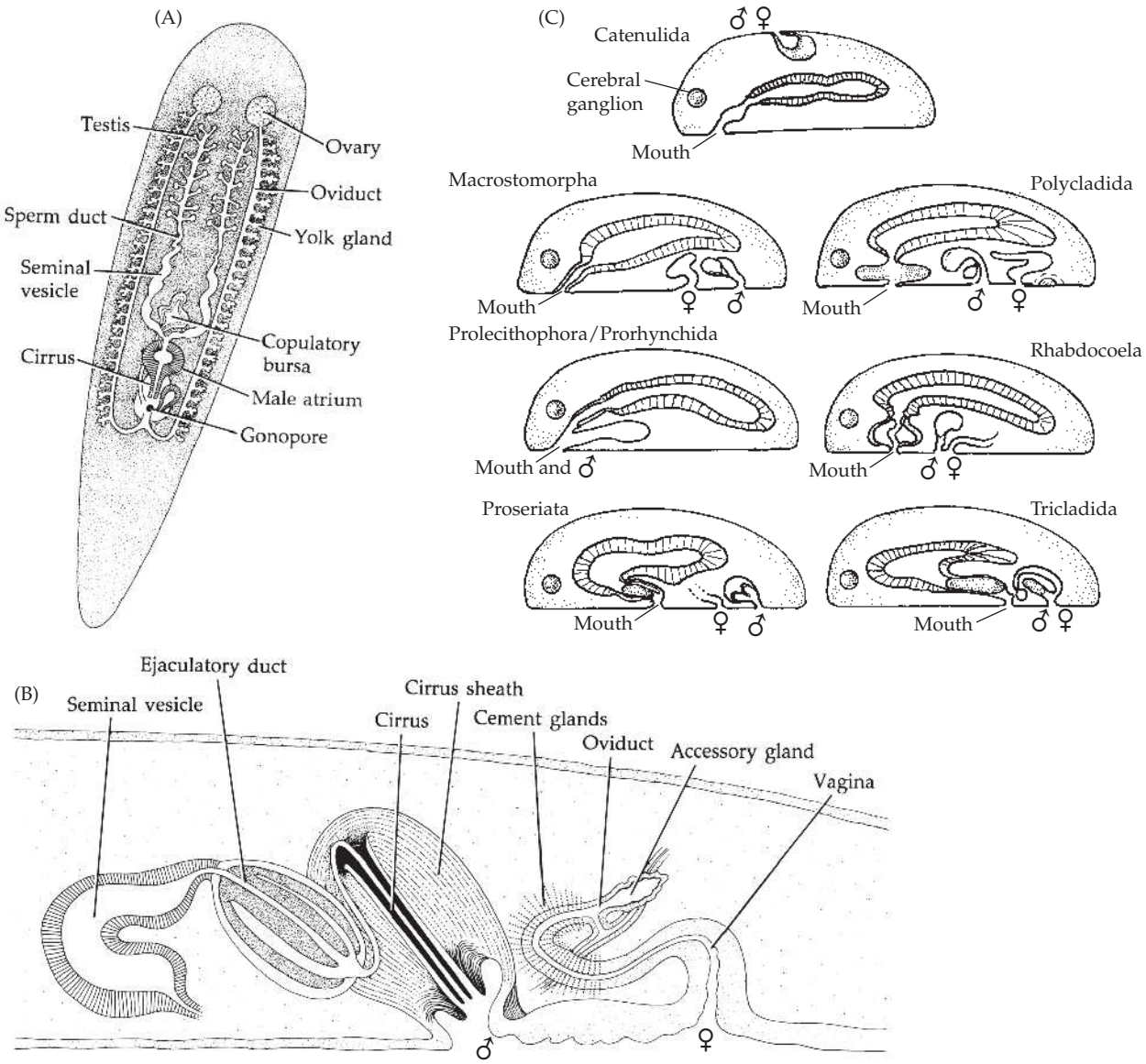

FIGURE 17.22 Reproductive systems of free-living flatworms. (A) Generalized triclad condition with separate ovaries and yolk glands (neoöphoran condition). (B) The copulatory structures of a triclad (sagittal section). (C) Generalized scheme of the relative position of male (♂) and female (♀) reproductive structures with respect to the location of the mouth in seven taxa.

in hypodermic insemination, and sperm lack bristles. In contrast, species in which the stylet is not hooked tend to copulate, and sperm do possess bristles. Bristles appear to maintain sperm in position within the female reproductive tract after mutual insemination by mating pairs. After pairs separate, each individual applies its mouth to its own vagina and "sucks," evidently removing unattached sperm. The sperm that have imbedded their feelers into the female reproductive tract are in position for fertilization, and bristles appear to assist in this process. Unattached sperm removed from the vagina are apparently eaten.

Ingestion of sperm from mating partners may in fact be widespread. In other free-living flatworms from several taxa, the presence of **Lang's vesicle** is associated with species that engage in copulation. Although this structure is thought to be a sperm storage organ, its significance is still in doubt. The structure is usually attached to the digestive system, suggesting that it may be involved in sperm digestion.

Once fertilization is accomplished, the zygotes are either retained by the parent within the uteri of the female reproductive tract or laid in various sorts of gelatinous or encapsulated egg masses (Figure 17.23B). Thus, most maternal free-living flatworms are obliged to contribute substantially toward the care of their embryos; they may be described as oviparous or ovoviviparous. Some freshwater triclads produce special overwintering zygotes, which are encapsulated and retained within the female reproductive tract until spring.

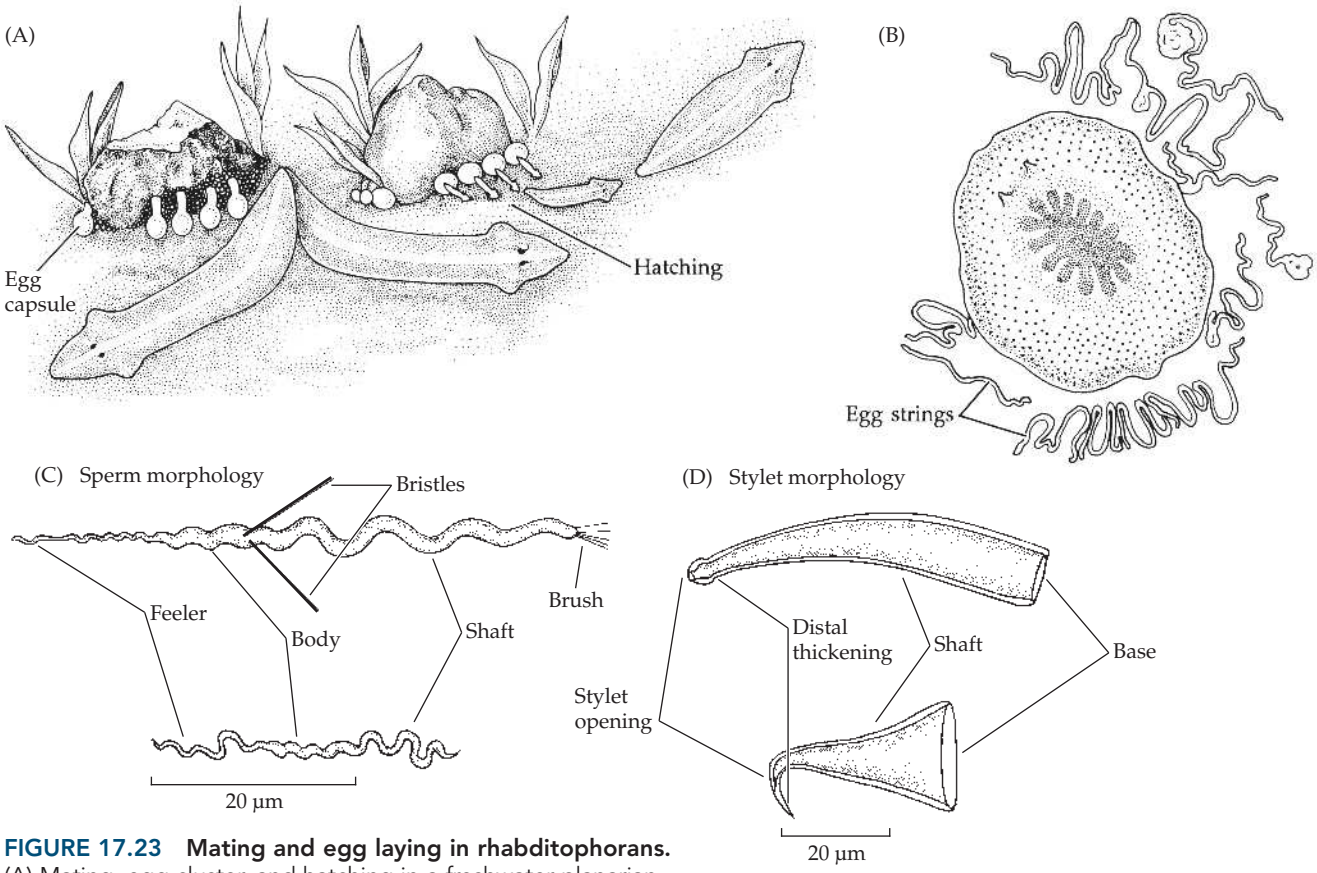

FIGURE 17.23 Mating and egg laying in rhabditophorans. (A) Mating, egg cluster, and hatching in a freshwater planarian. (B) Egg laying by the polyclad *Stylochus*. (C,D) Sperm and stylet morphology in two species of *Macrostomum*. Upper figures are *M. lignano*, a species in which individuals reciprocally copulate when mating. Lower figures are *M. hystrix*, a species in which hypodermic insemination occurs.

The general strategy of the vast majority of free-living flatworms is to produce relatively few zygotes, which are protected by brooding or encapsulation and undergo direct development. A few polyclads produce a **Müller's larva**, which swim about for a few days prior to settling and metamorphosing (Figures 17.24 and 17.25). This type of larva is equipped with eight ventrally directed ciliated lobes, by means of which it swims. A few species of parasitic polyclads of the genus *Stylochus* produce a **Götte's larva**, which bears four rather than eight lobes; and members of the freshwater catenulid genus *Rhynchoscolex* pass through a vermiform stage in their development that has been referred to as a larval form.

Early embryogeny differs greatly between the archoöphoran and neoöphoran flatworms. The endolecithal ova of the archoöphorans undergo some form of spiral cleavage (although some authors question the details of this process). The pattern and cell fates in many of these archoöphoran embryos are distinctly protostome-like, and this spiral cleavage has been well studied (especially in polyclads). Quartets of cells are produced, the fates of which may be described using Wilson's coding system (Chapter 4). By the end of spiral cleavage, the embryo is considered a stereoblastula, oriented with the derivatives of the first micromere quartet at the animal pole and the macromeres at the vegetal pole. The lq cells become the anterior ectoderm, cerebral ganglion, and most of the rest of the nervous system. The 2q derivatives contribute to

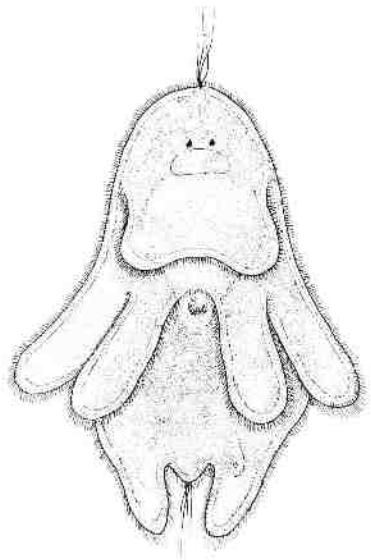

FIGURE 17.24 "Face-on" view of Müller's larva of a polyclad (*Planocera*).

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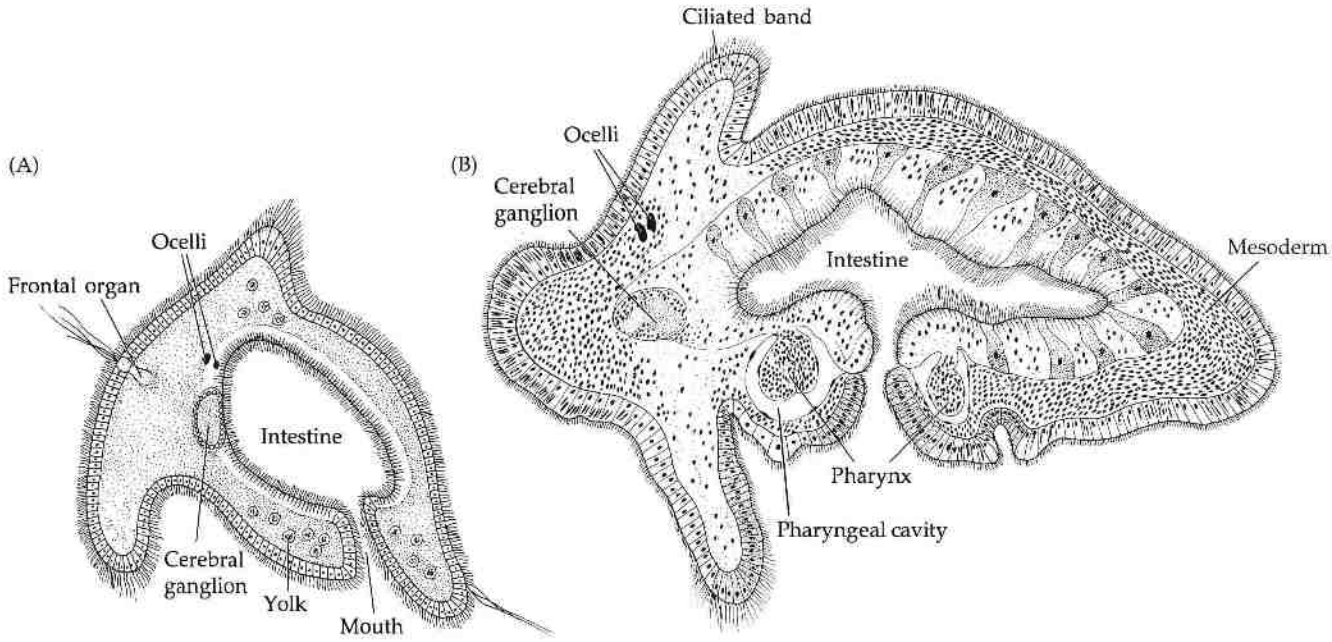

FIGURE 17.25 Polyclad development. (A) A Müller's larva (sagittal section). (B) A later larval stage, showing formation of the pharyngeal apparatus (sagittal section).

ectoderm and ectomesoderm, particularly that of the pharyngeal apparatus and its associated musculature. The remainder of the ectoderm and probably some ectomesoderm are formed from the derivatives of the third micromere quartet. The 4d cell, normally associated solely with endomesoderm in typical protostomes, divides to produce a $4d^1$ and $4d^2$ cell in polyclads. The $4d^1$ gives rise to endoderm and thus to the intestine; the $4d^2$ produces the endomesoderm from which the body wall and mesenchymal muscles, much of the mesenchymal mass, and most of the reproductive system are derived. The remaining cells (4a, 4b, 4c, and the 4Q) include most of the yolk and are incorporated into the developing archenteron as embryonic food.

Gastrulation is by epiboly of the presumptive ectoderm derived from some of the cells of the first three micromere quartets. The ectoderm grows from the animal pole to the vegetal pole, surrounding the 4q and 4Q cells. At the vegetal pole the ectoderm turns inward as a stomodeal invagination, which later elaborates as the pharynx and connects with the developing intestine (Figure 17.25). As development proceeds, the embryo flattens, with the mouth directed ventrally, and hatches as a tiny flatworm. If development is indirect, the larva emerges about the time the intestine is hollowing.

Because of the deposition of extracellular yolk with ectolecithal ova, the development of neoöphoran species is highly modified from the plan just described. Certain species of rhabdocoels and triclads have been most extensively studied, and the two groups differ—especially in the early stages. In both cases, cleavage is so distorted that cell fates and germ layer formation cannot easily be compared with the typical spiralian pattern. In the rhabdocoels, early cleavage leads to the formation of three masses of cells positioned along the presumptive ventral surface of the embryo beneath the mass of yolk (Figure 17.26A). The cell masses then produce a layer of cells that extends around to enclose the yolk. This covering thickens to several cell layers, the innermost eventually becoming the intestinal lining (and enclosing the yolk), the outermost becoming the epidermis. The anterior cell mass produces the nervous system; the middle cell mass produces the pharynx and associated muscles; the posterior cell mass forms the rear portion of the worm and the reproductive system.

Early development in triclads differs from that of other neoöphorans. During early cleavage, the blastomeres are loose within a surrounding mass of fluid yolk, a condition described as "blastomere anarchy." A few of the blastomeres migrate away from the others and flatten to produce a thin membrane enclosing a packet of the yolk including the remaining blastomeres (Figure 17.26B,C). These migrating blastomeres are often called **hull cells**, but the yolk-enclosing **hull membrane** they create can be variable and may not be homologous among flatworm taxa. Additional yolk cells are produced as a syncytial mass around a group of developing embryos and encapsulated, as many as 40 per capsule. Through migration and differentiation of various blastomeres, each embryo forms a temporary intestine, pharynx, and mouth, through which it ingests the yolky syncytium. The embryonic mouth eventually closes and the wall of the embryo thickens to form anterior, middle, and posterior cell masses, whose fates are similar to those in rhabdocoels.

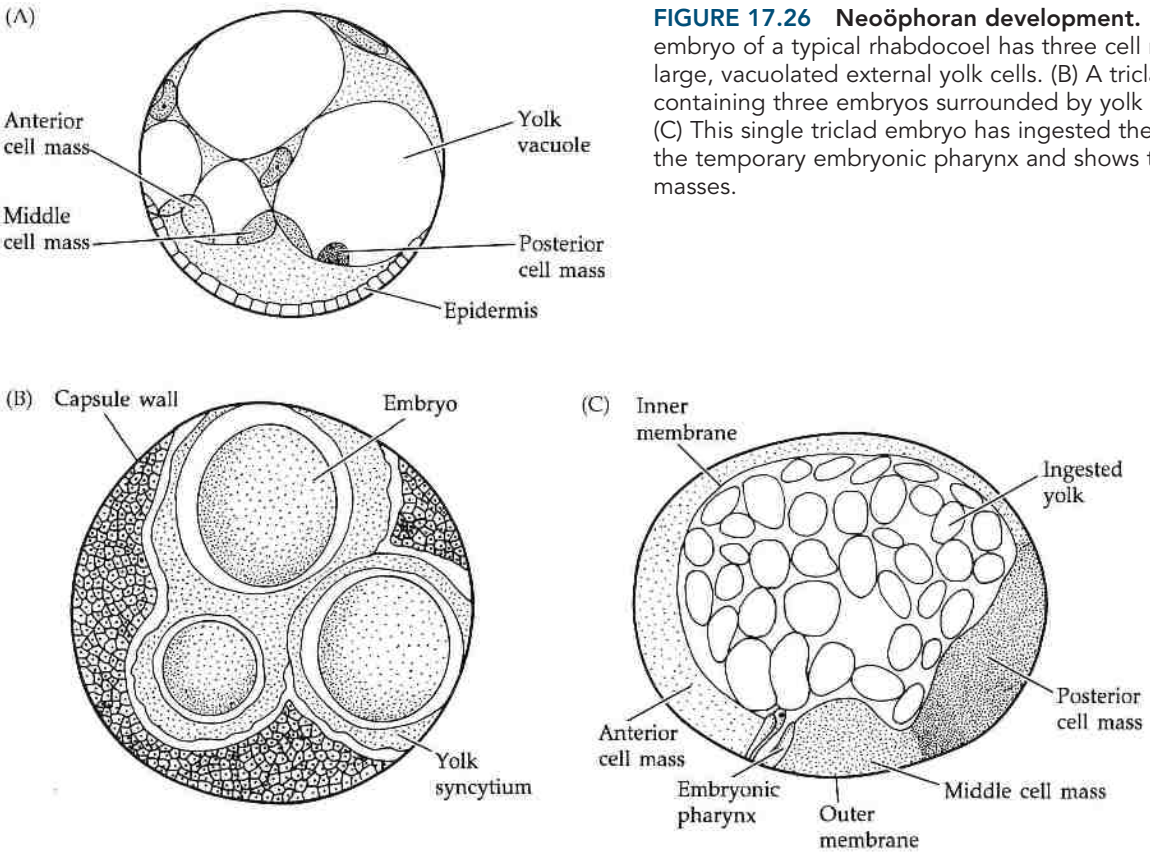

FIGURE 17.26 Neoöphoran development. (A) The embryo of a typical rhabdocoel has three cell masses with large, vacuolated external yolk cells. (B) A triclad egg capsule containing three embryos surrounded by yolk syncytium. (C) This single triclad embryo has ingested the yolk through the temporary embryonic pharynx and shows the three cell masses.

Sexual reproduction: Flukes Like the free-living flatworms, flukes are hermaphroditic and typically engage in mutual cross-fertilization. Self-fertilization occurs only in rare cases. There is a great deal of variation in the details of the reproductive systems among flukes, but most are built around a common plan similar to that in certain free-living flatworms (Figure 17.27). The male system includes a variable number of testes (usually many in the monogenean flukes and two in the digenean flukes), all of which drain to a common sperm duct that leads to a copulatory apparatus, usually an eversible cirrus. The sperm duct–cirrus junction is frequently enlarged as a seminal vesicle. Prostatic glands are commonly present, opening into the cirrus lumen near the seminal vesicle. All of these terminal structures are housed within a muscular **cirrus sac**, the contraction of which causes eversion of the cirrus as an intromittent organ (Figure 17.27C). There is usually a common genital pore that opens ventrally near the anterior end of the animal and leads to a shallow atrium, shared by both the male and female systems. Many monogenean flukes have simpler male systems than that just described, often lacking much elaboration of the terminal structures and possessing a simple **penis papilla** rather than an eversible cirrus.

The female reproductive system (Figure 17.27B) usually bears a single ovary connected by a short oviduct to a region known as the **ootype**. The oviduct is joined by a yolk duct (= vitelline duct) formed by the union of paired ducts, which carry yolk from the multiple laterally placed yolk glands. A seminal receptacle is usually present as a blind pouch off the oviduct. Extending anteriorly to the genital atrium is a single uterus, which is sometimes modified as a **vagina** near the female gonopore.

Sperm are produced in the testes and stored prior to copulation in the seminal vesicle (Figure 17.27C). During mating, two flukes align themselves such that the cirrus of each can be inserted into the female orifice of the other. Sperm, along with semen from the prostatic glands, are ejaculated into the female system by muscular contractions. The sperm move to, and are stored within, the seminal receptacle, and the mates separate. As eggs pass through the oviduct to the ootype, they are fertilized by sperm released from the seminal receptacle into the oviduct.

Flukes produce ectolecithal ova. The yolk glands produce yolk, which is deposited outside the eggs along with secretions that form a tough shell around the zygote. Thus encapsulated, the zygotes move from the ootype into the uterus, probably aided by secretions from clusters of unicellular **Mehlis's glands**. The zygotes may be stored within the uterus for various lengths of time prior to release through the female gonopore.

Some flukes possess an additional canal that arises from the oviduct and serves as a special copulatory duct.

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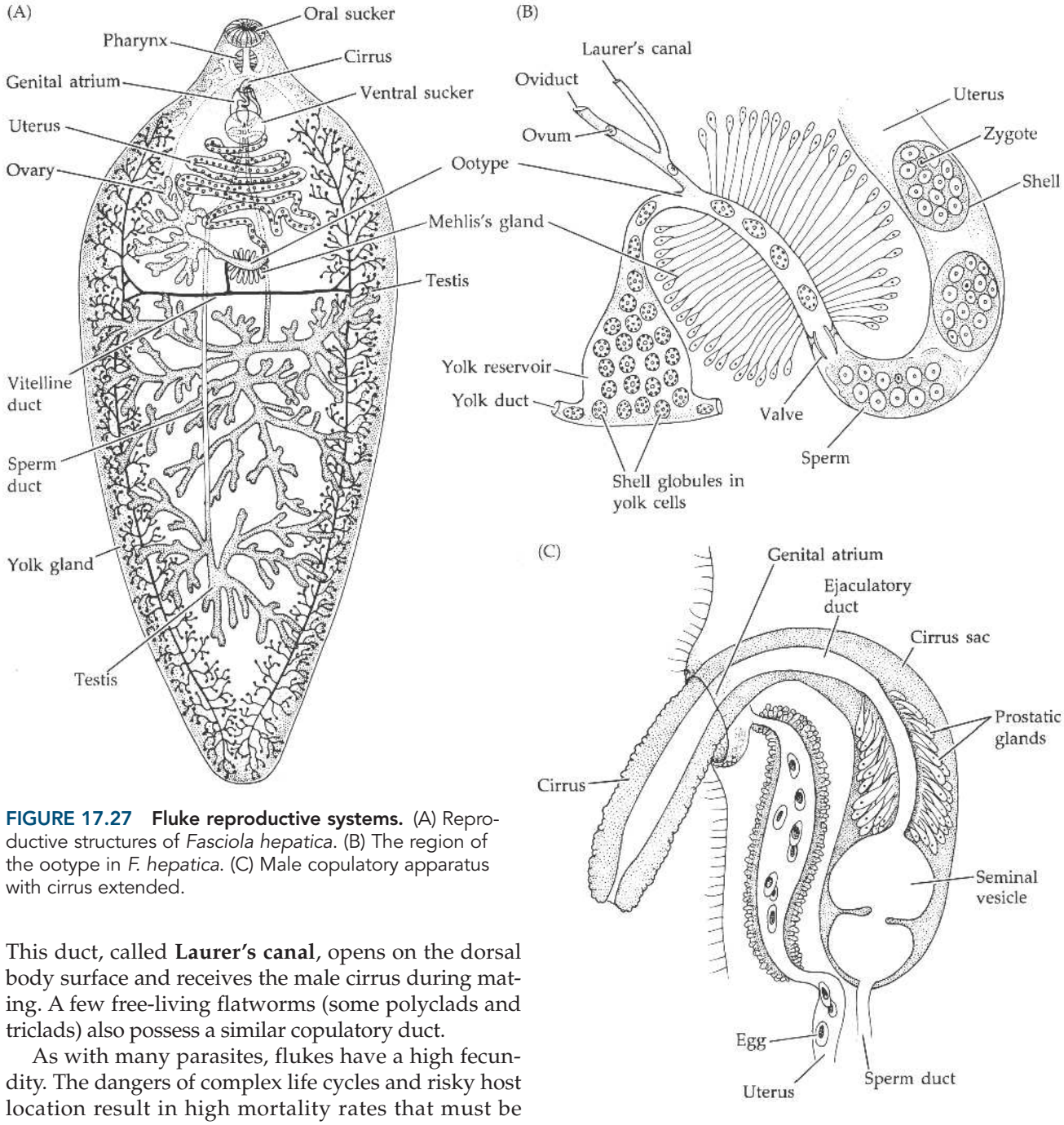

FIGURE 17.27 Fluke reproductive systems. (A) Reproductive structures of *Fasciola hepatica*. (B) The region of the ootype in *F. hepatica*. (C) Male copulatory apparatus with cirrus extended.

This duct, called **Laurer's canal**, opens on the dorsal body surface and receives the male cirrus during mating. A few free-living flatworms (some polyclads and triclads) also possess a similar copulatory duct.

As with many parasites, flukes have a high fecundity. The dangers of complex life cycles and risky host location result in high mortality rates that must be offset by increased zygote production or asexual processes. Flukes may produce as many as 100,000 times as many eggs as free-living species.

The early stages of development in flukes are usually highly modified because of the ectolecithal nature of the ova. In species where little yolk is present, cleavage is holoblastic, and cell fates and germ layer formation have been traced accurately. Development is virtually always mixed, involving one or more independent larval stages.

The life cycles of monogenean flukes are relatively simple and involve only a single host, hence the name. Most of the adults are ectoparasites on fishes, although some attach to turtles, various amphibians, and even some invertebrates. A few members of the Monogenea have taken up a mesoparasitic life style and reside in host body chambers that open to the environment (e.g., gill chambers, mouth, bladder, cloacal cavity). When the embryos are released from the uterus, they often attach to the host tissue by means of special adhesive threads on the shell. Upon hatching, a larval stage called an **oncomiracidium** is released to the environment (Figure 17.28). The oncomiracidium is densely ciliated and swims about until it encounters another appropriate host. The cues larvae use to locate particular hosts may be tactile or chemical and may vary depending on local densities of hosts and other larvae.

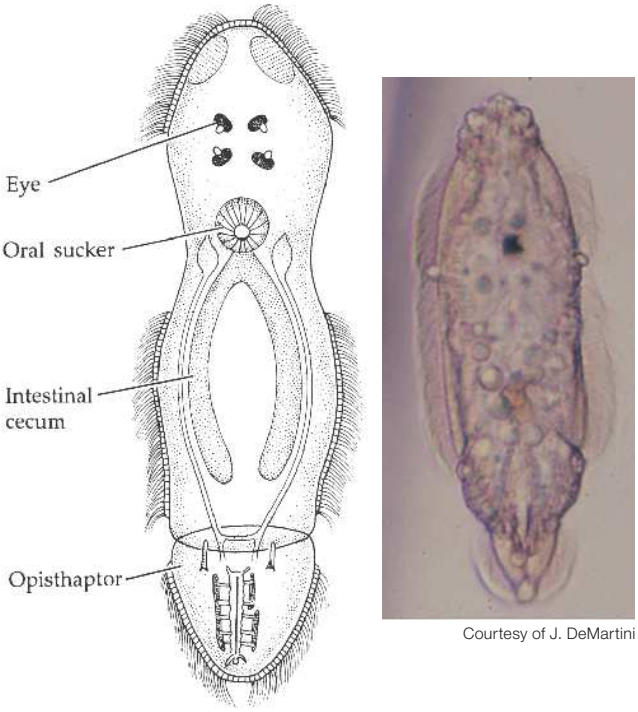

FIGURE 17.28 Drawing and photograph of an oncomiracidium larva of a monogenean fluke.

The prohaptor and especially the opisthaptor develop during the larval stage and facilitate attachment to the new host, whereupon the larva metamorphoses to a juvenile fluke. It is about this time that the ciliated larval skin is shed and the tegument (= neodermis) forms. There are many variations on this basic life cycle among members of the class Monogenea; we present two in outline form in Figure 17.29.

Digenean flukes (orders Diplostomida and Plagiorchiida) include some of the most successful parasites known. A good deal of variation exists, not only in adult morphology, but also in life cycles (Figure 17.30). In general, eggs are produced by adult worms in their definitive host. After fertilization, the zygotes are eventually discharged via the host's feces, urine, or sputum. Upon reaching water, they either are eaten by an intermediate host or hatch as free-swimming ciliated larvae called **miracidia**, which actively penetrate an intermediate host. Several asexual generations of larval forms occur in the intermediate host, eventually producing free-swimming forms called **cercaria**. The cercaria usually encyst within a second intermediate host, becoming **metacercaria**. Infection of the definitive host occurs when the metacercaria are eaten or, if there is no second intermediate host, when the cercaria penetrate directly. The larval skin is lost in the definitive host, and the syncytial tegument develops.

In their adult stages, nearly all of the digenean flukes are endoparasites of vertebrates. They are known to inhabit nearly every organ of the body, and many are serious pathogens of humans and livestock. The intermediate hosts of trematode flukes are gastropods, although some are known to use other invertebrates or even certain vertebrates. Most species of snails host one or more species of digenean flukes; the common California tidal flat gastropod *Cerithideopsis californica* serves as intermediate host to nearly two dozen species of digenean flukes, most of which ultimately infect shore birds. Almost all of the trematodes that infect *C. californica* castrate the snail, thus, theoretically, freeing up the host's energy reserves for their own purposes as they live out their lives producing their own offspring. Diplostomid flukes in the genus *Tylodelphys* usually parasitize the eyes and central nervous system of freshwater fishes. Swimmer's itch is a reemerging human disease caused by bird schistosome cercariae (e.g., *Trichobilharzia*), which can infect people in water bodies; the cercariae typically fail after penetrating human skin, but they can still cause dangerous symptoms. Space does not permit an account of more than a few of the life cycles of these worms. We begin with a general case, using the Chinese liver fluke *Clonorchis sinensis* (order Plagiorchiida) as an example. This trematode is widespread in the Far East. It displays all the common stages found in the life cycles of most digenetic flukes. In northern Thailand a related fluke, *Opisthorchis viverrini,* has a similar life cycle and pathology.

The adult Chinese liver fluke usually lives within the branches of the bile duct in humans. This animal may reach several centimeters in length and in high numbers causes serious problems, including cholangiocarcinoma, a rare but aggressive cancer of the

FIGURE 17.29 Life cycles of two monogenean trematodes. (A) The life cycle of *Dactylogyrus vastator*, a parasite of freshwater cyprinodont fishes. (B) The life cycle of *Polystoma integerrimum*, a parasite in the urinary bladders of frogs. This fascinating life history demonstrates the dramatic influences exerted by the developmental stage of the host on the development of the parasite. Under normal conditions, the adult fluke resides in the bladder of adult frogs. The fluke releases fertilized eggs into the water, where they hatch as oncomiracidia. These in turn become so-called gyrodactylid larvae, which attack the tadpole larval stages of the host. If the tadpole is very young, the fluke larvae attach to the external gills of the host and undergo precocious sexual maturation (progenesis) to produce more zygotes; these flukes die upon metamorphosis of the host. However, if the fluke larvae encounter more advanced tadpoles, they enter the branchial chambers and attach to the host's gills, where they reside until the host undergoes metamorphosis. At that time, the flukes leave the branchial chamber, migrate to the cloacal pore, and enter the host's bladder. Here the flukes live and grow, but they do not become sexually active until they are influenced by the host's sex hormones. Thus, sexual reproduction of the host and of its parasites are synchronized—a pattern that guarantees availability of larval hosts for larval parasites!

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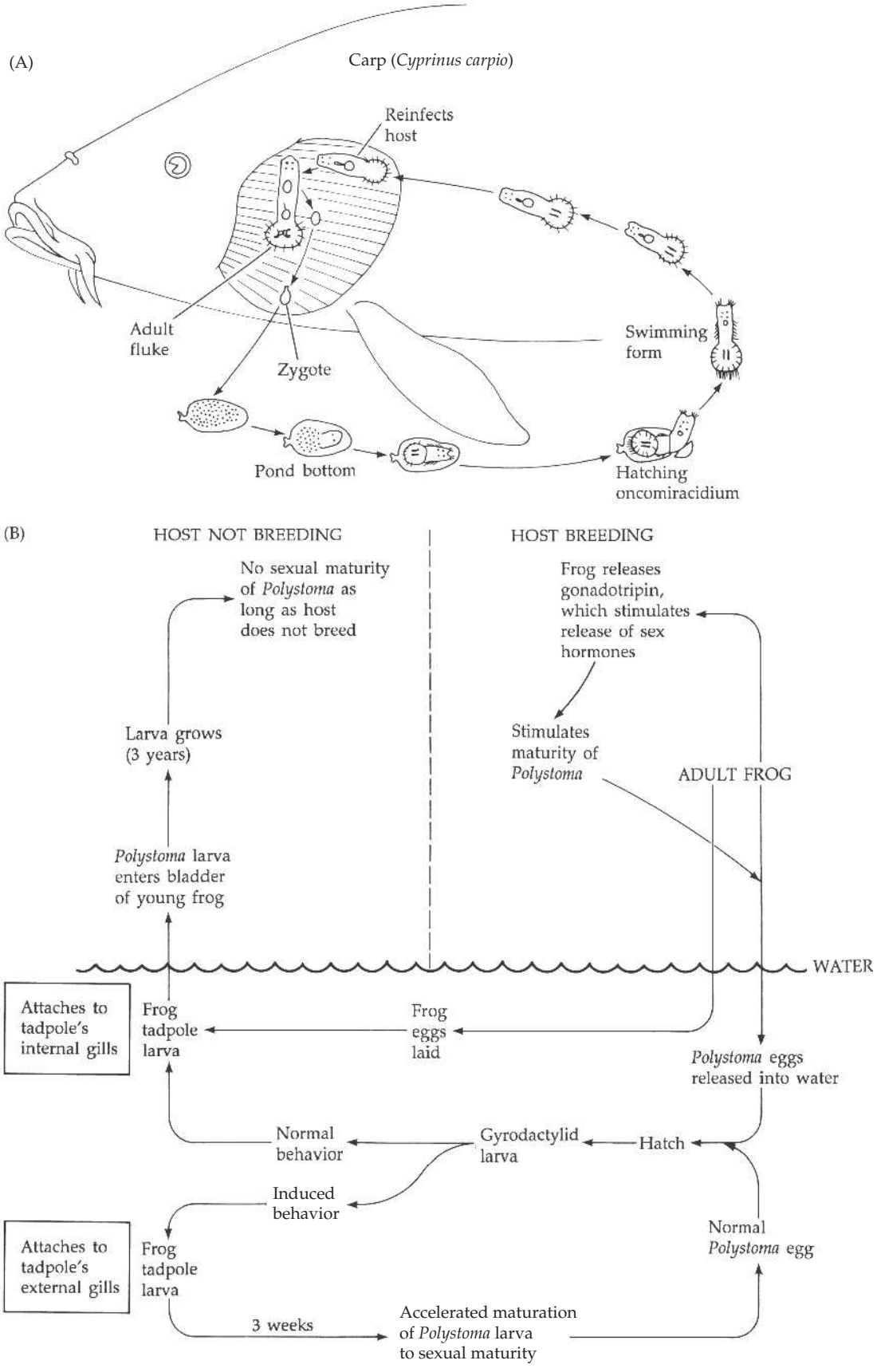

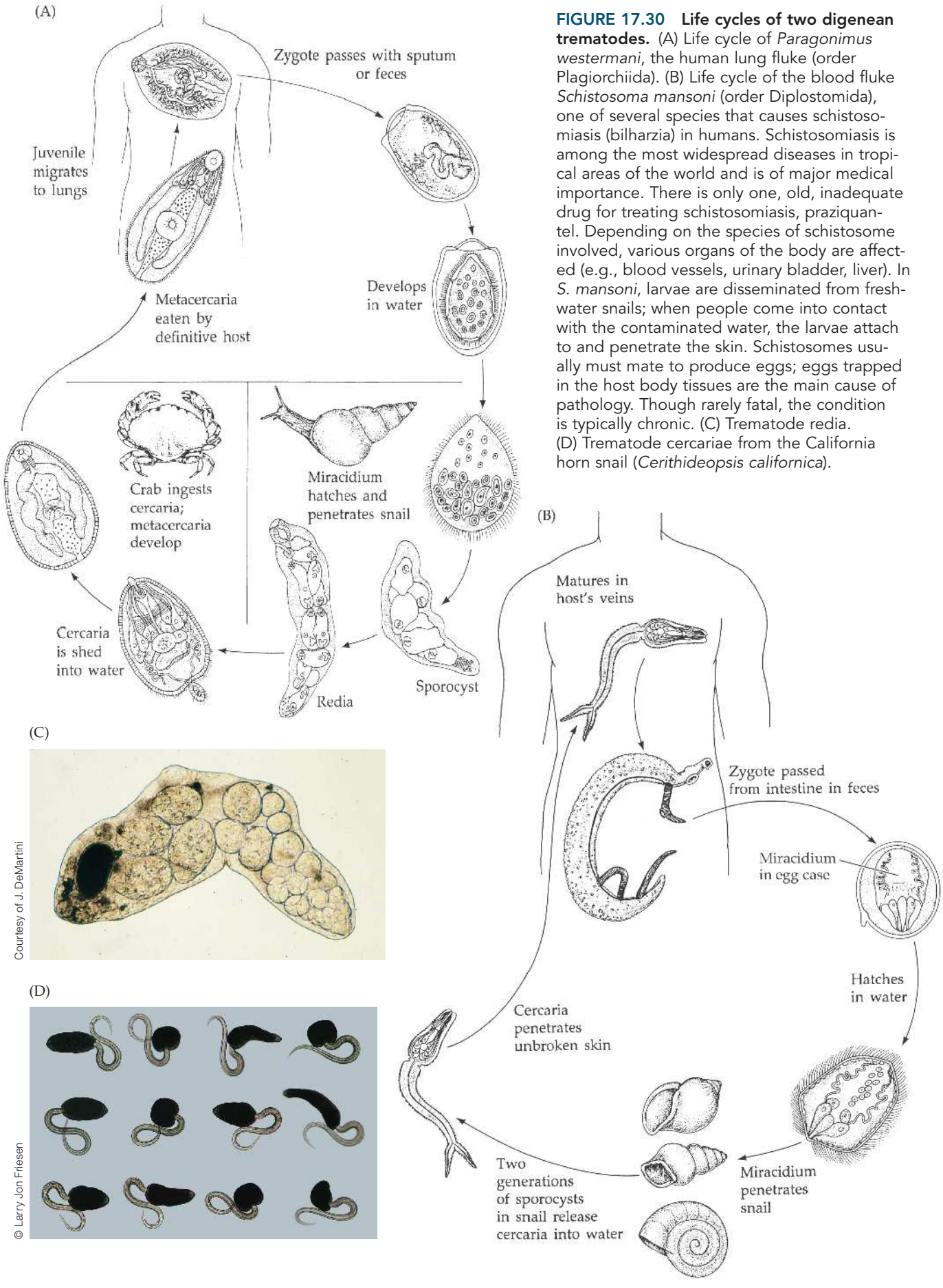

FIGURE 17.30 Life cycles of two digenean trematodes. (A) Life cycle of *Paragonimus westermani*, the human lung fluke (order Plagiorchiida). (B) Life cycle of the blood fluke *Schistosoma mansoni* (order Diplostomida), one of several species that causes schistosomiasis (bilharzia) in humans. Schistosomiasis is among the most widespread diseases in tropical areas of the world and is of major medical importance. There is only one, old, inadequate drug for treating schistosomiasis, praziquantel. Depending on the species of schistosome involved, various organs of the body are affected (e.g., blood vessels, urinary bladder, liver). In *S. mansoni*, larvae are disseminated from freshwater snails; when people come into contact with the contaminated water, the larvae attach to and penetrate the skin. Schistosomes usually must mate to produce eggs; eggs trapped in the host body tissues are the main cause of pathology. Though rarely fatal, the condition is typically chronic. (C) Trematode redia. (D) Trematode cercariae from the California horn snail (*Cerithideopsis californica*).

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bile duct. While still in the uterus of the female reproductive tract, the zygotes develop to miracidia, each housed within its original egg case. Once released from the female system and passed out of the host with the feces, the miracidia are eaten by the first intermediate host, a snail of the genus *Parafossarulus*. The ciliated, swimming miracidium hatches from its egg case in the gut of the snail and migrates into the digestive gland. Here each miracidium becomes an asexually active form called a **sporocyst**, within which germinal cells become yet another larval form called a **redia**. Subsequently, germinal cells within the redia produce the cercaria larvae. This double sequence of rapid asexual reproduction results in perhaps 250,000 cercariae from each original miracidium!

The cercariae leave the snail, swim about, and enter the second intermediate host, the Chinese golden carp (*Macropodus opercularis*). The cercariae of *C. sinensis* burrow through the skin of the fish and encyst in the muscle tissue as metacercaria. If the fish is insufficiently cooked and then eaten by a human, the metacercaria survive and are released from their cysts by the action of the host's digestive enzymes. Once freed, they migrate into the bile duct, metamorphose into juvenile worms, mature, and complete the cycle. Adult flukes can inhabit their hosts for many years, causing irritation and blockages. With this general life cycle in mind, we refer you to Figure 17.30 for a brief overview of two additional examples.

A critical point here are the strategies for survival displayed by these parasites. There is, of course, no assurance of finding the proper hosts at the proper times, and mortality is extremely high. The advantages of high specialization could be efficiency and reduced competition with other species, once established in a proper host. However, multiple infections and within-host competition can be intense, favoring a wide range of competitive adaptations among species, including in at least one trematode species (*Himasthla elongata*), soldier and reproductive castes within molluscan hosts, similar to those observed in social insects. Such adaptations imply the existence of strong selection, acting on larval as well as adult life stages. As we have emphasized earlier, the compensation for such high mortality is high fecundity coupled with asexual reproduction—and therein lies the expense. Another question is how so many different body plans can be produced by a single animal, but stem cell heterogeneity has an important role in driving the propagation of these complex life cycles.

Sexual reproduction: Tapeworms That the "business of animals is to reproduce themselves" is a lesson the cestodes demonstrate well. Most of their time, energy, and body mass are devoted to the production of more tapeworms. Like other flatworms, cestodes are hermaphroditic and practice mutual cross-fertilization when mates are available. However, some cestodes are known to self-fertilize. The orders Amphilinidea and Gyrocotylidea possess a single male and a single female reproductive system, whereas the remaining cestodes, which constitute a clade named Eucestoda (see the Classification section), contain complete systems repeated within each proglottid. There is a good deal of variation in the details of these systems; the following is a generalized description of the male and female systems as they occur in a single proglottid of a cestode (Figure 17.31).

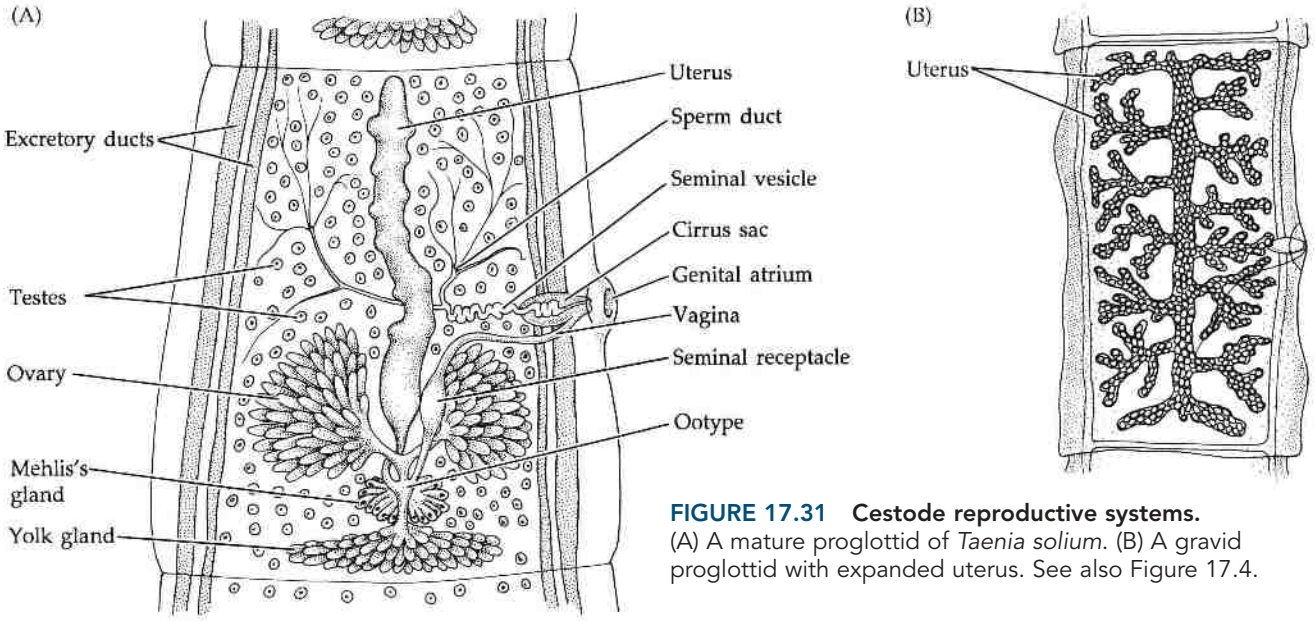

FIGURE 17.31 Cestode reproductive systems. (A) A mature proglottid of *Taenia solium*. (B) A gravid proglottid with expanded uterus. See also Figure 17.4.

The testes are numerous. Some are scattered throughout the mesenchyme, but most are concentrated along the lateral margins. Collecting tubules lead from the testes to a single coiled sperm duct, which extends laterally (as a seminal vesicle) to a cirrus housed within a muscular cirrus sac. The male system empties into a common genital atrium.

The female system usually includes two ovaries from which an oviduct extends to an ootype surrounded by shell glands. The uterus is a branched blind sac extending from the ootype. A duct extends from the female gonopore in the genital atrium to the oviduct; its junction with the oviduct, near the tube, is swollen as a seminal receptacle. The portion of the duct near the genital atrium is called the vagina. A diffuse yolk gland empties via a vitelline duct into the oviduct.

During mutual cross-fertilization the cirrus of each mate is inserted into the vagina of the other. Many tapeworms double back on themselves so that two proglottids of the same worm cross-fertilize; in some species, self-fertilization is known to occur within a single proglottid. Sperm are injected into the vaginal duct and are stored in the seminal receptacle. Eggs are fertilized as they move through the oviduct from the ovaries to the ootype. Capsule material and yolk cells are deposited around each zygote, and the zygotes are moved into the uterus for temporary storage.

The reproductive system of each proglottid matures and becomes functional with age as they are moved more posteriorly along the body by the production of new proglottids. If mating has occurred, the proglottids toward the posterior end become filled with an expanded uterus engorged with developing embryos (Figure 17.31B). These proglottids eventually break free from the body and are lost from the host with the feces, although in some cases the proglottids release embryos inside the host and the embryos pass out with the feces. Early development of tapeworm embryos is drastically modified from the pattern seen in free-living flatworms and varies somewhat among different groups. However, like all Neodermata, after fertilization the ectolecithal ova of cestodes show no vestiges of spiral cleavage, and even germ layer formation is often difficult or impossible to trace.

Most adult tapeworms live in the digestive tracts of vertebrates and usually require one or more intermediate hosts to complete their life cycles. A few can complete their life cycle in a single host. Depending on the number of hosts and other factors, tapeworm life cycles are quite variable, and we describe only two examples.

Taenia saginata (order Cyclophyllidea) is known as the beef tapeworm, since cattle are the intermediate hosts. The adults, which may exceed 1 m in length, reside in human small intestines (Figure 17.32A). As proglottids mature, they are released in the host's feces. The fertilized eggs break free into the environment as the proglottids disintegrate. By this time each zygote has developed to a stage called an **oncosphere**, surrounded by a resistant coat called an **embryophore**, which allows the embryo to remain in the environment for two or three months. Usually six tiny hooks are evident in the embryo; thus, the oncosphere is sometimes called a **hexacanth larva**.

If grazing cattle ingest the oncosphere, it is released from its covering, the hexacanth larva penetrates the intestinal wall using its hooks, and it is carried by the circulatory system to the cow's skeletal muscle. Here the hexacanth develops into a stage called the **cysticercus**, or bladder worm, which encysts in the connective tissue within the muscle of the intermediate host. Each cysticercus contains an invaginated developing scolex. If humans eat raw or poorly cooked infected beef, the scolex evaginates and attaches to the lining of the new host's small intestine, where the adult worm grows and matures. (Another tapeworm, *Taenia solium*, utilizes pigs as its intermediate host and follows a similar life cycle.)

The life cycles of some cestodes involve two or more hosts. An example is *Diphyllobothrium latum*, the so-called broad fish tapeworm (order Diphyllobothriidea) (Figure 17.32B). Nearly any fish-eating mammal, including humans, can serve as the definitive host for this tapeworm. Encapsulated zygotes are released from mature proglottids and shed in the host's feces. After one or two weeks in water, the embryos develop to the oncosphere (hexacanth) stage. At this time, each oncosphere is encased in a ciliated embryophore, and it hatches as a free-swimming larva called a **coracidium**. To successfully continue the life cycle, the coracidium must be eaten by the first intermediate host, a copepod (Crustacea). The cilia are shed and the released hexacanth larva bores through the gut wall into the host's body cavity, where it develops into a **procercoid** stage. Certain species of freshwater fish can serve as the second intermediate host. The fish eats the copepod, the procercoid bores through the gut and into the fish's muscle tissue, and there it grows into a segmented **plerocercoid** stage, complete with a tiny scolex. When a human consumes raw or undercooked infected fish, the plerocercoid attaches to the intestinal wall and matures.

Life cycles of parasitic flatworms can be a fascinating topic, and this lifestyle has resulted in great evolutionary success. Because of health and food industry implications, many life cycles are well studied and broadly available in public internet sites, such as the U.S. Centers for Disease Control and Prevention (CDC). We address the reader to these sites when they are interested in exploring the life cycles of many parasitic flatworms and other invertebrates.

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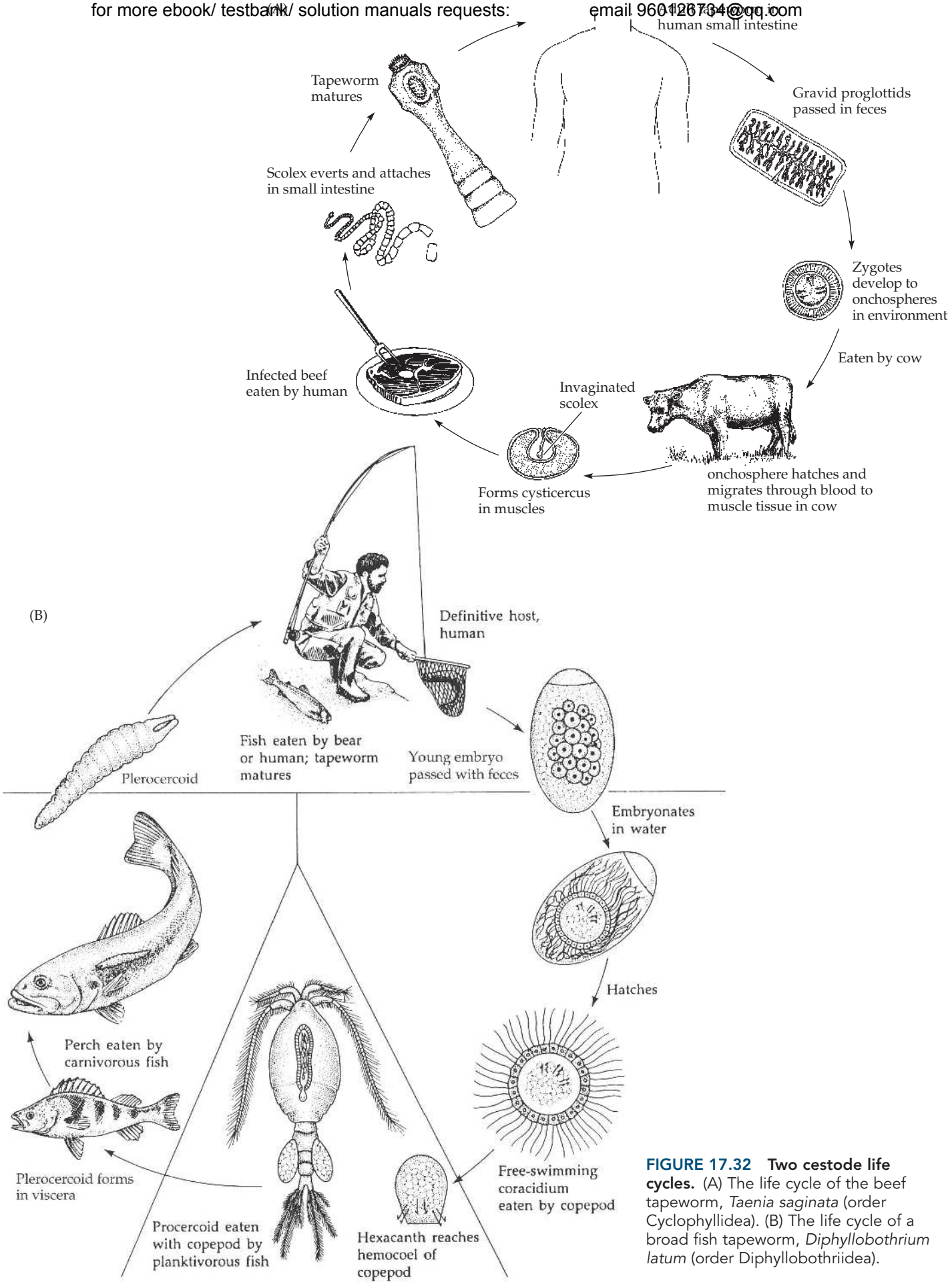

FIGURE 17.32 Two cestode life cycles. (A) The life cycle of the beef tapeworm, *Taenia saginata* (order Cyclophyllidea). (B) The life cycle of a broad fish tapeworm, *Diphyllobothrium latum* (order Diphyllobothriidea).

Platyhelminth Phylogeny

Ideas about the origin of flatworms, their relationships to other phyla, and evolution within the group have been debated for a very long time. The lack of a robust fossil record and the relative anatomical simplicity of flatworms have made morphology-based phylogenetic analysis difficult—there is a paucity of reliable characters that might identify and differentiate clades. In fact, unambiguous synapomorphies that define the phylum Platyhelminthes itself have yet to be clearly identified. Platyhelminth fossils consist mainly of structures left on hosts by parasitic species, or occasional evidence from host coprolites, although some trace fossils from the early Paleozoic have been assigned to this phylum.

For most of the twentieth century, flatworms were considered to be very primitive bilaterians, perhaps even the sister group to the rest of Bilateria. However, in 1963, the German zoologist Peter Ax suggested that flatworms might actually be more highly derived (in the protostome line) than previously thought and that they might represent a series of reductions from a vermiform coelomate ancestor—a case of extreme reduction by paedomorphosis (the retention by adult individuals of traits seen in young), perhaps through neoteny, wherein the somatic development of adults is slowed or delayed. The idea had some support, especially with regard to the acoelomorphs (then included in Platyhelminthes). There was also an idea that platyhelminths arose through progenesis (a type of paedomorphosis in which sexual development of larvae or young is accelerated), from developmental stages of early protostomes prior to the embryonic appearance of the coelomic cavities—that is, rapid maturation of larval or other stages that had solid bodies or still contained the blastocoel. By the 1990s other researchers, such as the Danish zoologist Claus Nielsen, also began to argue that Platyhelminthes were nested higher in the spiralian protostome line. And in the late twentieth century and early in this century, phylogenetic studies based on gene sequence data clearly supported the idea that flatworms are not at the base of the bilaterian clade, but indeed nested higher in the Spiralia as a likely sister group of Gastrotricha. Thus, the anatomical simplicity of these animals, such as lack of a circulatory system and through gut, appears to be the result of secondary reductions, not primitiveness.

We can safely assume that the original flatworm was free-living, although not necessarily assignable to any extant order. Peter Ax, Tor Karling, and Ulrich Ehlers have presented various versions of this "turbellarian archetype." These hypothetical ancestral flatworms are envisioned as having had a simple pharynx and a saclike gut without diverticula, such as seen in modern Catenulidea and Macrostomorpha (Figure 17.33A,B). There is also general agreement that the primitive flatworm was probably an

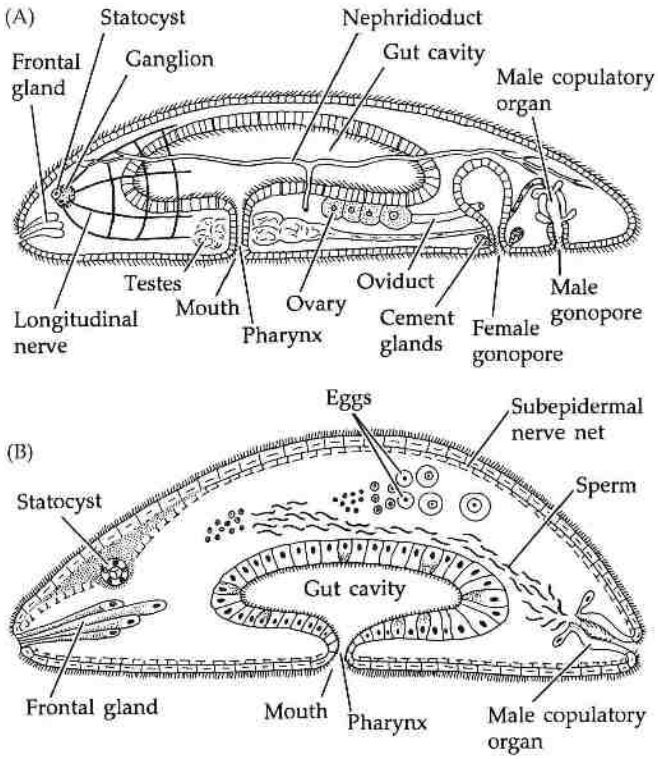

FIGURE 17.33 Two examples of hypothetical "turbellarian" archetypes. (A) Macrostomid-like archetype suggested by Peter Ax. (B) Archetype proposed by Tor Karling.

archoöphoran with endolecithal ova, spiral cleavage, and a single-layered, completely ciliated epidermis.

Fortunately, modern gene sequence analyses have begun to shed new light on the phylogeny of flatworms, including the removal of the Acoelomorpha (now in the phylum Xenacoelomorpha) and broad acceptance that platyhelminths comprise two major clades, Catenulidea and Rhabditophora. Molecular phylogenies also support the monophyly of Neodermata and also of its three major clades—Trematoda, Monogenea, and Cestoda (Figure 17.34).

The availability of genomic data sets for platyhelminths is uneven, clearly biased toward those of medical and veterinary importance. High-quality reference genomes exist for dozens of parasites, including the first platyhelminth genomes of *Schistosoma mansoni* and *Echinococcus multilocularis*, and detailed analyses of *S. haematobium* and *Taenia solium* as well as partial genomes of a couple dozen tapeworms, and about the same number for flukes, now exist. However, few free-living platyhelminths have been fully sequenced. These include *Macrostomum lignano* and the triclad *Schmidtea mediterranea*. In the fluke *Schistosoma*, two distinct mitochondrial gene orders have been found. The gene orders in free-living groups are often quite different from one another (and from the gene order of parasitic species). The use of transcriptomic data since 2015 has resulted in a number of

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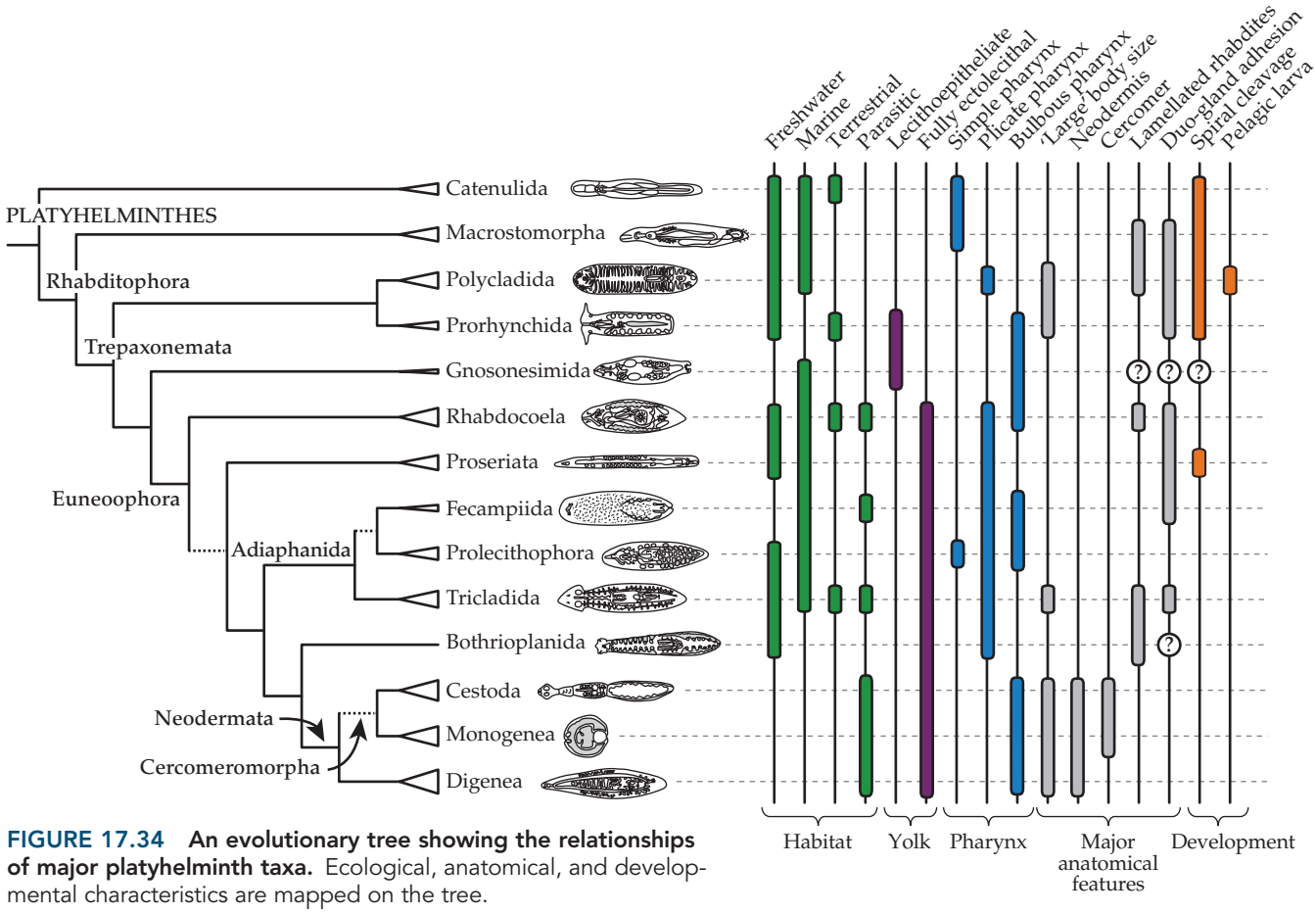

FIGURE 17.34 An evolutionary tree showing the relationships of major platyhelminth taxa. Ecological, anatomical, and developmental characteristics are mapped on the tree.

highly congruent hypotheses of relationships among the major platyhelminth lineages.

The phylogeny of Platyhelminthes shown in Figure 17.34 is based primarily on two simultaneous genomic studies (Laumer et al. 2015, Egger et al. 2015). Although many internal relationships remain enigmatic, the order Catenulida is now widely viewed to be the most basal of the platyhelminths and the sister group to Rhabditophora (containing the remaining platyhelminths). Catenulids are anatomically simple flatworms, with an unbranched pharynx and gut and a single biflagellate protonephridium. And they retain the spiral cleavage and endolecithal ova that characterize most phyla in the clade Spiralia. Rhabditophora comprises two clades, Macrostomorpha and Trepaxonemata, the latter being home to the majority of species in the phylum and including some of the best known free-living groups as well as the flukes and tapeworms.

All of the earliest-branching clades of flatworms, Catenulida, Macrostomorpha, and Polycladida share spiral cleavage and endolecithal eggs with other spriralian protostomes. The terrestrial/freshwater group Prorhynchida, a proposed sister group to the mainly marine, diverse, and well-known polyclad flatworms (Polycladida), retains spiral cleavage but has shifted to ectolecithal eggs. Molecular evidence strongly supports the sister-group relationship between the endolecithal polyclads and the ectolecithal Prorhynchida (a clade known as Amplimatricata), suggesting that prorhynchids independently evolved ectolecithal ova. The discovery of this likely evolution led to abandonment of the old taxon "Neoophora," which had held *all* the ectolecithal taxa (i.e., Prorhynchida, Rhabdocoela, Proseriata, and Acentrosomata). The last three groups now comprise the Euneoophora, the most highly derived flatworm lineage. These patterns confirm the basal nature of the archoöphoran plan. Gnosonesimora is likely the sister group to the Euneoophora. Recall that in the neoöphoran plan (seen in the order Prorhynchida and the superclass Euneoophora) there is an ovarian specialization into germinal and vitelline cell producing regions. It has been suggested that this separation of germ-line and yolk-line cells might allow these ectolecithal species to synthesize yolk at a higher rate than their endolecithal ancestors, thereby enhancing fecundity, and possibly allowing multiple embryos to develop within the same egg capsule, also enhancing fecundity by allowing conservation of resources for larval nutrition.

Phylogenetic relationships within the huge and complex Euneoophora lineage are still somewhat unsettled. The Rhabdocoela and Proseriata retain elements of spiral cleavage, suggesting their basal placement within this clade. Molecular analyses also suggest that rhabdocoels could be the sister group to the Proseriata +

Acentrosomata. Acentrosomata is notable for its loss of spiral cleavage. This is thought to be due to the evolutionary loss of the centrosome (and redirection of centriole formation) due to loss of three particular genes in species of Adiaphanida, Bothrioplanida, and Neodermata. It is this feature that led to their grouping under the name Acentrosomata. Centrioles, of course, play a critical role in the development of spindle fibers during cell division. In some cases, early embryogenesis in acentrosomate species is so chaotic that the blastomeres undergo what has been called dispersive cleavage, wherein they temporarily lose physical contact with one another and "drift" in a matrix of yolk. This process has been given the colorful name blastomere anarchy, and it characterizes Adiaphanida (triclads, prolecithophorans, and fecampiids) and Bothrioplanida. In these groups, centrioles are assembled in terminally differentiating ciliated cells through a so-called acentriolar pathway that triggers their assembly. This is the only known case of centrosome loss in the animal kingdom. Tricladida has been shown to be a monophyletic group. Bothrioplanids appear to be the last free-living ancestor to the Neodermata. There is no trace of spiral cleavage in neodermatans either, although they are not generally characterized by blastomere anarchy. There seems to be no question about the monophyly of the Neodermata, all of which are ectolecithal, lack spiral cleavage, and have larvae that shed their cilia early in their life cycle. However, there is still debate over relationships among the Monogenea, Cestoda, and Trematoda, as reflected in our phylogeny.

Phylum Gastrotricha: The Gastrotrichs, or Hairy-Bellied Worms

The phylum Gastrotricha (Greek *gasteros*, "stomach"; *trichos*, "hair") comprises about 860 species of marine, brackish, and freshwater protostomes. Most species are less than 1 mm long, although a few are only 60 μm in length while some reach 3.5 mm. Many gastrotrichs bear a superficial resemblance to flatworms and rotifers, but they are easily distinguished by their adhesive tubes and cilia restricted to the ventral surface. Under high magnification, tiny gastrotrichs appear as very charismatic invertebrates, with their "whiskered" faces and spiny or scaled, often bowling-pin-shaped bodies. Figure 17.35 illustrates some of the body forms within this phylum and some features of their external anatomy, and Box 17B lists the distinguishing features of the group. Marine gastrotrichs are meiofaunal and live in the interstitial spaces between sand grains, from the intertidal zone to abyssal depths (5,700 m). Freshwater species are found in surface detritus or among the filaments of aquatic plants and plantlike protists and sometimes form large blooms with densities of 2.6 million individuals per square meter; a few are semiplanktonic.

The gastrotrich body is typically divisible into a head and a trunk (Figures 17.35B,C and 17.36A), though many species lack such an obvious distinction. Externally, gastrotrichs possess a cuticle that surrounds all aspects of the body and is often smooth in appearance but may be elaborated into spines, bristles, scales, and/or plates (Figure 17.35). **Adhesive tubes**, a diagnostic character of most gastrotrichs, are also derived from the cuticle and generally contain a pair of glands that secrete adhesive and releaser substances (the **duo-gland adhesive system**). These tubes may be abundant (Macrodasyida) or sparse to absent (most Chaetonotida).

The gastrotrich head bears a terminal or subterminal mouth with stiff cilia or other cuticular elaborations. A ring of motile cilia often encompasses the head dorsally while other ciliary elaborations such as pits and tentacles are present on the sides (Figure 17.35F). A necklike constriction behind the head is present in many but not all gastrotrichs. The gastrotrich trunk (the main part of the body) is generally vermiform (Macrodasyida, *Neodasys*) or bowling-pin-shaped (Chaetonotida), and it contains most of the organ systems. The trunk terminates in a rounded, bilobed, tailed, or forked caudum that bears adhesive tubes.

The most recent molecular phylogenetic studies place gastrotrichs squarely within the protostome bilaterians and close to the base of the Spiralia, where they seem to arise near the Platyhelminthes or the Gnathifera (Gnathostomulida, Micrognathozoa, and Rotifera). Anatomically, however, gastrotrichs are more similar to the members of the Nematoida and Scalidophora clades because of their circumpharyngeal brain, bilayered cuticle, and myoepithelial pharynx.

GASTROTRICH CLASSIFICATION

ORDER CHAETONOTIDA (Figure 17.35A–C). Primarily freshwater, but also some marine, estuarine, and semiterrestrial (freshwater microhabitat) species; body usually bowling-pin-shaped, smooth or complex cuticle with a variable number of adhesive tubes (most with only 2 on caudal furca); pharynx with Y-shaped lumen, pharyngeal pores absent; 1 or more pairs of protonephridia present; hermaphroditic, parthenogenetic, or a combination of hermaphroditic and parthenogenetic.

SUBORDER MULTITUBULATINA Marine; strap-shaped body with smooth cuticle and anterior, posterior, ventral, and lateral adhesive tubes; hermaphroditic with complex reproductive organs. Monogeneric: *Neodasys*, with two known species.

SUBORDER PAUCITUBULATINA Mostly freshwater species but with many marine representatives;

The section on Gastrotricha was revised by Rick Hochberg.

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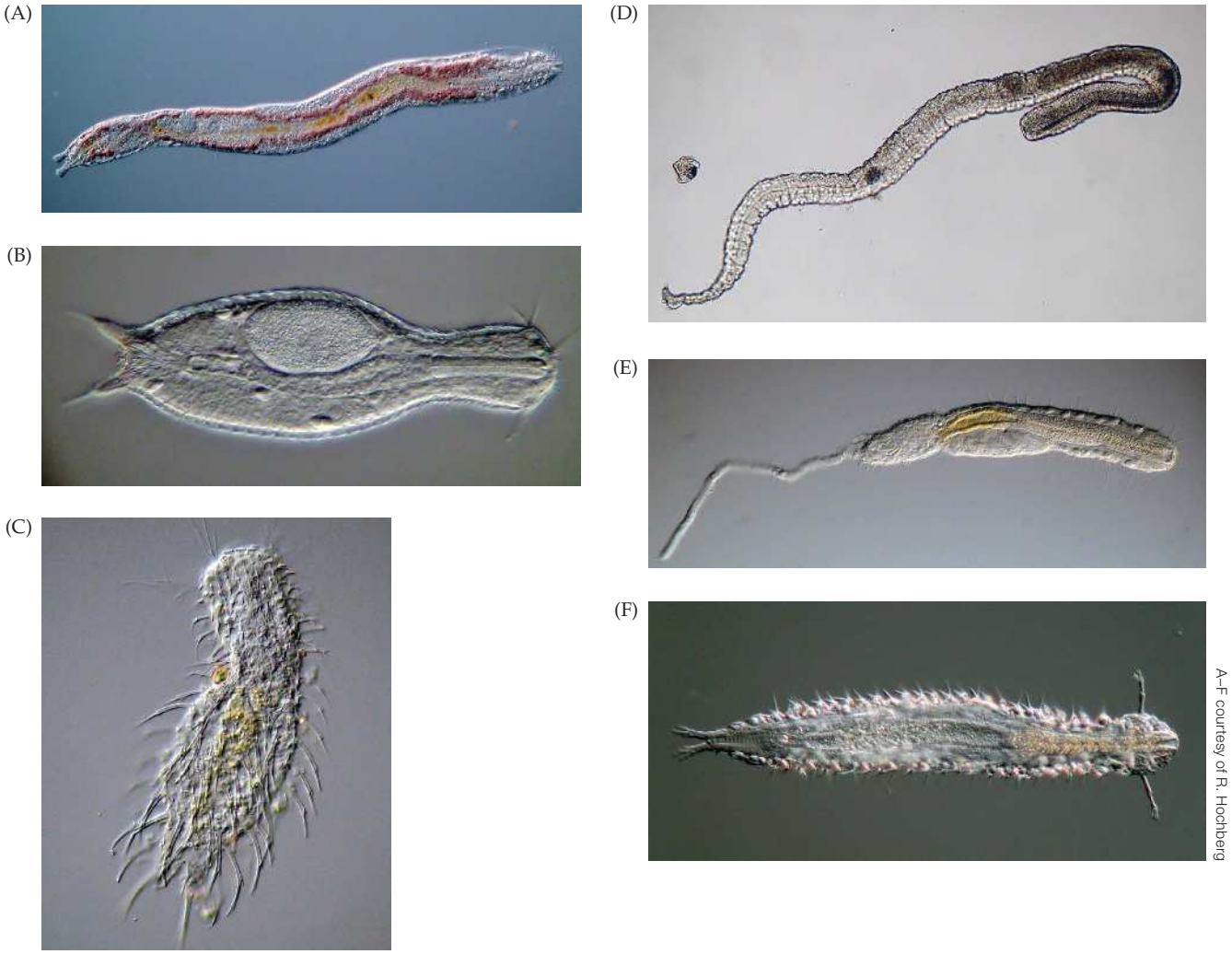

FIGURE 17.35 Representative gastrotrichs.
(A–C) Light micrographs of Chaetonotida. (A) *Neodasys*. (B) *Xenotrichula*. (C) *Chaetonotus*. (D–F) Light micrographs of Macrodasyida. (D) *Megadasys*. (E) *Urodasys*. (F) *Xenodasys*.

bowling-pin-shaped body often covered by elaborate cuticle, usually with 2 terminal adhesive tubes on caudal furca, though some with 4 (e.g., *Diuronotus*) and others with no tubes (e.g., *Neogossea*, *Kijanebalola*); hermaphroditic, parthenogenetic, or both (e.g., *Aspidiophorus, Chaetonotus, Dasydytes, Lepidodermella*).

ORDER MACRODASYIDA (Figures 17.35D–F). Mostly marine and estuarine gastrotrichs with only a single freshwater genus (*Redudasys*); body usually strap shaped, with smooth or elaborately sculptured cuticle, usually bearing numerous adhesive tubes along the head (ventral) and trunk (lateral, ventral, posterior, sometimes dorsal); pharynx with inverted Y-shaped lumen, pharyngeal pores present in all except species of *Lepidodasys*; usually with several pairs of protonephridia; hermaphroditic with complex reproductive organs; some may be parthenogenetic (e.g., Redudasyidae, some *Macrodasys, Turbanella, Urodasys*).

BOX 17B Characteristics of the Phylum Gastrotricha

1. Triploblastic, bilateral, unsegmented, acoelomate
2. Microscopic, body elongate or bowling-pin-shaped
3. Bilayered cuticle, smooth or with scales or spinelike elaborations; with exocuticle covering entire body including all cilia; cuticle not molted
4. Duo-gland adhesive tubes
5. Epidermis cellular or partly syncytial; epidermal cells monociliate or multiciliate; locomotory cilia on ventral surface only
6. Myoepithelial pharynx with triradiate lumen; complete gut
7. One pair or more of protonephridia, without special circulatory or gas exchange structures
8. Hermaphroditic, parthenogenetic, or hermaphroditic and parthenogenetic
9. Complex reproductive organs
10. Embryonic development poorly studied
11. Direct development

The Gastrotrich Body Plan

Body Wall

A gastrotrich's body is encased in a multilayered cuticle of varying thickness and complexity. It is never molted. The outer portion, or exocuticle (also called epicuticle), contains one or more lamellae that cover all external surfaces, including locomotory and sensory cilia (Figure 17.36E); the inner portion, or endocuticle, is thick and fibrous and produces the spines, scales, and adhesive tubes (Figure 17.35). The epidermis may be cellular as in Macrodasyida or partly syncytial as in most Chaetonotida; only ventral epidermal cells bear locomotory cilia (thus the derivation of the phylum name: "hairy belly"). Most species possess multiciliate epidermal cells; however, some species possess monociliate cells in some parts of their body. **Duo-gland adhesive organs**, consisting of at least one adhesive gland and one releaser gland (which are critical for rapid grip and release from sand grains in the interstitial environment), are present in most species and form cuticle-covered necklike tubes to the outside (Figure 17.36F). A similar system also occurs in some Platyhelminthes. Species of *Neodasys* lack the releaser gland, and neither gland is present in some semiplanktonic species (e.g., Neogosseidae). An epidermal gland system consisting of multiple, independent, unicellular exocrine glands is present in most species of Macrodasyida and hypothesized to secrete compounds that function as repellents against predators.

Internal to the epidermis are connective tissues such as a basal lamina (absent in many species) or in some cases large vacuolar **Y-cells** (some Macrodasyida and *Neodasys*) that function in hydrostatic support. Hemoglobin has been detected in the Y-cells of *Neodasys* and may be present in others. Muscles are present as circular, helicoidal, and longitudinal bands that insert on the cuticle via an intervening epithelial cell; dorsoventral and other muscle orientations may also be present.

Support and Locomotion

The cuticle and compact (acoelomate) body plan provide hydrostatic support while the complex array of muscles produces the bending and twisting movements that are characteristic of gastrotrich locomotion and essential for life between sand grains (which are "boulder size" for millimeters-long gastrotrichs). Most animals are highly flexible and in some genera such as *Megadasys* (Figure 17.35D) can stretch their already elongate bodies to nearly twice gliding length or contract into a tight ball. The adhesive tubes play a significant role during these activities. Some semiplanktonic freshwater gastrotrichs, such as species of Dasydytidae (Chaetonotida), have movable spines that permit a form of saltatory swimming.

Feeding and Digestion

Most gastrotrichs feed by pumping small food items into the gut by action of the pharynx, a myoepithelial tube that is surrounded by complex layered muscles. The pharyngeal lumen is either Y-shaped (Chaetonotida) or inverted Y-shaped (Macrodasyida) (Figures 17.36B,D). In most macrodasyidans, a pair of pharyngeal pores connects the pharyngeal lumen to the outside, thereby permitting the release of excess water imbibed with the food (Figure 17.36C). Gastrotrichs feed on nearly any organic material, alive or dead, of appropriately small size (bacteria, detritus, protists, unicellular algae).

The mouth is terminal or subterminal and often surrounded by a ring of stiff cilia or cuticular spines that may aid in food capture. A short buccal cavity connects the mouth to the elongate muscular pharynx lined with cuticle (a stomodaeum) (Figure 17.36). In species of Chaetonotida, a pharyngeal "valve" may be present at the junction of the pharynx and intestine (midgut). The endodermally derived portion of the gut is a straight tube that narrows posteriorly and leads to a ventral anus. The anus is preceded by a cuticle-lined hindgut in Chaetonotida, while in most Macrodasyida a hindgut is absent and the anus is presumably permanent or temporary. Digestion and absorption occur in the intestine, which is composed of cuboidal cells with a brush border; motile cilia may be present in some species and aid in food passage.

Circulation, Gas Exchange, Excretion, and Osmoregulation

Circulation and gas exchange occur by diffusion through the body wall. Some gastrotrichs are capable of anaerobic respiration when environmental conditions require it. Protonephridia are the primary excretory organs in gastrotrichs. Marine species such as most macrodasyidans and *Neodasys* possess multiple pairs of protonephridia that function solely in the removal of metabolic wastes. Their protonephridia are generally mono- or bicellular filtration organs, each with a single flagellum; they connect to the outside by way of a single ciliary canal cell and nephridiopore cell. In species that live in a hypo-osmotic environment, like most freshwater chaetonotidans, the single pair of protonephridia also function in osmoregulation. Their protonephridia are bicellular organs that lead to an elongate and convoluted canal cell (Figure 17.36A). The extra length of the canal cell in freshwater species is hypothesized to function for increased reabsorption of necessary salts and minerals from the primary urine before elimination.

Nervous System and Sense Organs

The central nervous system consists of a dorsal brain and one or more pairs of longitudinal nerve cords. The

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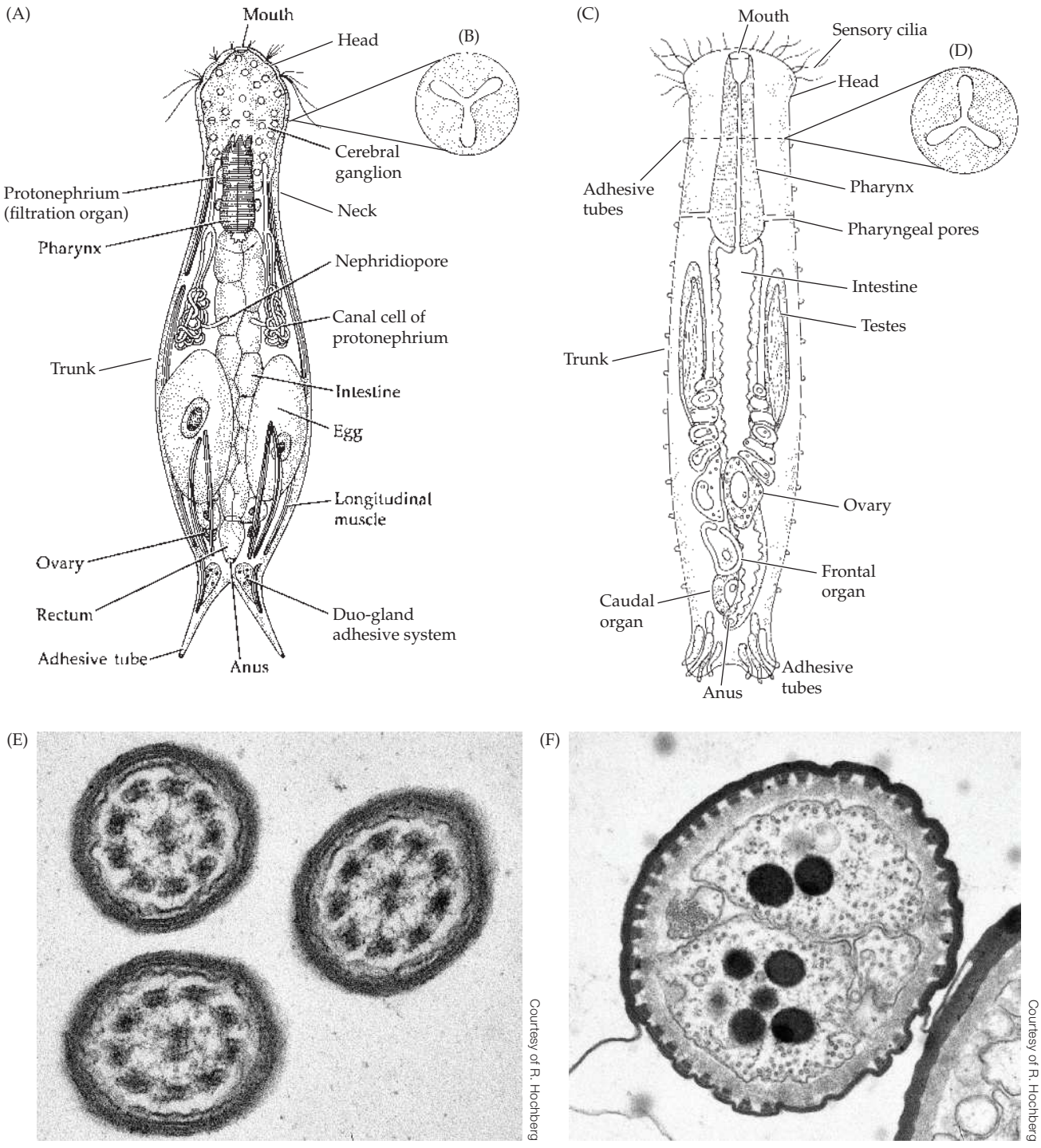

FIGURE 17.36 Anatomy of gastrotrichs. (A) Representative of Chaetonotida, *Paucitubulatina*. (B) Cross section through pharynx showing Y-shaped pharyngeal lumen. (C) Representative of Macrodasyida and (D) cross section through pharynx showing inverted Y-shaped pharyngeal lumen. (E–F) Transmission electron micrographs of (E) a cross section through locomotory cilia and (F) an adhesive tube.

brain consists of numerous cells that sit atop a ringlike commissure around the anterior region of the pharynx (Figure 17.36A). Cerebral neurons innervate the head and pharynx. The nonganglionated nerve cords arise from the brain and are interconnected by thin commissures; they unite at the posterior end.

Sensory receptors are ciliary in structure and concentrated in the head region but may be distributed over the entire body. Ciliary pits and tentacles on the heads of some species are likely chemosensory, while stiff, bristlelike cilia on the head and trunk probably have a tactile function. Several species possess

pigmented (red) ocelli that indicate probable photoreceptive capabilities; experiments have shown that species lacking ocelli still have spectral sensitivity. One species, *Pleurodasys helgolandicus*, possesses an unusual pair of drumstick-like organs that are hypothesized to function as gravity receptors.

Reproduction and Development

Most species of gastrotrichs are hermaphroditic or a combination of hermaphroditic and parthenogenetic. Strict parthenogenesis is rare and known from only a few species. The hermaphroditic reproductive system is best studied in Macrodasyida and often contains gametes and organs of sperm transfer and storage (Figure 17.36C). The male system comprises one or two testes with associated sperm ducts that lead to a single or paired ventral gonopores. A **caudal organ** that presumably functions in the transfer of sperm is present in most species, but in Hummondasyidae, and in some Macrodasyidae and Thaumastodermatidae, is it directly connected to the sperm ducts. Some species bear a sclerotized stylet within the caudal organ.

The female system includes one or two ovaries in the posterior body region. Other reproductive organs may include a **frontal organ** (seminal receptacle), as in Macrodasyida and *Neodasys*, or an **X-organ**, as in most Chaetonotida. The ovaries are generally compact or somewhat diffuse. Oocytes mature anteriorly in most species and become positioned above the intestine and in proximity to the frontal organ when present; oviducts are rare, but some species do have a distinct uterus. Yolk is produced within the oocyte itself. Mutual cross-fertilization leads to the direct exchange of sperm or spermatophores (via hypodermic impregnation or some other mechanism) in all species, but sperm is stored in the frontal organ of most macrodasyidans. The X-organ in chaetonotidans is a bilobed syncytial organ in the posterior trunk that develops during the sexual phase and is thought to play a role in reproduction, although its function has never been demonstrated. Fertilization is always internal and precedes the production of an eggshell by the egg itself. Oviposition is through the body wall of most species, and it might occur through a temporary or perhaps permanent pore, or in some cases via rupture of the body wall.

Historically, most freshwater chaetonotidans were assumed to be strict parthenogens until small packets of rodlike sperm were discovered next to their midgut. The sperm develop after the production of the parthenogenetic ova and in synchrony with the meiotic (sexual) ova, suggesting they are not vestigial male gametes; such a condition is referred to as **postparthenogenetic hermaphroditism**. Cross-fertilization has never been observed in these species. Two forms of parthenogenetic eggs are produced: the first few eggs (tachyblastic) hatch quickly and are important for rapid population growth, while the last egg (opsiblastic) may overwinter before hatching. A third and more rare type of egg, called the plaque-bearing egg, is thought to be the result of sexual reproduction, but its development has never been followed.

Few embryological studies have been conducted on gastrotrichs, and those few have shown that the main cleavage events are somewhat contradictory. In general, cleavage is holoblastic and subequal (i.e., the blastomeres are of approximately equal size); however, after the initial equatorial division, there is an apparent divergence in cleavage patterns between the two orders. The second cleavage plane of the posterior blastomere is meridional in macrodasyidans but equatorial in chaetonotidans, which leads to different fates for the developing tissues. In neither case is a spiral-like cleavage pattern evident. By the fifth division, a bilaterally symmetric embryo has developed. Gastrulation occurs by invagination followed by epiboly of the secondary ectoderm over presumptive mesoderm. A stomodaeum forms in both orders, but a proctodeum has been noted only for chaetonotidans. The U-shaped embryo continues to grow and elongate in the eggshell for several hours (to several days) prior to hatching.

Development is direct, juveniles being small versions of adults, though without noticeable reproductive organs and with fewer adhesive tubes (in Macrodasyida). Maturation is rapid and the animals usually are sexually mature within a few days after hatching. Individuals of most species probably live only a few weeks.

Chapter Summary

This chapter introduced you to the recently recognized clade Rouphozoa, a lineage of spiralian protostomes that includes two phyla: Platyhelminthes (flatworms) and Gastrotricha (hairy-bellied worms). For many years, flatworms had been regarded as basal bilaterians because of their seemingly simplified anatomy and lack of a through gut (absence of an anus). By the 2010s, however, phylogenomic analyses were indicating that platyhelminths and gastrotrichs comprise a sister group embedded well within the spiralian clade. Few anatomical apomorphies have been identified that define Rouphozoa, and both phyla seem to be characterized by features that are plesiomorphic for the Spiralia in general (dense body ciliation, protonephridia, etc.). One putative synapomorphy of Rouphozoa is the presence of duo-gland adhesive organs, although similar organs also exist in other groups as well (e.g., annelids, nematodes). Both

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phyla are acoelomate, and their precise placement among the spiralian protostomes remains unresolved.

Nearly 30,000 species of platyhelminths have been described, including free-living, commensal, and parasitic forms from marine, freshwater, and terrestrial environments. Most are dorsoventrally flattened and all lack discrete circulatory or gas exchange structures and an anus. They possess a unique system of neoblast cells and produce mucus with specialized rhabdoids/rhabdites. Most are hermaphroditic, with complex reproductive systems and biflagellate sperm. Development is direct or indirect, with unique larvae in the large order Polycladida (Götte's and Müller's larvae). Platyhelminthes include many important parasitic species, including the flukes and tapeworms. About 860 species of marine, brackish-water, and freshwater gastrotrichs have been described, all being microscopic (60 μm to 3.5 mm). The cuticle is well developed, smooth or with scales or spines, and the epidermis is cellular or partly syncytial. The pharynx has a distinctive triradiate lumen, and the gut is complete.

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CHAPTER 18

Introduction to Ecdysozoa

Scalidophora (Phyla Kinorhyncha, Priapula, Loricifera)

This chapter is the first of seven that describe animals belonging to the large protostome clade Ecdysozoa, first introduced in Chapter 8. Unlike the Spiralia, Ecdysozoa can be defined by clear morphological synapomorphies, including their three-layered cuticle that is molted, a process regulated by ecdysteroid hormones (where known). The cuticle consists of a proteinaceous exocuticle and an endocuticle with chitin or collagen, with the epicuticle forming from the apical zone of the epidermal microvilli. The cuticle contains chitin in all ecdysozoans, at least in some stages of the life cycle or in particular regions of their body. Ecdysozoans do not have external epithelial cilia, nor a ciliated larva with an apical organ, and they never undergo spiral cleavage. Cilia may be present, however, in association with certain cuticular structures, such as the scalids and buccal papillae of priapulans, the clavoscalids of loricriferans, and sensory spots on kinorhynchs.

Introduction to Ecdysozoa

Ecdysozoa contains eight phyla (and about 83% of known animal diversity), commonly organized into three subclades: Scalidophora, Nematoida (see Chapter 19), and Panarthropoda (see Chapter 20). The latter two subclades have robust morphological and sometimes molecular support, but while Scalidophora has strong morphological support, it is not always recovered as a clade in molecular analyses. The relationships of the three ecdysozoan clades have not been firmly determined, and they appear as an unresolved trichotomy in our tree of the Metazoa (see Chapter 28). Some evidence suggests

The sections on Kinorhyncha and Priapula were revised by Martin Vinther Sørensen. The section on Loricifera was revised by Katrine Worsaae and Reinhardt Møbjerg Kristensen.

Classification of The Animal Kingdom (Metazoa)

- PHYLUM PORIFERA
- PHYLUM CTENOPHORA
- PHYLUM PLACOZOA
- PHYLUM CNIDARIA

Bilateria (a.k.a. triploblasts)

- PHYLUM XENACOELOMORPHA

Nephrozoa

PROTOSTOMIA

Spiralia

- PHYLUM DICYEMIDA (=RHOMBOZOA)

GNATHIFERA

- PHYLUM CHAETOGNATHA
- PHYLUM GNATHOSTOMULIDA
- PHYLUM ROTIFERA
- PHYLUM MICROGNATHOZOA

PLATYTROCHOZOA

- PHYLUM ENTOPROCTA
- PHYLUM CYCLIOPHORA

Lophotrochozoa

- PHYLUM MOLLUSCA
- PHYLUM NEMERTEA
- PHYLUM ANNELIDA*

LOPHOPHORATA

- PHYLUM PHORONIDA
- PHYLUM BRYOZOA (=ECTOPROCTA)
- PHYLUM BRACHIOPODA

Rouphozoa

- PHYLUM GASTROTRICHA
- PHYLUM PLATYHELMINTHES

Ecdysozoa

SCALIDOPHORA**

- PHYLUM KINORHYNCHA
- PHYLUM PRIAPULA
- PHYLUM LORICIFERA

NEMATOIDA

- PHYLUM NEMATODA
- PHYLUM NEMATOMORPHA

PANARTHROPODA

- PHYLUM TARDIGRADA
- PHYLUM ONYCHOPHORA
- PHYLUM ARTHROPODA
  - SUBPHYLUM CHELICERATA
  - MANDIBULATA
    - SUBPHYLUM MYRIAPODA
    - PANCRUSTACEA
      - SUBPHYLUM CRUSTACEA***
      - SUBPHYLUM HEXAPODA

DEUTEROSTOMIA

- PHYLUM CHORDATA

AMBULACRARIA

- PHYLUM HEMICHORDATA
- PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida

** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent

*** Paraphyletic (excludes Hexapoda)

that Nematoida and Scalidophora might comprise a sister group, and they do share a number of morphological similarities, though nothing that is fully unique to the two groups. This putative clade has been given the name Cycloneuralia. However, most molecular phylogenetic analyses have failed to find support for Cycloneuralia, often placing Nematoida as a sister group to Panarthropoda, and Priapula sometimes as a sister group to all other ecdysozoans, a hypothesis that is in part supported by the large diversity of priapulan-like forms in the Cambrian, some of which may be stem-group priapulans or stem-group ecdysozoans.

The Scalidophora

The clade Scalidophora includes three phyla of marine infaunal animals, two exclusively meiofaunal (Kinorhyncha and Loricifera) and Priapula, which can be megainfaunal or meiofaunal as juveniles or even as adults. These three phyla may seem to have little in common, given the variation in body plans: the segmented trunk of kinorhynchs, the wormlike body of priapulans, and the loricated trunk (i.e., covered by a hard protective shell) of loriciferans. However, Scalidophora has been supported by a series of morphological characters. The name of the clade derives from the presence of scalids on the introvert—short spines, triradiate in cross section (at some ontogenetic stage), with ciliary receptors from one or more monociliated sensory cells. Another proposed synapomorphy uniting the three phyla is the presence of inner and outer retractor muscles in the introvert, the muscles attaching via **tanycytes**—extremely elongated epidermal cells with intermediate filaments. The protonephridia of scalidophorans are also unique, with a compound filter built by two or more terminal cells. And finally, scalidophorans are also characterized by the presence of **flosculi**, special sensory spots with external cuticular micropapillae surrounding a central pore and a few ciliary receptors. However, despite these seemingly strong synapomorphies, some morphologists have questioned Scalidophora based on similarities of the loriciferan larva to that of nematomorphs, including hexaradial symmetry in their internal armature as well as musculature (hexaradial symmetry is also found in some cephalic structures in nematodes).

While the clade Scalidophora has been largely endorsed by morphologists, the monophyly of this grouping has not been thoroughly tested with molecular data, and when tested, it has not been supported. Earlier molecular results, based on one or two genes, did not find a consistent placement for Loricifera. The first phylogenomic analysis including data for Loricifera recovered a sister-group relationship between Loricifera and Priapula, although without significant support, but the analysis did not include Kinorhyncha or Nematomorpha. A more recent phylogenomic analysis, with a data set designed to resolve ecdysozoan relationships, failed to recognize Scalidophora. For those molecular studies including at least Kinorhyncha and Priapula, many recovered their sister-group relationship with variable support, although other recent ones have suggested that Priapula is the sister group to all other ecdysozoans. Mitochondrial gene data fail to recognize Scalidophora, instead resolving Kinorhyncha and Priapula as a grade toward the stem of Ecdysozoa. So, although we continue to use Scalidophora in this edition of our text, we recognize that this clade still needs further testing.

The oldest suspected scalidophoran fossils are treptichnid burrows dating to the base of the Cambrian, thought to have been produced by a priapulan-like creature, and the annulated, introvert-bearing, lower Cambrian *Markuelia*. The latter includes several described fossil species that are among the earliest known ecdysozoans in the fossil record. Likewise, a series of articulated priapulan-like fossils, in addition to scalids, teeth, and hooks preserved as small carbonaceous fossils, are known since the Fortunian stage of the earliest Cambrian. However, positive identifications are difficult to make without being able to provide a clear morphological definition of Scalidophora that can be recognized in fossils. Several other, younger fossils have been assigned to Scalidophora or one of its constituent phyla, especially Priapula and Loricifera (see the Phylum Priapula and Phylum Loricifera sections).

Phylum Kinorhyncha: The Kinorhynchs, or Mud Dragons

Among the most intriguing of ecdysozoans are members of the phylum Kinorhyncha (Greek *kineo*, "movable"; *rhynchos*, "snout"), sometimes called "mud dragons." Since their discovery in 1841 on the northern coast of France, about 300 species of kinorhynchs have been described from around the world, nearly all of which are less than 1 mm in length. Most live in marine sands or muds, from the intertidal zone to a depth of 9,500 m. However, specimens have also been recorded from algal mats and kelp holdfasts, sandy beaches, and brackish estuaries; others live on hydroids, bryozoans, sponges, or sediment aggregations in polychaete tubes or on shells of molluscs.

The body of a kinorhynch is composed of three regions: a head, a short neck region, and a segmented trunk (Figure 18.1). Families and genera are often diagnosed by the composition of the segments, whereas species differences often relate to distribution of spines and setae. Kinorhynchs are one of three truly segmented metazoan clades (the other two being Annelida and the Panarthropoda), although the genetic developmental process of segment formation in kinorhynchs is not yet understood. The major characteristics of kinorhynchs are given in Box 18A.

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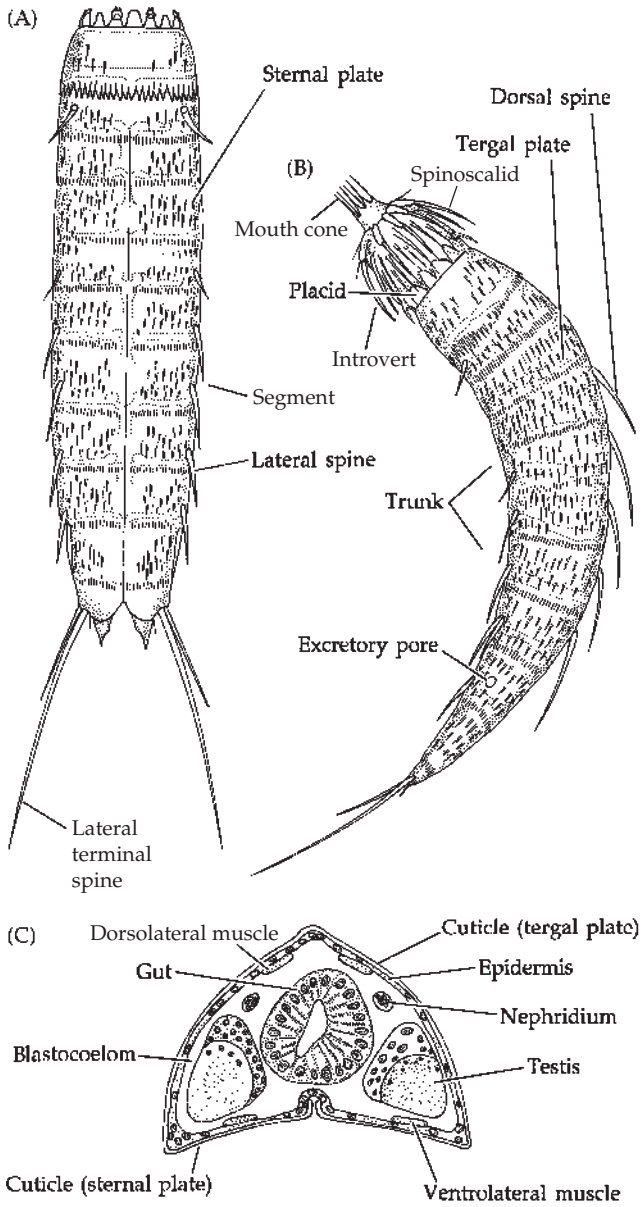

(D)

Courtesy of Martin V. Sorensen

FIGURE 18.1 Kinorhynchs. (A,B) External anatomy of the kinorhynch *Echinoderes*. (A) Ventral view with head retracted. (B) Lateral view with head extended. (C) A trunk segment (cross section) of a kinorhynch; note the arrangement of the body wall structures and the organs within the blastocoelom. (D) *Echinoderes* sp., a meiofaunal species, with head extended.

The kinorhynch head is formed by a retractable mouth cone with nine outer **oral styles**, and an introvert with numerous appendages called **spinoscalids** (Figures 18.1 and 18.2A). By using the ten anterior-most primary spinoscalids as markers, the remaining spinoscalids on the introvert can be divided into ten sectors, where the spinoscalids follow either a bilateral or pentaradial symmetry pattern. Functionally, the two units can be distinguished by the way they move when the head is retracted into the trunk. The mouth cone can be withdrawn by simple retraction in which muscles attached to its proximal base drag it into the introvert. When the head retraction continues into the trunk, the introvert is inverted, meaning that the anterior-most spinoscalids and the part of the introvert that joins the mouth cone are the first to retract.

The kinorhynch neck is composed of a number of plates, called **placids**, and when the head is retracted, the placids act as a closing apparatus (Figure 18.2B). In some genera the placids are hard structures that are

BOX 18A Characteristics of the Phylum Kinorhyncha

1. Triploblastic, bilaterally symmetrical, body segmented (both externally and internally)
2. Blastocoelomate or, in some species, acoelomate
3. Body divided into head, neck, and 11-segmented trunk
4. Head divided into mouth cone and introvert with scalids
5. Segments formed by complete cuticular rings, or composed of tergal and sternal plates
6. Epidermis cellular without locomotory cilia
7. Gut complete
8. With one pair of protonephridia in segment 8, nephridiopores opening on segment 9; without special circulatory or gas exchange structures
9. Direct development through six juvenile stages; juveniles molting their cuticle at the transition between each stage
10. Gonochoristic
11. Embryonic development and cleavage patterns not well understood
12. Found in marine and brackish benthic habitats; most common in mud, but also found in sand or inhabiting epizoic or epiphytic habitats

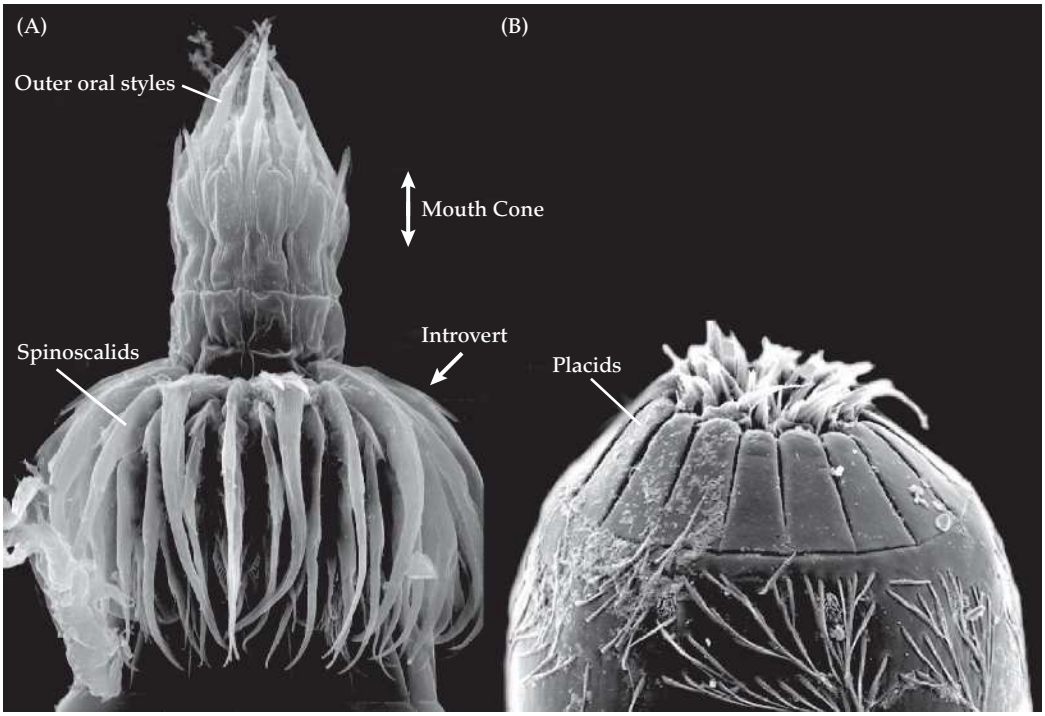

FIGURE 18.2 Scanning electron microscopy showing extended and retracted head of a kinorhynch. (A) Extended head, showing the external morphology of the mouth cone and introvert. (B) Retracted head, with the placids of the neck acting as closing apparatus.

easily recognized, whereas in other genera they are thinner and softer, and more difficult to see. Within the genus *Cateria*, the placids are extremely soft and in one species completely lost, whereas they are fused into a neck ring in the genus *Franciscideres*. The number of placids differs among genera and ranges from 4 to 16.

The kinorhynch trunk consists of 11 segments in all adults. Most trunk segments are made up of a dorsal (tergal) plate and a pair of ventral (sternal) plates (Figures 18.1A and 18.3). The anus is located on the last segment and is usually flanked by strong lateral terminal spines. The segmented body plan is reflected internally by the epidermal glands, nervous system, and muscles.

During juvenile development, and in some species during adult life as well, kinorhynchs shed their cuticle. This supports their position among the ecdysozoan protostomes, even though it is still uncertain whether molting is mediated by the hormone ecdysone.

CLASSIFICATION OF KINORHYNCHA

CLASS CYCLORHAGIDA Neck usually with 14–16 placids that work as a closing apparatus, although in one group a clamshell-like first trunk segment may assist;

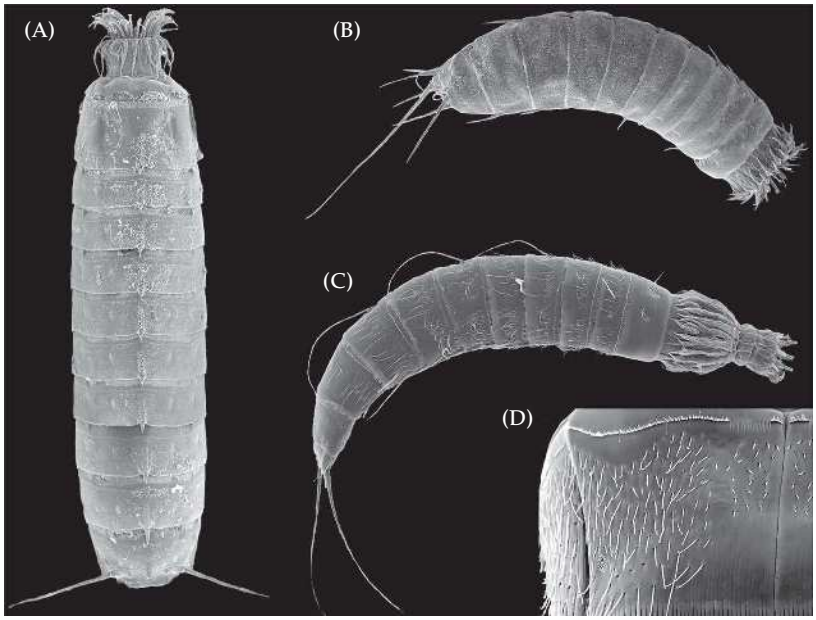

FIGURE 18.3 Scanning electron microscopy of Kinorhyncha. (A) The allomalorhagid genus *Pycnophyes*, and the cyclorhagid genera (B) *Centroderes* and (C) *Meristoderes*. (D) Close-up of right sternal plate. Note the articulations with the left sternal plate, and the tergal plate.

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trunk oval, inverted heart-shaped, or slightly triangular in cross section; numerous cuticular trunk spines and tubes present; trunk segments usually with dense covering of cuticular hairs or denticles. The class includes genera such as *Centroderes* (Figure 18.3B), *Echinoderes* (Figure 18.1D), *Meristoderes* (Figure 18.3C), and *Semnoderes*.

CLASS ALLOMALORHAGIDA Neck with 9 or fewer placids. Trunk either triangular or completely round in cross section. Midterminal spine never present in adults. The class includes genera such as *Paracentrophyes*, *Neocentrophyes*, *Pycnophyes*, *Dracoderes*, and *Franciscideres* (Figure 18.3A).

The Kinorhynch Body Plan

Body Wall

Beneath the thick, well-developed, chitinous cuticle is a nonciliated epidermis (Figure 18.1C) that contains elements of the nervous system. Largely internal to the epidermis but still attached to the cuticle are bands of cross-striated dorsal and ventral longitudinal muscles. All ventral muscles, and most dorsal ones, attach to cuticular thickenings at the anterior segment margins and run to the anterior margin of the following segment. Other dorsal muscles run throughout the trunk. The head is retracted by introvert and mouth cone retractor muscles that have anterior attachment points in the most anterior part of the introvert and have posterior attachments between trunk segments 3 to 6. A series of segmentally arranged dorsoventral muscles creates the increased hydrostatic pressure that protracts the introvert and **mouth cone** when the retractor muscles relax, and diagonal muscles contribute to lateral movement of the trunk (Figure 18.4).

Support and Locomotion

Body shape in kinorhynchs is more or less fixed by the rigid plates of the supportive cuticular exoskeleton, but the animals are able to flex and even twist at the points of articulation between adjacent segments. Segmented trunk musculature facilitates movements of the articulated cuticular plates. Intersegmental muscle fibers assist with dorsoventral and lateral trunk movements. In the absence of external cilia, burrowing is accomplished by extending the head into the substratum, anchoring the anterior spines, and then pulling the rest of the body forward. It has also been suggested that the numerous glandular cells that open along the trunk may be involved in locomotion, that is, by creating a push in a forward direction when mucus is released from the glands.

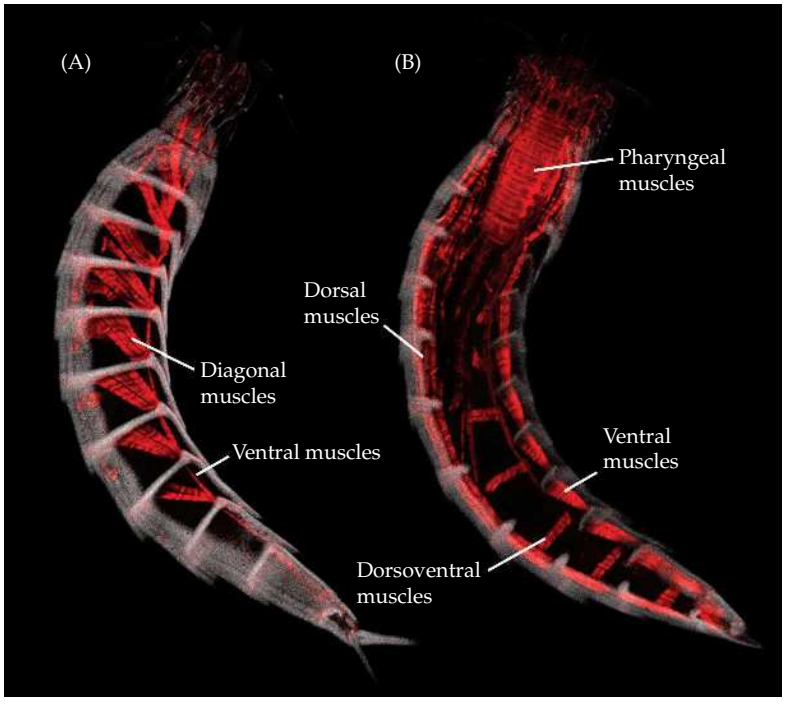
Feeding and Digestion

Kinorhynchs are probably direct deposit feeders, ingesting the substratum and digesting unicellular algae and/or other organic material therein; they have been found with their guts full of benthic diatoms. However, the details of feeding and the exact nature of their food are not known.

The digestive system is remarkably arthropodlike. The mouth leads into a buccal cavity located within the mouth cone and subsequently to a muscular pharynx (Figure 18.5). The buccal cavity, pharynx, and esophagus are lined with cuticle. Protractors, retractors, and circular muscles coordinate eversion and retraction of the introvert and mouth cone. Various paired glands are often associated with the esophagus, but their functions are uncertain. The esophagus connects with an elongate, straight midgut, which leads to a short, cuticle-lined proctodeal hindgut (rectum) and the anus on the last segment. So-called "digestive glands" often arise from the midgut.

Circulation, Gas Exchange, Excretion, and Osmoregulation

Gas exchange takes place by diffusion across the body wall, and circulation and internal transport are accomplished



Courtesy of Martin V. Sørensen

FIGURE 18.4 Confocal laser scanning microscopy showing trunk muscles of the kinorhynch *Echinoderes* (lateral view). (A) Optical slices through lateral part of trunk. (B) Optical slices through medial part of trunk.

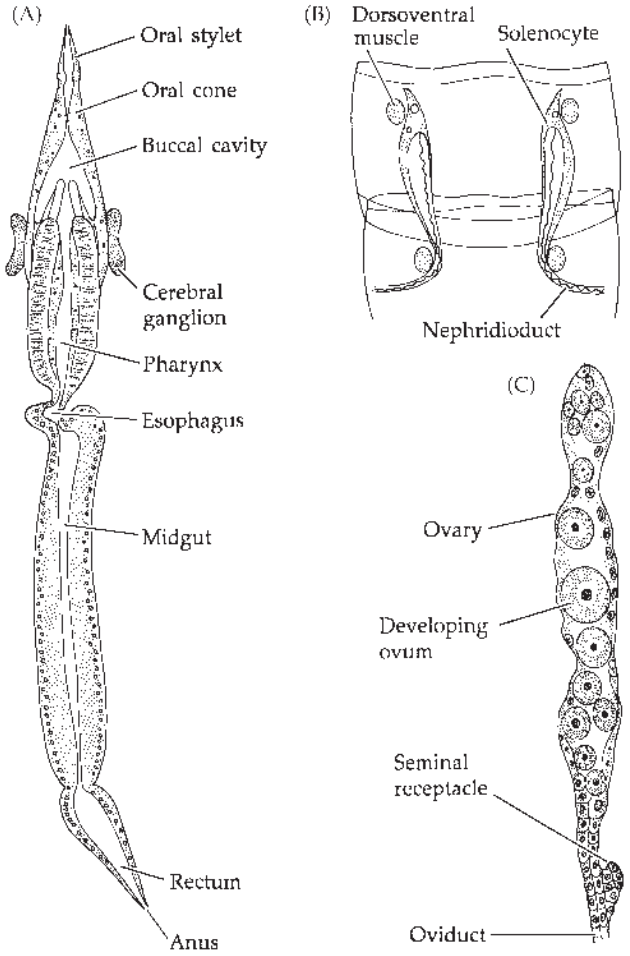


FIGURE 18.5 Internal anatomy of kinorhynchs. (A) The digestive tract of *Pycnophyes*. (B) The nephridial arrangement in two segments of *Pycnophyes*. (C) The simple female reproductive system of a kinorhynchs.

primarily by body movements. Kinorhynchs possess one pair of solenocyte protonephridia in segment 8, each with a short nephridioduct that opens laterally through a nephridiopore on segment 9 (Figure 18.5B). Excretory and osmoregulatory physiology is likely interesting, although largely unstudied; some estuarine and intertidal species can tolerate large fluctuations in salinity, and some live in salinities as low as 3.5 parts per thousand in the Gulf of Finland.

Nervous System and Sense Organs

The central nervous system of kinorhynchs is relatively simple and is intimately associated with the epidermis. The brain is arranged in a ringlike manner around the pharynx (Figure 18.5A) and is composed of anterior and posterior aggregations of somata and a neuropil. Ten radially arranged longitudinal nerves arise from the neuropil. The two midventral longitudinal nerves converge in the trunk region forming the ventral nerve cord that has ganglia in each segment in most species. Sensory receptors include introvert spinoscalids and mouth cone styles (in the head region) and sensory spots and spines (on the trunk). Some species have pigmented eyespots in the anterior region of the introvert.

Reproduction and Development

Kinorhynchs are gonochoristic and possess relatively simple reproductive systems. External morphological differences between males and females are usually restricted to the most posterior segments. In both sexes, paired saclike gonads lead to short gonoducts that open separately on the terminal segment. In the males, the gonopore may be associated with two or three cuticular, hollow, penile spines that presumably aid in copulation, although their precise function is uncertain. The female gonads comprise both germ cells and nutritive (yolk-producing) cells. Each oviduct bears a diverticulum that forms as a seminal receptacle prior to ending at a gonopore between segments 10 and 11 (Figure 18.5C).

Mating has never been observed in kinorhynchs, and egg laying and early development (e.g., cleavage patterns) have not been adequately studied. Fertilized eggs are coated with a protective envelope of silt and detritus and then deposited in sediment. Embryos develop directly and hatch as juveniles with 9 segments. The juvenile reaches maturity after six molts and gradually changes into the adult morphology during these molts. New segments are added by elongation and by subsequent subdivision of the terminal segment. The mature condition with 11 trunk segments is often reached in juvenile stage 5. Molting among adults has been reported as well.

Phylum Priapula: The Priapulans, or Penis Worms

Twenty-two extant species (and several fossil species) are assigned to the phylum Priapula (from *Priapus*, the Greek god of reproduction, symbolized by his enormous penis). These odd creatures were recorded in Linnaeus's *Systema Naturae*, where he mentioned the species *Priapus humanus* (literally, "human penis"). Since that time priapulans have been associated with several different invertebrate phyla, but today morphological evidence supports their alliance with the other scalidophoran ecdysozoans, perhaps most closely related to the kinorhynchs. Molecular evidence is currently less conclusive, but some recent analyses also support the scalidophoran affinity. The major characteristics of priapulans are given in Box 18B.

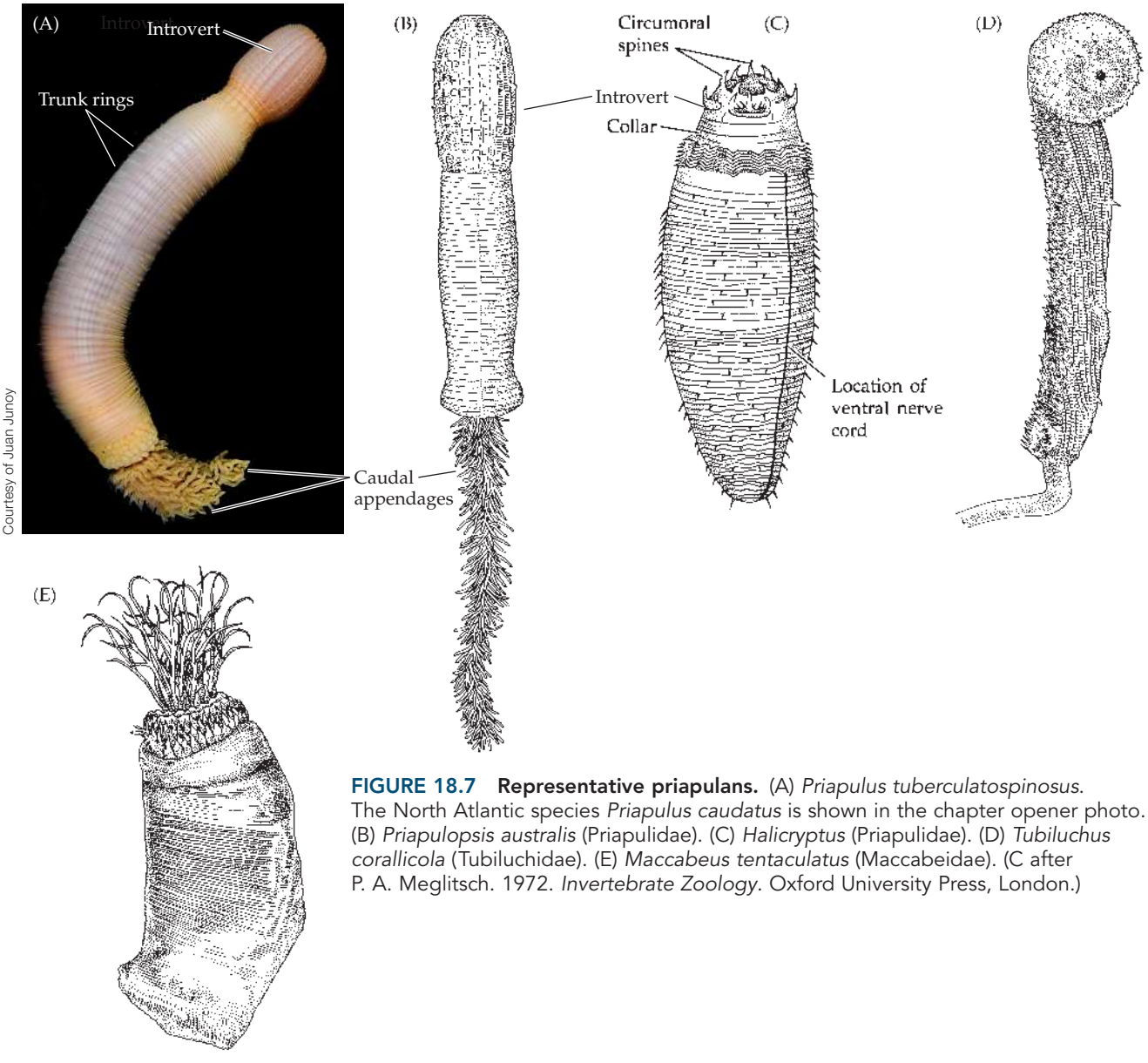
Three genera (*Tubiluchus*, *Meiopriapulus*, and *Maccabeus*) comprise meiofaunal species that measure 1.5 mm to about 5 mm (Figure 18.6), whereas the remaining four genera (*Acanthopriapulus*, *Halicryptus*, *Priapulopsis*, and *Priapulus*) are macrofaunal, with the largest species, the Alaskan *Halicryptus higginsi*, reaching a length

Courtesy of G. Giribet

FIGURE 18.6 **The meiofaunal priapulan *Tubiluchus corallicola*.**

of almost 40 cm. Priapulans are cylindrical vermiform creatures. The body comprises an introvert, sometimes a neck region, a trunk, and sometimes a "tail" or **caudal appendage** (Figure 18.7). The whole introvert can be inverted, and it is equipped with short, hook-shaped scalids that are considered homologous with the spinoscalids of loriciferans and kinorhynchs. When present, the caudal appendage varies in shape and function among species.

Large priapulans are active infaunal burrowers in relatively fine marine sediments and occur primarily in boreal and cold temperate seas. A few species construct tubes. Adults of one species, *Halicryptus spinulosus*, lives in anoxic, sulfide-rich sediments in the Baltic Sea and shows remarkable abilities to both tolerate and detoxify high sulfide levels in its body. In contrast, the



Courtesy of Juan Junoy

FIGURE 18.7 **Representative priapulans.** (A) *Priapulus tuberculatospinosus*. The North Atlantic species *Priapulus caudatus* is shown in the chapter opener photo. (B) *Priapulopsis australis* (Priapulidae). (C) *Halicryptus* (Priapulidae). (D) *Tubiluchus corallicola* (Tubiluchidae). (E) *Maccabeus tentaculatus* (Maccabeidae). (C after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

BOX 18B Characteristics of the Phylum Priapula

1. Triploblastic, bilaterally symmetrical, unsegmented (may be superficially annulated), and vermiform
2. Body cavity lining probably not peritoneal; presumably blastocoelomate; one species coelomate
3. Introvert with hooked spines
4. Nervous system radially arranged and largely intraepidermal
5. Gut complete
6. With (often multicellular) protonephridia associated with the gonads as a urogenital system
7. Many with unique caudal appendage (in adults) that may serve for gas exchange
8. No circulatory system
9. Thin cuticle that is periodically shed; without epidermal cilia
10. With unique loricate larva, with cuticular lorica that is shed at metamorphosis to adult stage
11. Gonochoristic
12. Cleavage radial-like; the blastopore giving rise to the anus
13. Marine and benthic; mostly burrowers

small meiofaunal forms burrow or live interstitially among sediment particles, and they appear to be most diverse in subtropical and tropical waters.

Fossil stem- and crown-group priapulans are, so far, known only from the Cambrian record, where they are rather common. They may have been one of the major predator groups in the Cambrian seas, and they were almost certainly more diverse in Paleozoic times than they are today. The most abundant fossil species, *Ottoia prolifica*, resembles the extant *Halicryptus spinulosus*. Recent work confirms that *O. prolifica* and the closely related *O. tricuspida*, which date from the middle Cambrian, were serious carnivores, their introvert being lined with rows of hooks, teeth, and spines for dealing with their prey. The iconic trace fossil *Treptichnus pedum*, which defines the base of the Cambrian, has been postulated to be the result of the burrowing behavior of priapulan-like animals.

PRIAPULAN CLASSIFICATION

Classes and orders are usually not recognized within the Priapula; the phylum is divided into the three extant families:

FAMILY PRIAPULIDAE (Figure 18.7A–C). Relatively large (4–40 cm); trunk with superficial annulations; caudal appendage (absent from *Halicryptus spinulosus*) either a grapelike cluster of fluid-filled sacs (called vesiculae) or a muscular extension with cuticular hooks. Nine species, 4 genera: *Acanthopriapulus*, *Halicryptus*, *Priapulopsis*, and *Priapulus*

FAMILY TUBILUCHIDAE (Figures 18.6 and 18.7D). Small (less than 5 mm long); trunk not annulated; caudal appendage vermiform and muscular. Tubiluchids live in sediments of shallow tropical waters. Eleven species, 2 genera (*Tubiluchus* and *Meiopriapulus*)

FAMILY MACCABEIDAE (= CHAETOSTEPHANIDAE) (Figure 18.7E). Very small (less than 3 mm long); meiofaunal; trunk with rings of tubercles and posterior longitudinal ridges with hooks; no caudal appendage; posterior end of abdomen extensible and mobile, used for burrowing (posterior end first). Maccabeids are found in the Mediterranean Sea and Indian Ocean. Monogeneric, with only two described species (*Maccabeus tentaculatus* and *M. cirratus*)

Priapulan Body Plan

Body Wall, Support, and Locomotion

The priapulan body is covered by a thin, flexible cuticle that forms a variety of spines, warts, and tubercles (Figure 18.7). Hook-shaped scalids are often present around the mouth and on the introvert, and these are generally considered homologous with the spinoscalids of kinorhynchs and loriciferans. In all three groups the scalids function as sensory structures and assist in locomotion. Priapulans move through sediments by means of the introvert and peristaltic body muscle action. The cuticle contains chitin and is periodically shed as the animal grows. Beneath the cuticle lies an unciliated epidermis of thin, elongate cells with large fluid-filled intercellular spaces. Beneath the epidermis are well-developed layers of circular and longitudinal muscles. There are also complex muscle layers and bands associated with the pharynx, and a set of introvert retractor muscles (Figure 18.8A).

Adult priapulans have a large body cavity that may extend into the caudal appendage. The body cavity is lined by a simple noncellular membrane secreted by surface cells on the retractor muscles and is therefore a blastocoel (blastocoelom). The only exception to this is the meiofaunal species *Meiopriapulus fijiensis* that does possess a small epithelium-lined compartment around the foregut, and this cavity is apparently a true coelom. The fluid of the body cavity contains motile phagocytic amebocytes and free erythrocytes with hemerythrin.

Maintenance of body form and support are provided by the hydrostatic skeleton of the body cavity. The contraction of circular muscles around this cavity also facilitates protrusion of the introvert by increasing the internal pressure. Priapulans that move through the substratum do so largely by peristaltic burrowing, probably using the various hooks and other cuticular extensions to hold one part of the body in place while the rest is pushed or pulled along. *Maccabeus* is thought to use its ring of posterior cuticular spines for anchorage within its burrow (Figure 18.7E).

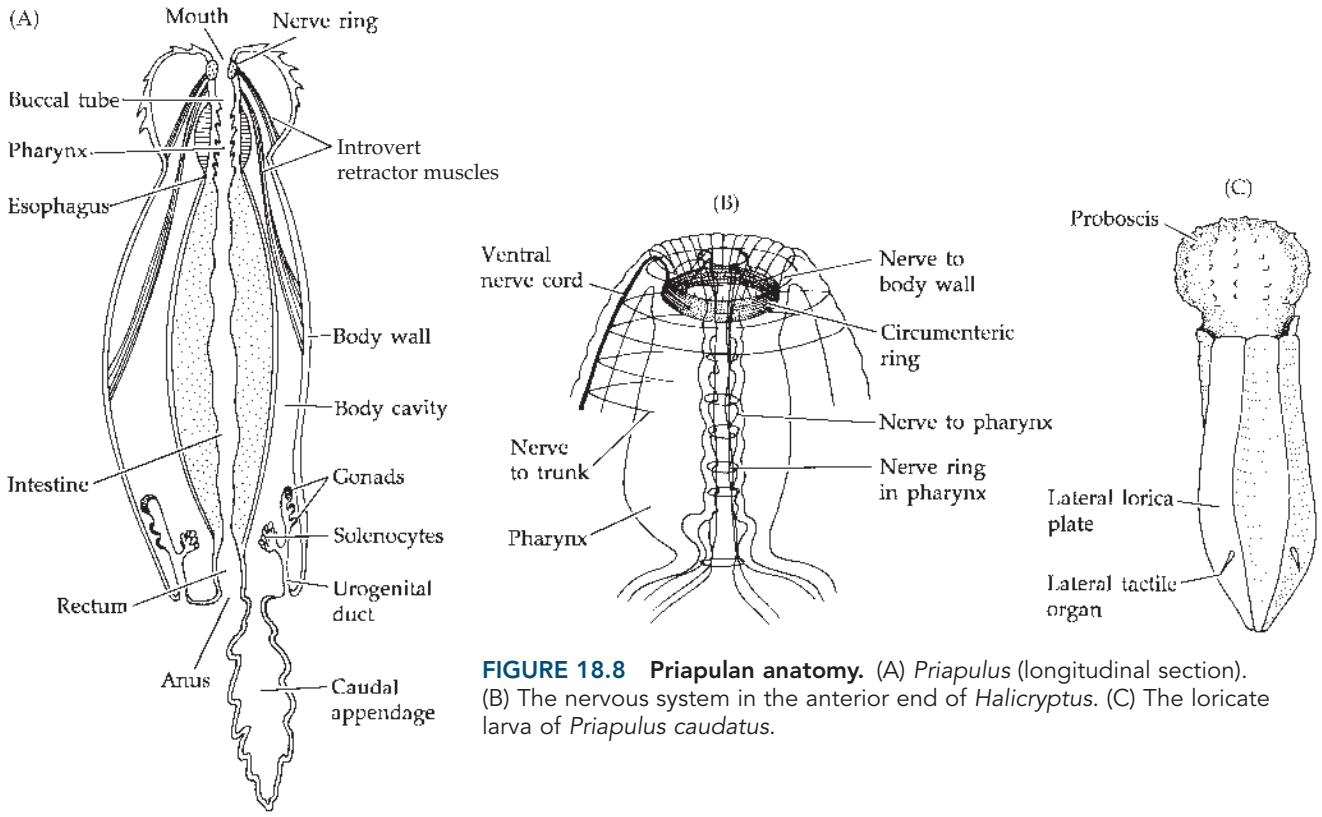


FIGURE 18.8 Priapulan anatomy. (A) *Priapulus* (longitudinal section). (B) The nervous system in the anterior end of *Halicryptus*. (C) The loricate larva of *Priapulus caudatus*.

Feeding and Digestion

Most priapulans (i.e., members of the family Priapulidae) live in soft sediments and prey on soft-bodied invertebrates such as polychaetes. During feeding, a portion of the toothed, cuticle-lined pharynx is everted through the mouth at the end of the extended introvert. As the prey is grasped, the pharynx is inverted; the introvert then retracts and the prey is drawn into the gut.

Tubiluchus corallicola (Figure 18.7D) lives in coral sand, as well as silty and muddy sediments, and feeds on organic detritus. The pharynx is lined with pectinate teeth, which the animal uses to sort food material from the coarse sediment particles. *Maccabeus tentaculatus*, a tube dweller, is a trapping carnivore. Eight short scalids, called **trigger spines**, arranged around the mouth opening are assumed to be touch sensitive, and these are in turn ringed by 25 branched scalids. It is suspected that when a potential prey touches the trigger spines, the other scalids quickly close as a trap.

The digestive system is complete and either straight or slightly coiled (Figure 18.8A). The portion of the gut that lies roughly within the bounds of the introvert comprises the buccal tube, pharynx, and esophagus, all of which are lined with cuticle and together constitute a stomodeum. In members of the genus *Tubiluchus*, the stomodeum also includes a region behind the esophagus called a **polythridium**, which bears a circlet of two rows of plates and may be used to grind food. The midgut or intestine is the only endodermally derived section of the digestive tract and is followed by a short proctodeal rectum. The anus is located at the posterior end of the abdomen, either centrally or slightly to one side. Nothing is known about the digestive physiology of priapulans, although it is likely that digestion and nutrient absorption occur in the midgut.

Circulation, Gas Exchange, Excretion, and Osmoregulation

Internal transport takes place through diffusion and movement of the fluid in the body cavity. The presence of the respiratory pigment hemerythrin in the body fluid cells suggests oxygen transport or storage functions, and many priapulans are known to live in marginally anoxic muds. In those species with a vesiculate caudal appendage, the lumen of that structure is continuous with the main body cavity, and such caudal appendages may function as gas exchange surfaces.

Clusters of solenocyte protonephridia lie in the posterior portion of the body cavity and are associated with the gonads as a urogenital system or complex (Figure 18.8A). Priapulan protonephridia are possibly unique in being composed of two or more terminal cells. A pair of urogenital pores opens near the anus. Priapulans inhabit both hyper- and hyposaline environments, so the protonephridia may function in both osmoregulation and excretion.

Nervous System and Sense Organs

The priapulan nervous system is intraepidermal and is constructed for the most part on a radial plan within the cylindrical body (Figure 18.8B). The brain is ring

shaped and wrapped around the buccal tube in the anterior part of the introvert. The main ventral nerve cord arises from this ring and gives off a series of ring nerves and peripheral nerves along the body. In addition, longitudinal nerves extend from the main nerve ring along the inner pharyngeal lining and are connected by the ring commissures.

Priapulans have several types of sensory structures. All introvert scalids, except the locomotory scalids in *Meiopriapulus fijiensis*, probably have a sensorial function, and smaller sensory structures—the so-called **flosculi**—are distributed over the trunk region. A flosculus is a sensory structure that includes a central sensory cilium surrounded by a circle or collar of seven modified microvilli. Besides scalids and flosculi, different setae, tubuli, and anal hooks may have receptor cells and hence serve a sensory function.

Reproduction and Development

Priapulans are gonochoristic, although males are unknown in *Maccabeus tentaculatus*. The reproductive organs are similarly placed and connected in both sexes. The paired gonads are drained by genital ducts, which are joined by collecting tubules from the protonephridia to form a pair of urogenital ducts exiting posteriorly through urogenital pores (Figure 18.8A).

Whereas macroscopic priapulans have external fertilization and spawn gametes into the water (first the males and then the females), at least species in the microscopic genus *Tubiluchus* appear to have internal fertilization. Cleavage is holoblastic, appears to be radial, and results in a coeloblastula (some accounts differ) that undergoes invagination. Gene expression studies on developing embryos of *Priapulus caudatus* have led to the surprising discovery that the anus is formed directly from the blastopore, whereas the mouth opening is formed by a group of ectodermal cells at the animal hemisphere of the embryo, thus these animals have deuterostomous development despite being part of the clade Protostomia. Gastrulation starts at the 64-cell stage with the invagination of the vegetal-most cells into a small blastocoel and the epibolic movement of the animal blastomeres toward the vegetal pole.

Direct development occurs only in *Meiopriapulus fijiensis*, in which the females brood the embryos. All other species develop through a series of **loricate larvae** (Figure 18.8C), which in some ways resemble loriciferans. The trunk of the larva is encased within a thick cuticular lorica into which the introvert can be withdrawn. The larvae live in benthic muds and are probably detritivores. The lorica is periodically shed as the larva grows; it is finally lost as the animal metamorphoses to a juvenile priapulan. At that time the caudal appendage forms in those species that possess this structure. The larvae of different genera vary somewhat in cuticular shape and ornamentation. Detailed larval development is best known for *Priapulus caudatus*. The newly hatched larva has a functional introvert, but mouth and anus are still closed, and no lorica is present yet. The lorica appears after the first molt, and additional scalids are added to the introvert. A mouth appears after the next molt, and during the following molts the trunk changes shape from being circular in cross section to having the flattened, bilateral symmetrical shape that typically is found in the *Priapulus* larvae. The exact number of larval stages is uncertain.

Phylum Loricifera: The Loriciferans

It may be apparent to you by now that interstitial habitats (the meiobenthic realm) are home for a host of bizarre and specialized creatures. Studies by zoologists D. Waloszek and K. J. Müller revealed that a rich meiofaunal ecosystem was in place as early as the upper Cambrian Era. And recently discovered microfossils now suggest that a rich meiofauna was already present in the early Cambrian, offering a solution to the problem (Darwin's dilemma) that the Cambrian Explosion appears to have sprung "out of nothing." Studies on modern meiofauna continue to reveal new animals, previously undescribed taxa, and myriad examples of convergent evolution associated with success in this environment. Among these recently discovered groups is the Loricifera, first named and described by Reinhardt Møbjerg Kristensen in 1983. The name Loricifera (Latin *lorica*, "corset"; *ferre*, "to bear") refers to the well-developed cuticular lorica encasing most of the body (Figure 18.9; Box 18C). The description of the phylum was initially based upon a single widespread species, *Nanaloricus mysticus*, but 37 other species have since been described. Most loriciferans have been found at depths of about 20–450 m in coarse marine sediments. One species, *Pliciloricus hadalis*, was collected in the western Pacific at a depth of over 8,000 m. Others, as yet undescribed, have been recorded from additional deep-sea muddy bottom locations. Most recently, a new type of larval form, called the **Shira-larva**, was described from depths of more than 3,000 m; it resembles Cambrian fossils from Australia. However, more surprising was the description in 2017 of an exceptionally preserved Cambrian loriciferan, *Eolorica deadwoodensis*, from western Canada. This fossil looks very similar to species in the extant family Pliciloricidae. To date, all 38 described extant species of loriciferans have been placed in three families (Nanaloricidae, Pliciloricidae, and Urnaloricidae) in a single order, Nanaloricida. All are free-living. Figures 18.9, 18.10 and 18.11 provide overviews of loriciferan anatomy.

In 2010, three species of loriciferans (all new to science) were discovered living and reproducing in a fully anoxic, high-sulfide, hypersaline basin in the deep Mediterranean Sea, called L'Atalante. Although prokaryotes and a few protists have long been known to spend their entire life in anoxic conditions, this was the first report of a metazoan proven to do so and to have obligate anaerobic metabolism. All three species lack mitochondria but

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have hydrogenosomes in their cells, as seen in some ciliate protists. In this deep basin, these loriciferans occur in the highest abundance ever recorded for this phylum (up to 701 individuals per square meter). *Spinoloricus cinziae* (Figures 18.9E–F), one of the three new species from this hypersaline basin, was formally described in 2014.

The loriciferan body is minute (85–800 μm long, the abyssal *Titaniloricus inexpectatovus* a giant among them) but complex, containing over 10,000 cells. The adults of most are about the same size as large meiobenthic ciliated protists. It is divided into a head (introvert and mouth cone), neck, thorax, and loricate abdomen. The head, neck, and most of the thorax can telescope into the lorica. The mouth is located at the end of an introvert, called the **mouth cone,** that projects from the head and contains six protrusible **oral stylets** in some species. Furthermore, the mouth cone also can have up to eight **oral ridges**, each with a furca at the base where the eight muscles attach. Nine rings of spinelike **scalids** (200–400 scalids in all) of various shapes also protrude from the spherical head, most apparently with intrinsic muscles. In the pliciloricids, some of these projections bear joints near their bases, reminiscent of articulated limbs. The first ring consists of 8 anteriorly directed **clavoscalids**; the remaining eight rings of **spinoscalids** are directed posteriorly. In at least some species of

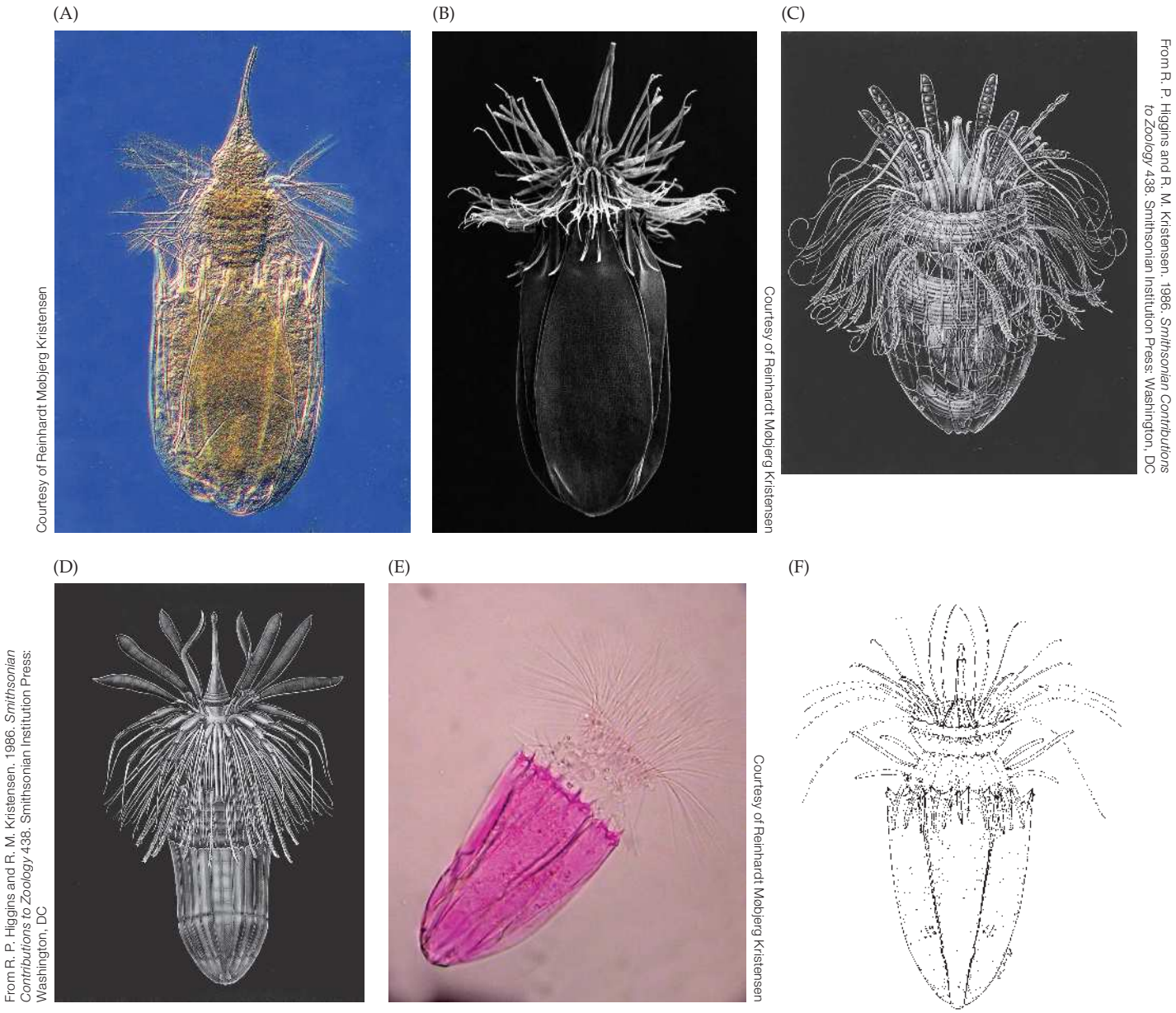

FIGURE 18.9 Representative loriciferans. (A) *Nanaloricus mysticus*, the first described loriciferan (photograph of the male allotype specimen for the species; Roscoff, France). (B) *Nanaloricus* sp. (an undescribed species from northwest France). (C) *Pliciloricus enigmaticus* (male), from the USA. (D) *Pliciloricus gracilis*, male, from the USA. (E,F) *Spinoloricus cinziae*, dorsal views in micrograph and line drawing. This is the first known metazoan living in an anoxic environment; from a deep basin in the Mediterranean Sea.

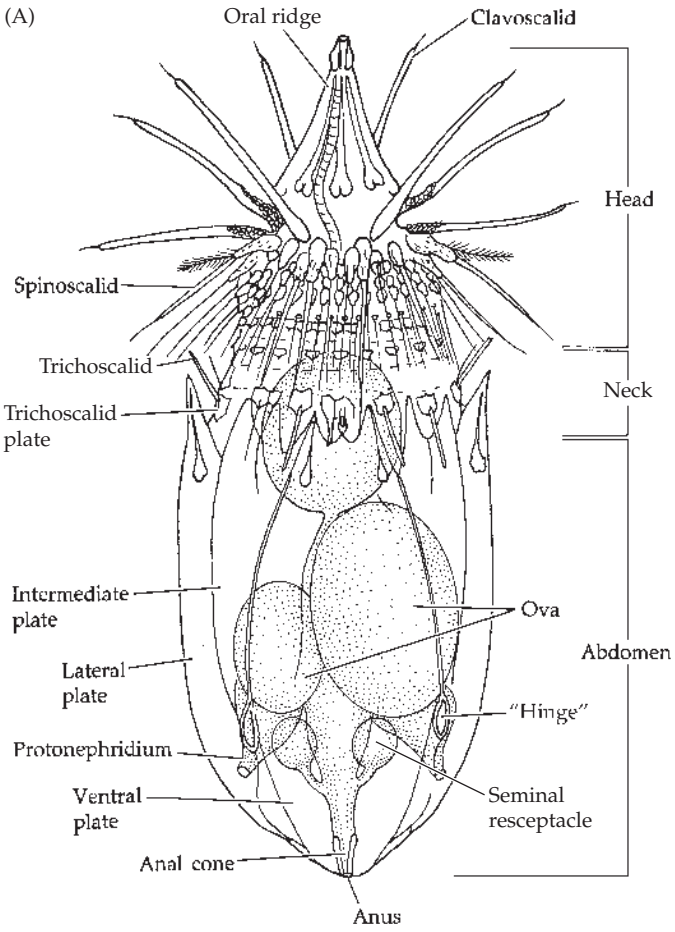

FIGURE 18.10 Anatomy of Loricifera. (A) An adult female loriciferan, *Nanaloricus mysticus* (ventral view). (B) The anterior end of *Nanaloricus mysticus*.

Nanaloricidae, the number of clavoscalids differs between males and females. The males may have 6 of the clavoscalids each split into three branches, resulting in a total of up 20 clavoscalids. The clavoscalids seem to be chemoreceptors, while the spinoscalids are both mechanoreceptors and locomotory. The 15 trichoscalids of the neck can be double or single. Recently it was discovered that the trichoscalids are attached to large cross-striated muscles, and in the family Nanaloricidae the adults use them to "jump" more than three times their own length, whereas in the family Pliciloricidae the trichoscalids may be used for swimming.

The lorica comprises six to ten plates in the family Nanaloricidae, which bear anteriorly directed spines around the base of the neck. In the family Pliciloricidae there are no plates, but there are cuticular plicae. In the genus *Pliciloricus* there are about 22 plicae, but in the genera *Rugiloricus* and *Titaniloricus* there are 30 to 60 plicae. Beneath the cuticle and the body wall there are several muscle bands, including those responsible for retraction of the anterior parts. The body cavity is presumably a blastocoelom (as is typical for the members of Scalidophora) and varies from rather spacious in Pliciloricidae to virtually absent in *Nanaloricus* (which would thus be acoelomate in the adult). Two musculatized **toes** occur caudally in the larva, on the abdomen, and function in both locomotion and adhesion. In the family Nanaloricidae, the Higgins larva has leaflike cuticular structures called **mucrones**. These structures may be involved in the swimming behavior of the larva.

The digestive tract is complete. A long, tubular, buccal canal leads from the mouth to a muscular pharynx bulb and esophagus (Figure 18.10B). The pharynx has both circular and longitudinal muscles. The lumen of these anterior gut structures is lined with cuticle. Behind the esophagus is a long midgut leading to a

BOX 18C Characteristics of the Phylum Loricifera

1. Triploblastic, bilaterally symmetrical, unsegmented, never vermiform, without epidermal cilia
2. Body cavity lining probably not peritoneal; presumably blastocoelomate or acoelomate
3. Body divided into a head (with a mouth cone and an introvert), neck, thorax, and loricate abdomen; the head-neck-thorax telescoping into the lorica
4. Mouth located on mouth cone, beset with spines (stylets); head (introvert) and neck with 7–9 rings of scalids
5. Gut complete
6. Without circulatory or gas exchange systems
7. One to two pairs of protonephridia, situated in gonads
8. Gonochoristic, parthenogenic (neotenous larvae), or hermaphroditic; development always including a unique, toed larva
9. All in marine interstitial environments (sand or mud); from shallow waters to the deep sea

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From R. P. Higgins and R. M. Kristensen. 1986. *Smithsonian Contributions to Zoology* 438. Smithsonian Institution Press: Washington, DC

Courtesy of Reinhardt Møbjerg Kristensen

FIGURE 18.11 The Higgins larva of two loriciferans. (A) *Pliciloricus gracilis* (ventral view; note the oral stylets and the tubular toes). (B) *Armorloricus elegans* (dorsal view; note the toes have mucrones for swimming).

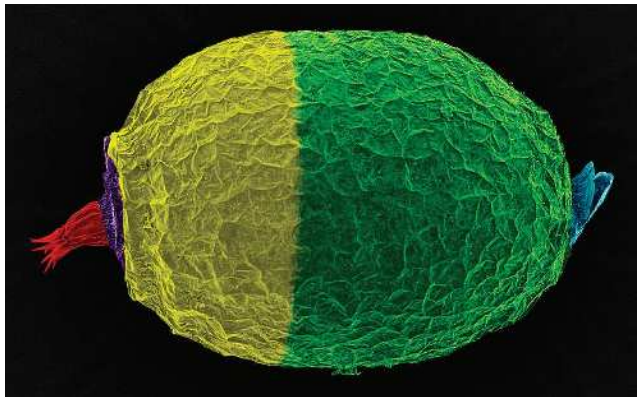
short, cuticle-lined rectum and an anus located on an anal cone. One pair of salivary glands is associated with the buccal tube. Little is known about feeding in loriciferans, but some apparently eat bacteria.

The central nervous system includes a large circumpharyngeal ganglion and a number of smaller ganglia associated with the various body regions and parts. A large ventral nerve cord also bears ganglia. At least some of the scalids are probably sensory in function; however, videos have shown that at least the trichoscalids are involved in a jumping behavior.

Loriciferans are gonochoristic, although one species (*Rugiloricus renaudae*) is hermaphroditic. Males and females differ externally in the form and number of certain scalids. The male reproductive system comprises two dorsal testes in the abdominal body cavity, probably a blastocoelom. The female system includes a pair of ovaries and probably in a few species of *Nanaloricus* also two seminal receptacles. Fertilization is suspected to be internal. Loriciferans have one or two pairs of monoflagellate protonephridia that are uniquely located within the gonads.

Little is yet known about early development in loriciferans. In most species, a feeding, benthic **Higgins larva** develops. This larva (Figure 18.11) is built along the same general body plan as the adult, but it possesses a pair of "toes" at the posterior end that are used for locomotion. These toes are thought to also have adhesive glands at their bases. Early stages apparently contain yolk reserves in the cells of the body cavity. The cuticle is periodically shed as the individuals grow in size. In some species the larva metamorphoses to a so-called "postlarva" (juvenile), which resembles an adult female but lacks ovaries. In others, larval metamorphosis involves a molt directly to an adult.

The original discovery of loriciferans was a fortunate event because the first species described, *Nanaloricus mysticus* (Nanaloricidae), proved to have the simplest life cycle in the phylum with the only life stages being the Higgins larva, free-living postlarva, and adult. In the second described genus, *Rugiloricus*, a strongly modified postlarval stage was discovered (in *R. cauliculus*). Successive complexity was added to loriciferan life cycles, first with the discovery of parthenogenetic phases, and then with the newly discovered Urnaloricidae, which lack free adults (Figures 18.12 and 18.14). And we now know that deep-sea species hasten their life cycle by producing neotenous larvae, which give rise to two to four additional larvae by parthenogenesis. The larvae of some loriciferans can encyst for a period of time, before metamorphosis, and this process might include a new type of larva—the so-called "ghost larva." The newest discovered loops in these complex life cycles are shown in Figure 18.13. *Rugiloricus manuelae* lacks free-living postlarvae, similar to what is seen in the genus *Pliciloricus*. Figure 18.13 shows a typical life cycle for species in the family Pliciloricidae, and Figure 18.14 shows the hypothetical life cycle of the urnaloricid, *Urnaloricus gadi,* with two question marks—where are the adults?



Courtesy of Reinhardt Møbjerg Kristensen

FIGURE 18.12 Colored SEM micrograph of the main life cycle stage of *Urnaloricus gadi*. Cyst-forming megalarva (about 400 µm long) with color-coded body regions: red, introvert; purple, neck; yellow, thorax; green, abdomen; blue, posterior opening with gonopore.

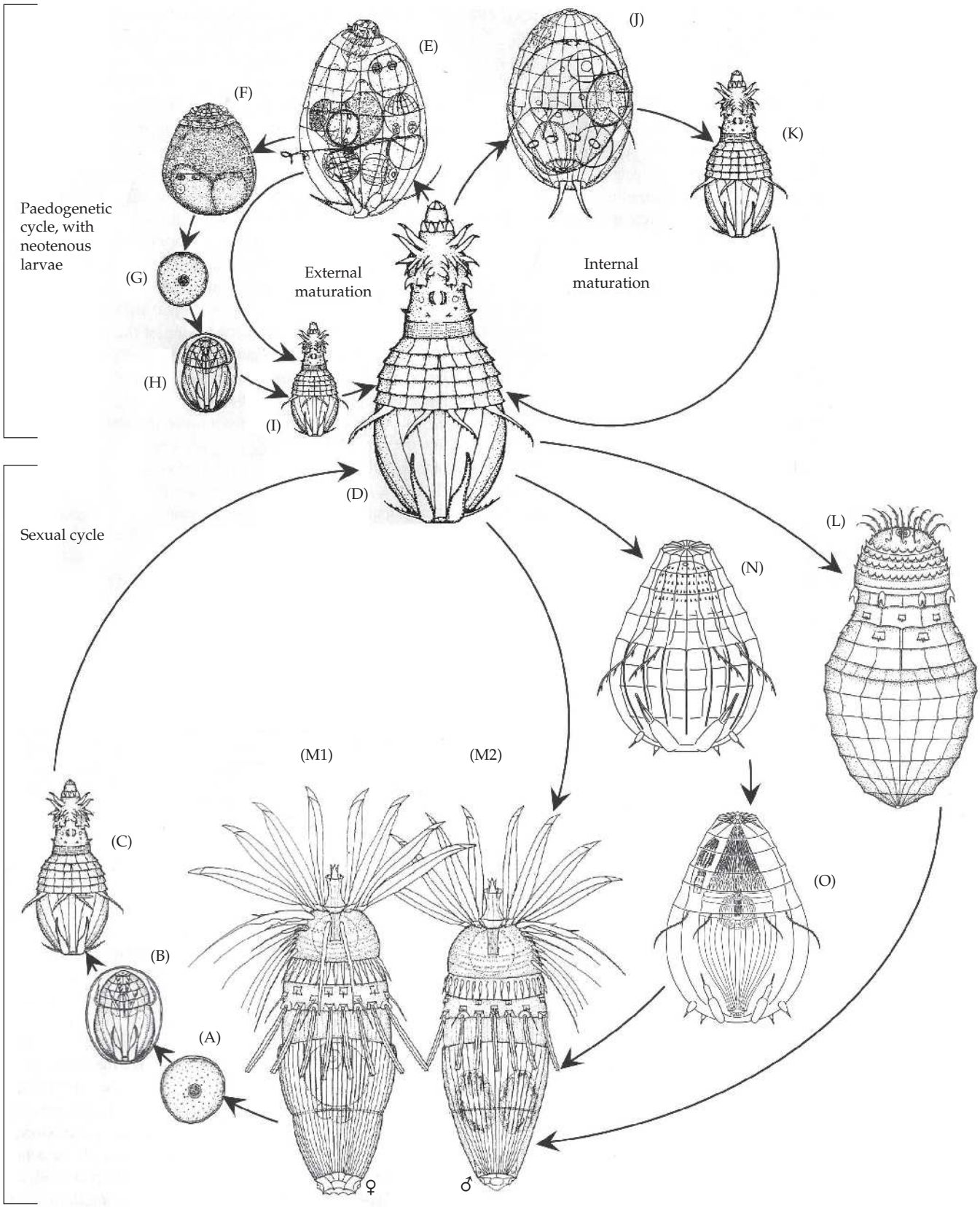


FIGURE 18.13 The life cycle of Pliciloricidae, with all the newly discovered "loops" in the life history. (A) Egg. (B) Embryo in the egg. (C) First instar Higgins larva. (D) Late instar Higgins larva. (E) Penultimate larva with ghost larva and embryos inside. (F) Free ghost larva. (G) Egg. (H) Embryo in egg. (I) First instar Higgins larva. (J) Penultimate larva with ghost larva and embryos inside. (K) First instar Higgins larva. (L) Free postlarva. (M1) Adult female. (M2) Adult male. (N) Last instar Higgins larva with postlarva inside. (O) Last instar Higgins larva with postlarva and young adult inside. (From F. Pardos and R. M. Kristensen. 2013. *Helgol Mar Res* 67: 623–638. https://hmr.biomedcentral.com/articles/10.1007/s10152-013-0349-0)

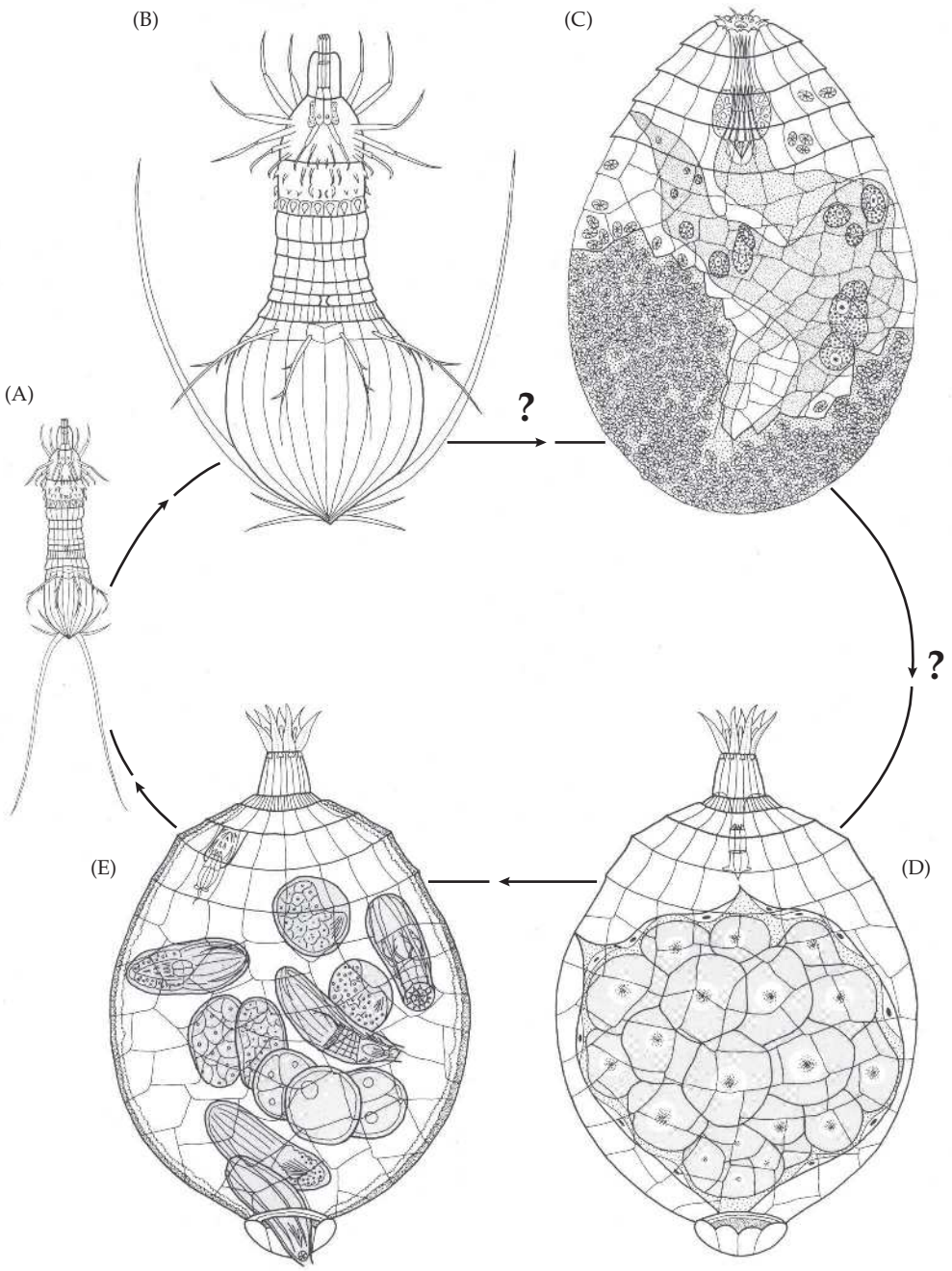


FIGURE 18.14 The hypothetical life cycle of *Urnaloricus gadi* (Urnaloricidae) from Faroe Bank, North Atlantic. (A) First instar Higgins larva emerges from the encysted megalarva. (B) Last instar of Higgins larva found in the sediment. (C) Pre-megalarva with head structure retracted and the cuticle partly covered with coccoliths. (D) Cyst-forming megalarva with large oocytes and a single cuticle. (E) Cystlike megalarva with three layers of cuticle. Inside are embryos and fully developed Higgins larvae. One larva is exiting via the posterior gonopore.

Chapter Summary

This chapter introduced you to two important clades, Ecdysozoa (also described in Chapter 8) and Scalidophora. Ecdysozoa is well supported by both molecular phylogenies and morphology, and it is notable for its distinct three-layered cuticle that is molted by way of ecdysteroid hormonal control. Ecdysozoans also lack external epithelial cilia (except for those associated with sensory structures), do not have ciliated larvae (nor apical organs), and never undergo spiral cleavage. Of the eight ecdysozoan phyla, three (Kinorhyncha, Loricifera,

(*Continued*)

Chapter Summary (*continued*)

Priapula) belong to a putative clade called Scalidophora. Kinorhyncha and Loricifera are exclusively meiofaunal, while priapulans can be mega- or meiofaunal. All three phyla are strictly marine and benthic, are probably blastocoelic (with the one exception noted for *Meiopriapulus*), possess a proboscis bearing unique triradiate spines called scalids, and have other shared apomorphies. However, the clade Scalidophora remains to be confirmed by molecular phylogenetics.

All 300 or so species of kinorhynchs (the mud dragons) are less than 1 mm in length. They live in marine sediments or on algae, from the littoral to 9,500 m. Their body is divided into a head, neck, and 11-segmented trunk. On the head, the proboscis forms a retractable mouth cone and introvert covered with spines or scales, and the retracted introvert is closed by other scales called placids. All these structures, as well as the trunk spines, are what give these creatures a "dragon" appearance. Loriciferans were discovered in 1983, and today nearly 40 species have been described. The name refers to a cuticular lorica encasing most of the body. They are minute animals that live in marine sediments from 20 m to over 8,000 m. As in kinorhynchs, the proboscis forms a retractable mouth cone and introvert (covered with protrusible stylets and scalids in some species). Priapulans comprise a small phylum (22 extant described species) of strange wormlike marine burrowing or interstitial animals. They range in size from 1.5 mm to 40 cm. As with kinorhynchs and loriciferans, the proboscis forms a retractable mouth cone and introvert covered with various spines. Many priapulans have a caudal appendage that might serve for gas exchange.

Future research on the Scalidophora will likely focus on embryology and genomics, which are in its infancy for this clade, with only a single poor-quality genome available for Priapula (at the time of this writing), and none for Loricifera or Kinorhyncha. The relationships among scalidophorans, and to the other ecdysozoan phyla, remain to be further evaluated. Virtually nothing is known about the embryonic development of Loricifera. Also, because priapulan-like animals were so diverse and abundant in the Cambrian, it would be interesting to understand why this group is relatively marginal in today's oceans.

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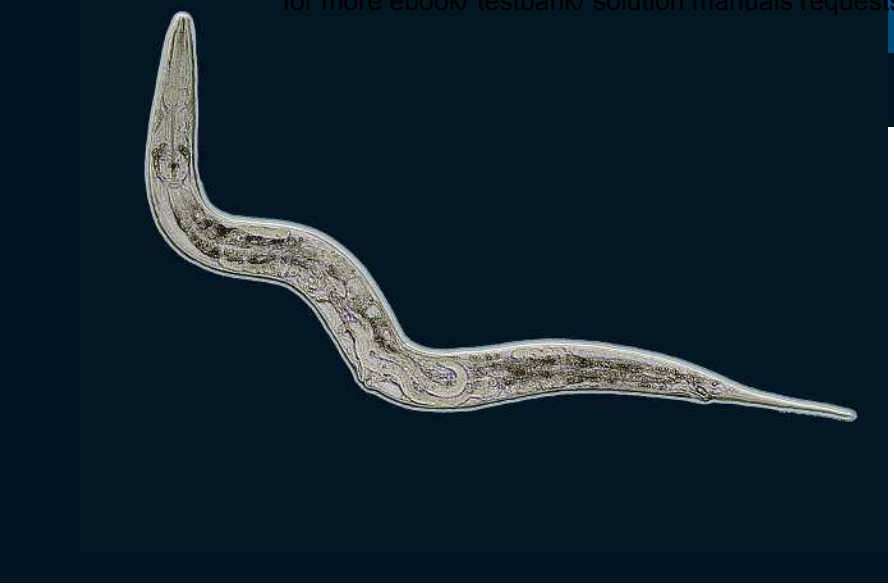

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CHAPTER 19

Nematoida

Phyla Nematoda and Nematomorpha

As noted in Chapter 18, the eight ecdysozoan phyla are generally organized into three subclades: Scalidophora (phyla Kinorhyncha, Priapula, Loricifera; see Chapter 18), Panarthropoda (phyla Onychophora, Tardigrada, Arthropoda; see Chapter 20), and Nematoida (treated in this chapter). The Nematoida include two phyla, Nematoda (nematodes, or roundworms) and Nematomorpha (nematomorphs, or horsehair worms). Nematoid worms epitomize the vermiform animal body plan, some being so long and thin they are sometimes referred to as "threadworms." The clade Nematoida is well supported by both molecular and morphological data. Adults in both phyla share a special cuticle, mostly without chitin (chitin is restricted to the cuticular pharynx of nematodes and to the juvenile cuticle of nematomorphs). Neither phylum has protonephridia, and both lack circular musculature in the body wall. The epidermis has epidermal cords, and it is likely that two such cords, dorsal and ventral, are ancestral for the clade Nematoida. The epidermal cords include longitudinal nerve strands. Males in both phyla possess a cloaca, the exception being the marine nematomorphs (genus *Nectonema*) in which the posterior part of the intestine is reduced and therefore cannot form a cloaca. In female nematodes, however, the genital opening is separate from the anus and often far away from it, in the middle region of the body. One further corresponding character is the lack of cilia in sperm cells, although both taxa have highly modified spermatozoa that are not comparable with each other in their structure, and lack of cilia is common in terrestrial animals. As in the other ecdysozoan taxa, nematoids lack locomotory epidermal cilia.

The section on Nematomorpha was revised by Andreas Schmidt-Rhaesa.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

FIGURE 19.1 Examples of the phylum Nematoda.
(A) *Allantonema* sp. (order Tylenchida), an insect parasite. (B) *Sphaerulariopsis* sp. (order Tylenchida), an insect parasite. (C) *Heterodera glycines* (order Desmodorida), a plant parasite. (D) *Tylenchulus semipenetrans* (order Tylenchida), a plant parasite. (E) *Greeffiella* sp. (order Desmoscolecida), a free-living marine species. (F) *Hexamermis* sp. (order Mermithida), a parasite of various invertebrates. (G) *Heterorhabditis bacteriophora* (order Rhabditida), an insect pathogen. (H) *Draconema* sp. (order Desmodorida), a free-living marine species. (I) *Caenorhabditis elegans* undergoing facultative vivipary, or endotokia matricida (juveniles are seen escaping the mother's body).

Nematodes and nematomorphs are both slender worms. Specimens of the nematode order Mermithida (Figure 19.1F) can be easily confused with nematomorphs, because both are insect parasites with a free-living phase and large body size (usually in the range of several tens of centimeters). However, they are differentiated by the surface structure of the cuticle and the shape of the ends of their bodies. Nematomorphs emerge from their hosts as adults with diagnostic characters for identification to species; mermithid nematodes emerge as postparasitic juveniles and must undergo a final molt to reach the adult stage.

Nematodes molt three or four times during their development; the preadult stages resemble the adults in general and are therefore called juveniles (although the term "larva" is often applied as well, especially with parasitic species). In nematomorphs, only one molt has been observed—at the end of a growth phase of the parasitic juvenile. Nematomorphs possess a true larva, which is microscopic (< 1 mm) and morphologically completely different from the adult.

While Nematoda is a species-rich taxon with a great variety of lifestyles that has adapted to nearly every habitat on Earth, Nematomorpha are all very similar in their life cycle, which includes a parasitic phase and a free-living phase for reproduction.

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Phylum Nematoda: Roundworms

Nematodes, the roundworms, are in the curious position of simultaneously being one of the least-known and one of the best-known animal phyla. How is this possible? They are one of the least known because, while nearly 27,000 species have been described, estimates of numbers of undescribed species range into the millions. Molecular studies have revealed that many named species are actually complexes of several genetically distinct species that are so far difficult or impossible to discriminate based on morphology. It has been suggested that every living animal and plant on Earth is host to one or more parasitic nematode species. Nematodes are nearly ubiquitous, they exist in almost every habitat and ecosystem on Earth (except the very driest), on every continent, and they are almost certainly the most abundant animals on the planet. Nematoda is the most abundant and speciose animal phylum in most marine sediments, including the abyss. It is one of the best-known animal phyla because the free-living soil nematode *Caenorhabditis elegans* has been adopted as a model organism in many fields, including neurobiology, developmental biology, toxicology, and genetics. Thousands of scientists around the world have focused their research on *C. elegans* with the goal of fully understanding every aspect of its biology and the developmental fate of every embryonic cell. *Caenorhabditis elegans* has a number of features that make it both relevant and powerful as a model for biological research. It is easy and inexpensive to maintain in laboratory conditions, it has a short life cycle (about three days), it produces a large number (300+) of offspring, and it has a transparent body that allows easy observation of all its cells. *Caenorhabditis elegans* is about 1 mm long and is a diploid, primarily self-fertilizing hermaphroditic roundworm. It was the first multicellular organism to have its entire genome sequenced. The complete cell lineage of *C. elegans*, from zygote to hatchling, is known, and its cell lineage is invariant—every individual is produced by the exact same sequence of cell divisions, which has been fully mapped. And with 959 somatic cells in adult hermaphrodite individuals, it is one of the best-documented cases of eutely. Males in this species, which are maintained at low numbers in natural populations, have 1,031 somatic cells. Once the target number of cells has been reached, growth in body size can only be accomplished by increases in the size of the cells themselves.

An enormous amount of literature exists on other nematodes as well, much of it dealing with parasitic species of economic or medical importance. Many of the large parasitic forms, such as the trichina worm (*Trichinella spiralis*), have been known since ancient times. Parasitic nematodes are sometimes called threadworms or pinworms.

Not all species of roundworms have the typical threadlike appearance, and their size may vary from a few microns to several meters in length (Figure 19.1). One of the smallest species known is *Hapalomus minutus*, just 80 μm (0.08 mm) long from sandy beaches and coral reefs. At the opposite end of the spectrum is the human Guinea worm (*Dracunculus medinensis*), up to 1.2 m long, and *Placentonema gigantissima*, the sperm whale nematode with females reaching over 8 m in length. Most free-living and plant-parasitic species are smaller than 1 mm.

Gastrointestinal nematode parasites have been shown to be important drivers of selection in wild vertebrate communities, and estimates of the number of undescribed nematodes that are parasites of vertebrates alone are on the order of 25,000 species. Skin-penetrating parasitic nematodes infect around one billion people worldwide. Nematodes can be found in aquatic (marine and freshwater) and terrestrial ecosystems ranging from the tropics to the poles, and at all elevations. In 2011, a nematode 500 μm (0.5 mm) long was even found living in ancient waters several miles below the Earth's surface in South Africa. Named *Halicephalobus mephisto*, after Mephistopheles (in reference to the devil in the Faust legend), this is the deepest-living metazoan yet discovered. It is thought to inhabit water-filled rock fractures and feed on subterranean bacteria. Some species are generalists, but many have very specific habitats. For example, the sour paste nematode, *Panagrellus redivivus*, described by Linnaeus in 1767 (as *Chaos redvivum*), was isolated from bookbinding glue.

Marine roundworms are considered the most diverse and widespread group of nematodes, occurring from shores to the abyss, and about 11,400 species have so far been described. Most studies of free-living marine meiobenthic communities have shown nematodes to be the most species-rich phylum in that environment. However, in spite of their abundance, marine nematodes are poorly known, most species remain undescribed, and their importance in benthic systems is little appreciated, though their relative abundance is sometimes used in biomonitoring. Some terrestrial soil environments yield as many as three million nematodes per square meter, and many thousands of nematodes occur in a handful of garden soil.

Many soil nematodes can undergo a resting phase, a period of extreme quiescence, or even cryptobiosis (nearly complete suspension of their metabolism) when conditions become unfavorable. Roundworms even survive the extreme cold and dryness of the Antarctic Dry Valleys in an anhydrobiotic state.

Nematodes have developed a multitude of parasitic lifestyles, which is why they can affect almost every animal and plant on Earth, including us. In fact, it has been estimated that up to one-third of all humans, mainly in the developing world, carry a nematode infection. Some cause serious damage to crops and livestock, and some are pathogenic to humans. More crop losses worldwide are caused by nematodes than

all arthropods combined. Most pet owners eventually encounter parasitic nematodes, as they are commonly seen in the feces and vomit of dogs and cats. The filarial worm, *Onchocerca volvulus*, is transmitted to humans through the bites of black flies and causes an eye disease called "river blindness" that is thought to infect nearly 40 million people in Latin America and Africa.

Nematodes (Greek *nema*, "thread"; *odes* "resembling") are vermiform blastocoelomates or acoelomates, with thin unsegmented bodies that are usually distinctly round in cross section (Box 19A). They possess digestive, nervous, reproductive, and excretory (though not of the nephridial type) systems but lack a discrete circulatory or respiratory system. To the untrained and unaided eye, most nematodes look very much alike, but there are significant variations in external body form, especially among the meiofaunal species (Figures 19.1 and 19.4). Although poorly known from the fossil record, a few species have been described from Early Cretaceous Lebanese amber, Late Cretaceous Burmese amber, and some Cenozoic amber. The earliest known unambiguous nematode is the lower Devonian *Palaeonema phyticum*. However, some specialists have suggested the Cambrian "Orsten" species *Shergoldana australiensis* might be a nematode or perhaps a member of the stem-group Nematoida, due to the similarity of its anterior end with that of nematomorphs.

BOX 19A Characteristics of the Phylum Nematoda

1. Triploblastic, bilateral, vermiform, unsegmented, and blastocoelic (or acoelic)
2. Body round in cross section and covered by a layered cuticle (chitin present in the pharyngeal cuticle of some species); growth in juveniles accompanied by cuticular molting until reaching the adult form; generally with four juvenile stages
3. Body wall with only longitudinal muscles (no circular muscles), with muscle arms
4. With unique cephalic sense organs (amphids); some with unique caudal sense organs (phasmids)
5. Complete digestive system; various oral structures arranged in radially symmetrical pattern
6. Most with unique secretory-excretory system, composed of one or two renette cells or a set of collecting tubules
7. Without special circulatory or gas-exchange structures
8. Epidermis cellular or syncytial, forming longitudinal cords housing nerve cords
9. Gonochoristic; wide range of reproductive modes
10. With unique cleavage pattern; not radial or spiral
11. Eutely present in at least some species (or some organs)
12. Found in marine, freshwater, and terrestrial environments, free-living and parasitic, sometimes with complex life cycles

Classification of Phylum Nematoda

Chitwood and Chitwood's 1933 anatomy-based classification of roundworms long prevailed, with a division of the phylum into Aphasmidia and Phasmidia, later changed to Adenophorea ("gland bearers") and

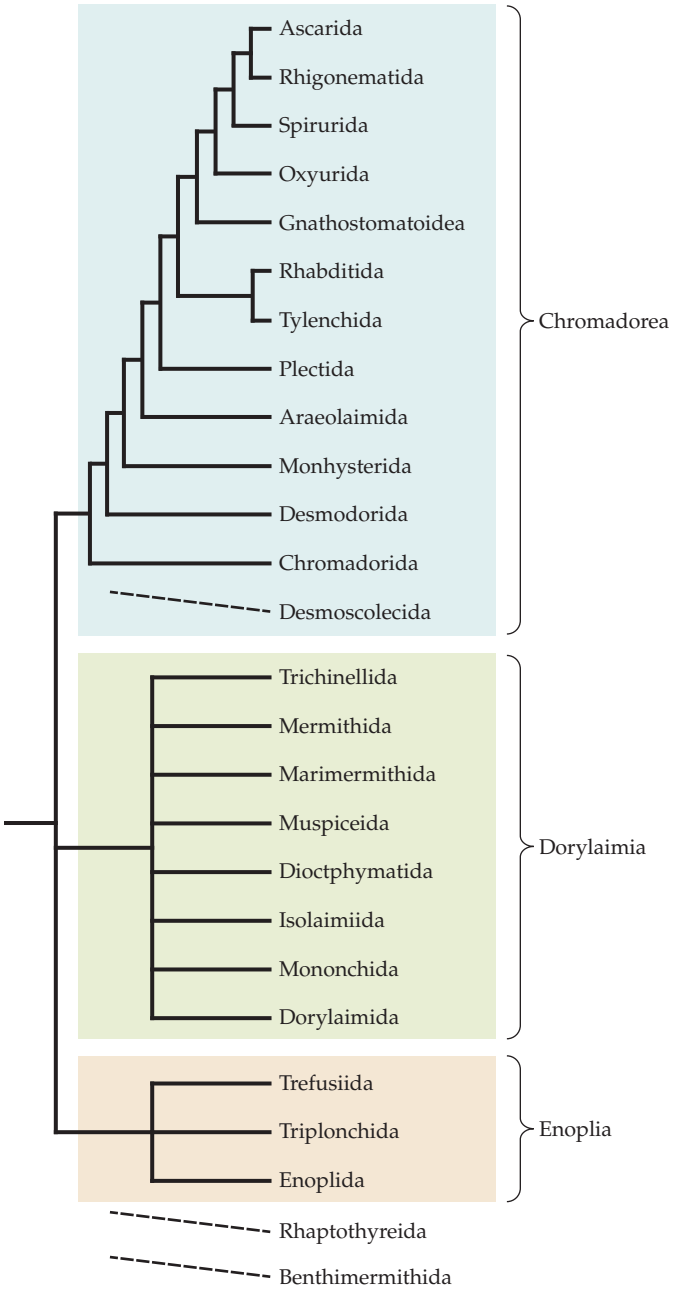

FIGURE 19.2 Nematoda molecular phylogenetic framework. Consensus phylogenetic view of Nematoda, combined from De Ley and Blaxter (2002), Sudhaus (2011), and Schmidt-Rhaesa (2014).

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Secernentea ("secretors"), respectively. More recent work, however, found Secernentea to be a derived clade within Chromadorea, whereas Adenophorea is probably paraphyletic (although the name is commonly still used). Molecular phylogenetics, bioinformatics, and digital communication technologies have substantially impacted nematode systematics over the past two decades. Blaxter et al. (1998) created the first molecular framework for the classification of Nematoda, using small subunit (SSU) rRNA sequences from 53 nematode species. Since then, SSU rRNA sequences available in public databases have increased enormously, some recent phylogenies have included over a thousand terminal taxa, and a phylogenomic analysis based on 56 nematode genomes has been published (International Helminth Genomes Consortium, 2019). (More than a hundred nematode genomes are currently available in public databases.) A new classification is emerging from the molecular data, but much more work remains to be done, as it fails to recognize many of the traditional nematode orders. The molecular framework confirms the presence of three principal early nematode lineages, named Chromadorea, Enoplia, and Dorylaimia (Figure 19.2), although the exact order of appearance of these three lineages (and relationships of their contained subclades) is not yet resolved. Thus, our consensus/working classification recognizes the three classes–Chromadorea, Enoplia, and Dorylaimia–and simply lists the major subclades alphabetically as orders. For a more detailed look at nematode classification, see De Ley and Blaxter (2002, 2004), Holterman et al. (2006), Meldal et al. (2007), and Schmidt-Rhaesa (2014), with some more recent changes based on genomics.

CLASS CHROMADOREA

- ORDER ARAEOLAIMIDA
- ORDER ASCARIDA
- ORDER CHROMADORIDA
- ORDER DESMODORIDA
- ORDER DESMOSCOLECIDA
- "ORDER GNATHOSTOMATIDA"
- ORDER MICROLAIMIDA
- ORDER MONHYSTERIDA
- ORDER OXYURIDA
- ORDER PLECTIDA
- "ORDER RHABDITIDA"
- ORDER RHIGONEMATIDA
- ORDER SPIRURIDA
- ORDER STRONGYLIDA
- ORDER TYLENCHIDA

CLASS ENOPLIA

- ORDER ENOPLIDA
- ORDER TREFUSIIDA
- ORDER TRIPLONCHIDA

CLASS DORYLAIMIA

- ORDER DIOCTOPHYMATIDA
- ORDER DORYLAIMIDA
- ORDER ISOLAIMIIDA
- ORDER MARIMERMITHIDA
- ORDER MERMITHIDA
- ORDER MONONCHIDA
- ORDER MUSPICEIDA
- ORDER TRICHINELLIDA

INCERTAE SEDIS

- BENTHIMERMITHIDA
- RHAPTOTHYREIDA

SYNOPSIS OF MAJOR GROUPS

CLASS CHROMADOREA With porelike or slitlike amphids, which vary from labial pores or slits to postlabial elaborate coils and spirals; cuticle usually annulated, sometimes ornamented with projections and setae; phasmids present or absent, generally posterior; esophagus usually divided into bulbs, with 3 to 5 esophageal glands; excretory system glandular or tubular, female with 1 or 2 ovaries.

ORDER ARAEOLAIMIDA A large clade with ~400 described species; mainly marine, but some species in humid terrestrial habitats. *Aphanolaimus*, *Araeolaimus*, *Odontophora*, *Sabatieria*, etc.

ORDER ASCARIDA (= ASCARIDIDA) Parasitic in the small intestines or lungs of mammals; including the human parasite *Ascaris lumbricoides* (the most common human helminth infection worldwide) and the pig parasite *A. suum*.

ORDER CHROMADORIDA Marine, free-living (occasionally in fresh water or soil). *Acantholaimus* (mostly in deep sea), *Achromadora* (on mosses and wet soils), *Chromadora*, *Chromadorita*, *Euchromadora*, *Neochromadora*, *Paracanthonchus*, etc.

ORDER DESMODORIDA Very large order of almost solely marine nematodes that includes the subfamily Stilbonematinae, long threadlike roundworms covered with a layer of symbiotic chemolithoautotrophic prokaryotes. *Aponema*, *Draconema*, *Desmodora*, *Ethmolaimus*, *Globodera*, *Heterodera*, etc.

ORDER DESMOSCOLECIDA Small to minute, free-living, almost exclusively marine (some

freshwater and moist soil species in the genus *Desmoscolex*). Most species recognizable by an annulated cuticle covered with minute mineral particles. *Desmoscolex*, *Greeffiella*, etc.

"ORDER GNATHOSTOMATIDA" Some workers put this cosmopolitan group within the order Spirurida, but this has not been supported by recent molecular studies. And, despite some anatomical features that seemed to unite the gnathostomatidans, the grouping is almost certainly artificial, and further studies are necessary to unravel the phylogenetic relationships of its genera. These are large, 2–6 cm or longer worms with distinctive pseudolabia that may bear teeth or long ramified appendages; the pseudolabia allow for retraction and expansion of the head in many genera. All are parasites, the hosts typically being aquatic and cold-blooded vertebrates, although the genus *Gnathostoma* is parasitic in mammals. Adult worms usually burrow into the mucosa of the host's stomach or intestine, or in sea otters into the esophagus or kidneys. In two nonmarine genera, *Gnathostoma* and *Spiroxys*, embryogenesis is known to occur in fresh water, and the motile second-stage juveniles (J2) are ingested by copepods (the obligatory intermediate hosts), where they develop into the infective third stage (J3) in the coelomic cavity. J3 stages re-encapsulate in the muscles and mesentery of the final host.

ORDER MICROLAIMIDA Lacking any known anatomical synapomorphies. Cuticle striated, annulated, smooth or punctate; buccal cavity usually with more or less pronounced dorsal tooth and smaller subventral teeth. Erected by Leduc et al. (2017), on the basis of molecular studies, to house the rare, free-living marine Paramicrolaimidae as well as *Molgolaimus* (formerly in Desmodorida and not included in our tree).

ORDER MONHYSTERIDA A large and complex lineage of roundworms with nearly 1,000 described species. Marine, freshwater, and terrestrial. *Astomonema*, *Gammarinema* (known only from the gill chambers of malacostracan Crustacea), *Linhomoeus*, *Parastomonema*, *Rhynchonema*, *Theristus*, etc.

ORDER OXYURIDA Pinworms usually parasitic in the guts of vertebrates, comprising 4 families and including the human pinworm, *Enterobius vermicularis*. Known from almost every primate genus. The life cycle is direct, with no free-living stage; transmission occurs through ingestion of eggs. Also *Gyrinicola, Oxyuris*, *Skrjabinema*, *Syphacia*, *Trypanoxyuris*, etc.

ORDER PLECTIDA An enigmatic order that may be paraphyletic; many marine species, as well as some in fresh water, soil, fungal mats, rotting wood, and thermal springs. *Anaplectus*, *Aphanolaimus*, *Deontolaimus* (*D. monohysteria* is a commensal in the gill chamber of the terrestrial hermit crab *Coenobita scaevola* in the Indian Ocean); also *Chronogaster*, *Leptolaimus*, *Metateratocephalus*, *Plectus*, *Tylocephalus*, etc.

"ORDER RHABDITIDA" Rhabditids comprise a large, nonmonophyletic group of saprobic or bacterivorous roundworms living in many types of organic matter, such as decomposing plants, algal deposits on beaches, decaying fruits, rotting cacti, material from frass tunnels of insects, dung of vertebrates, and cadavers of invertebrates and vertebrates. In various rhabditid lineages physiological adaptations to living in ephemeral terrestrial habitats and to life cycles in tight association with other animals have generated a set of features that facilitated the evolution of parasites in arthropods, molluscs, and vertebrates. *Caenorhabditis elegans* is an important model species, whereas species of *Heterorhabditis* are used as biocontrol agents of pest insects. Many rhabditid species are cosmopolitan. In one lineage, the diplogastrids, the first molt takes place within the embryonic eggshell (e.g., *Butlerius*, *Koerneria*, *Odontopharynx, Pristionchus*). We include two superfamilies, Anguillicoloidea and Camallonoidea (sometimes placed in a separate order, Camallanida), among the Rhabditida. Anguillicoloids are parasites in the swim bladders of freshwater eels; camallonoids are parasites in the guts of predatory vertebrates. Other important genera include *Camallanus*, *Cucullanus*, *Cephalobus*, *Myolaimus*, and *Steinernema.*

ORDER RHIGONEMATIDA Recent molecular analyses have not supported older views of rhigonematids as a family of Oxyurida, nor Ascarida, and this poorly understood and mostly parasitic group is treated as an order until further resolution can be obtained. *Brumptaemillus*, *Rhigonema*, *Zalophora*, etc.

ORDER SPIRURIDA Gut and tissue parasites of vertebrates (except fishes) that typically utilize an invertebrate intermediate host. In the superfamily Filarioidea (parasites of amphibians, reptiles, birds, and mammals), the eggs are thin shelled, like a sheath, and contain the miniaturized first-stage juvenile (J1), the infective **microfilaria** (e.g., *Brugia*, *Dracunculus*, *Onchocerca*, *Loa*, *Mansonella*, *Pelecitus, Wuchereria*). Filariae are tissue or cavity dwellers and can be anywhere in the host (coelomic cavity, blood and lymphatic vessels, subcutaneous tissues, the surface of the skin, the brain, etc.). Filarial nematodes are transmitted by blood-feeding arthropods, most often dipterans such as mosquitoes, midges, and simuliid and tabanid flies.

ORDER STRONGYLIDA The "bursate nematodes" are a monophyletic taxon characterized by an expansion of the tail in males as a copulatory organ, the caudal bursa. Early molecular studies suggest strongylids may be a clade within the larger order Rhabditida, and hence are not included in our phylogenetic tree. The supporting rays of the bursa are the channels through which nerve tissue runs to sensory papillae at the extremities. The bursa is divided into paired ventral and lateral lobes, with a single median dorsal lobe (these lobes may be variously fused). A large order (420 genera) with many important parasitic species, including the "hookworms" (family Ancylostomatidae, parasites

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of mammals). Two common hookworm infections in humans are caused by the species *Ancylostoma duodenale* (Old World hookworm) and *Necator americanus* (New World hookworm). Hookworm eggs are deposited in the stools of infected people. If these end up in the environment, they can hatch into juvenile worms, which can then penetrate the skin. One type can also spread through contaminated food. Risk factors include walking barefoot in warm climates where sanitation is poor. Species in this order infest all classes of terrestrial vertebrates on all continents, primarily as gastrointestinal parasites but also as pulmonary infections. Some species of *Stephanurus* infect the renal system of squids. The families Chabertiidae and Haemonchidae are of importance in livestock and ruminant health. Most strongylid life cycles are direct, with the host infection occurring by ingestion or skin penetration by the third juvenile stage (J3). Some species use molluscs or annelids as intermediate hosts. Lungworms (suborder Metastrongylina) infect the respiratory system, and occasionally other tissues, of mammals; eggs or juveniles released by female worms are carried in the blood and lodge in pulmonary capillaries, the juveniles breaking into the alveoli and eventually ascending the trachea, there being swallowed to pass into the feces. Also *Oesophagostomum*, etc.

ORDER TYLENCHIDA The largest and most economically important group of plant-parasitic nematodes, tylenchids have diverged to exploit all plant parts (one group even parasitizes the hemocoel of arthropods). Economically important genera include *Anguina* (seed galls, etc.), *Globodera* (pathogens of potatoes and other Solanaceae), *Pratylenchus* and *Meloidogyne* (root endoparasites that attack bananas, cereals, coffee, corn, legumes, and many fruits), *Hirschmanniella* (important rice pathogens), *Tylenchulus* (citrus parasite), and *Rotylenchulus* (a cotton pathogen). Also *Allantonema*, *Anguina*, *Aphelenchus*, *Bursaphelenchus*, *Criconema*, *Helicotylenchus*, *Sphaerulariopsis*, etc.

CLASS ENOPLIA With pocketlike amphids, not spiral, usually postlabial; cuticle smooth or finely striated; phasmids present or absent; esophagus cylindrical or bottle shaped with 3 to 5 esophageal glands; simple nontubular excretory system, usually a single cell; female generally with 2 ovaries; male generally with 2 testes.

ORDER ENOPLIDA A large and diverse taxon of large-bodied, mostly marine species (a few freshwater and terrestrial species are known). *Belbolla*, *Bernardius*, *Enoplus*, *Halalaimus*, *Oncholaimus*, *Oxyonchus*, *Syringolaimus*, *Viscosia*, etc.

ORDER TREFUSIIDA The orders Trefusiida and Triplonchida were once viewed as subgroups within the order Enoplida, but this has not been supported by recent molecular studies, which tend to place the lineages as coequal in an unresolved trichotomy. *Trefusia*, *Tripylina*, *Trischistoma*, etc.

ORDER TRIPLONCHIDA A large and diverse group of mostly free-living species found in nearly every habitat on Earth. Many soil, moss, freshwater, marine, and subterranean species, including a large radiation in Lake Baikal. *Trichodorus, Paratrichodorus* (vectors of plant-pathogenic tobraviruses), *Tobrilus*, and many others.

CLASS DORYLAIMIA A clade suggested by recent molecular phylogenetic studies.

ORDER DIOCTOPHYMATIDA A small clade of vertebrate parasites, especially in carnivorous mammals and birds; humans can be accidently infected. About 20 species, including the giant kidney worm *Dioctophyme renale* with body length exceeding 1 m (the second-largest known nematode). *Dioctophyme. renale* infects carnivorous mammals and occasionally others (horses, cows) and rarely humans; the infective third-stage juveniles (J3) occur in oligochaetes, which are consumed by the final hosts. Also *Eustrongylides*, *Hystrichis*, *Soboliphyme* (with its impressive cephalic sucker), etc.

ORDER DORYLAIMIDA A diverse order (18 families; over 2,640 described species), all free-living except plant parasites of the family Longidoridae, and found in nearly every habitat on Earth. Soil species can be highly diverse (100 g of soil may contain more than a dozen species in temperate regions); 0.3 to 1 cm long. Some free-living species are vectors of plant parasites. *Dorylaimus*, *Eudorylaimus*, *Longidorella*, *Tylencholaimus*, *Xiphinema*, etc.

ORDER ISOLAIMIIDA A monogeneric order, *Isolaimium*, with 12 described species of free-living terrestrial roundworms. Phylogenetic placement of this order is unclear.

ORDER MARIMERMITHIDA Rare parasites of marine invertebrates during their juvenile stage; adult worms free-living. Very large, 1 to 15 cm long. Seven described species. Worldwide at all depths. *Aborjinia*, *Marimermis*, *Thalassonema*, etc.

ORDER MERMITHIDA Large insect parasites; emerge from their hosts as postparasitic juveniles that undergo a final molt to reach the adult stage. *Hexamermis*, *Mermis*, etc.

ORDER MONONCHIDA Free-living soil and freshwater nematodes; ~460 described species, 1 to several millimeters in length. *Anatonchus*, *Clarkus*, *Iotonchus*, *Miconchus*, *Mylonchulus*, etc.

ORDER MUSPICEIDA Poorly known, mostly tiny parasites in the skin, eyes, and vascular and muscular sysems of vertebrates. Lacking phasmids (their caudal glands were once interpreted as phasmids). Nine genera, including *Maseria*, *Muspicea*, and *Robertdollfusa*.

ORDER TRICHINELLIDA (= TRICHOCEPHALIDA) Parasites of vertebrates. *Huffmanela*, *Trichinella*, *Trichina, Trichuris,* etc.

INCERTAE SEDIS

ORDER BENTHIMERMITHIDA Rare marine nematodes, in littoral to deep sea. Juveniles typically parasitic in various invertebrates; adults free-living and nonfeeding, ranging in size from <1 mm to over 17 cm. *Trophomera*, etc.

ORDER RHAPTOTHYREIDA Rare marine nematodes found at depths of 800 to 4,600 m. Mouth and gut vestigial, amphids large and featherlike; thought to live symbiotically with autotrophic prokaryotes (as seen in siboglinid worms and their chemoautotrophic bacterial symbionts). Once placed in the class Enoplea, molecular studies have left its relationships uncertain. Two species: *Rhaptothyreus typicus* and *R. minor*.

The Nematode Body Plan

Body Wall, Support, and Locomotion

Nematodes possess a relatively conserved basic body plan that consists of an external cylinder (the body wall) and an internal cylinder (the digestive system), which are separated by a blastocoelic (pseudocoelomic) body cavity filled with fluid under pressure, although in some small species this cavity does not exist. The blastocoel is not lined by mesodermally derived

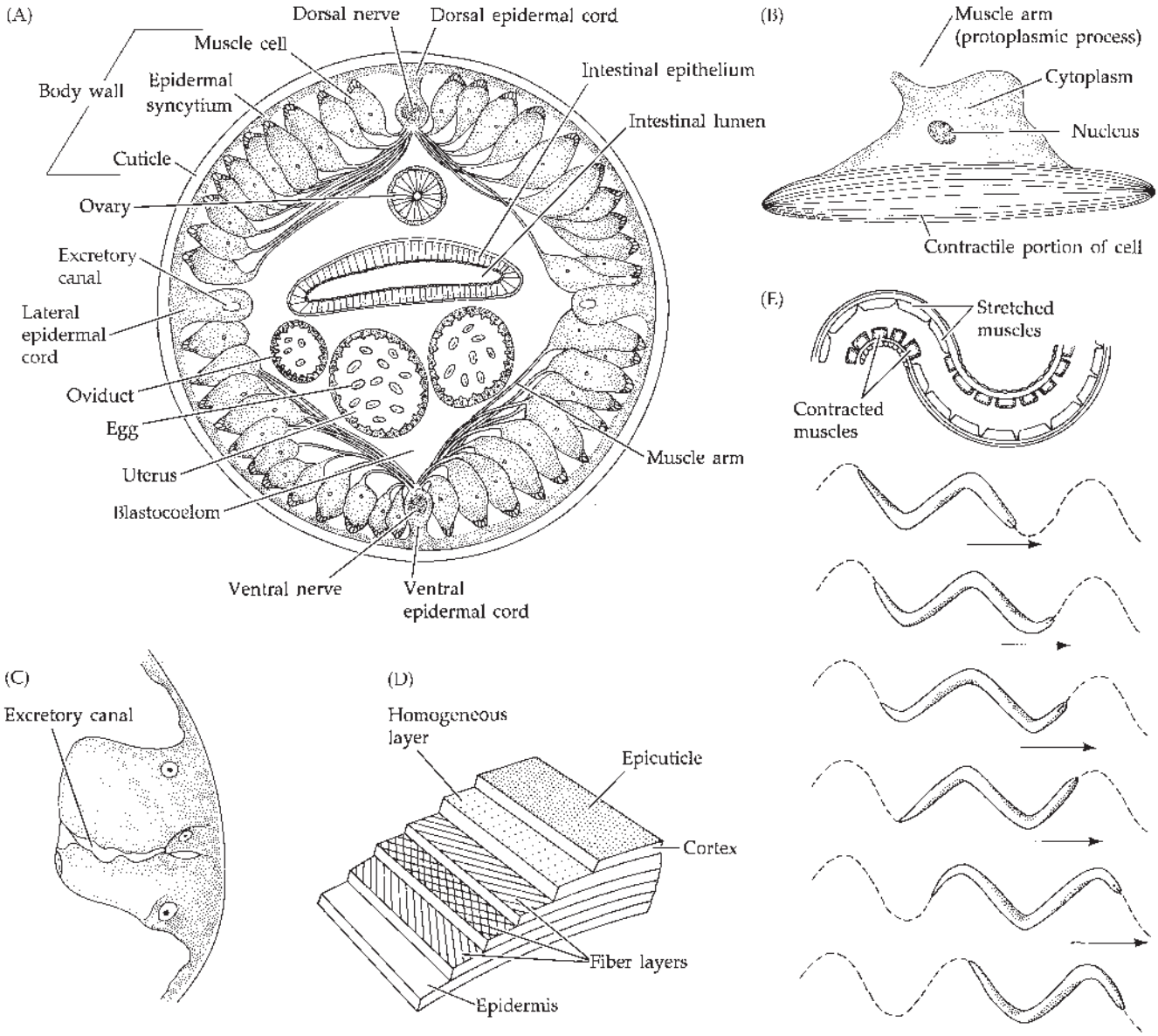

FIGURE 19.3 Selected anatomical and locomotory features of nematodes. (A) Stylized section through a female nematode such as *Ascaris*. (B) A single longitudinal muscle cell, illustrating the origin of the muscle arm. (C) The lateral epidermal cord of *Cucullanus* (order Rhabditida). (D) The layers of the cuticle. (E) Undulatory locomotion in a free-living nematode results from the action of the longitudinal muscle fibers. The concave areas along the body represent positions of muscle contractions; the convex areas are regions of the muscle stretching. Leverage is gained against surrounding objects of the substratum in the environment.

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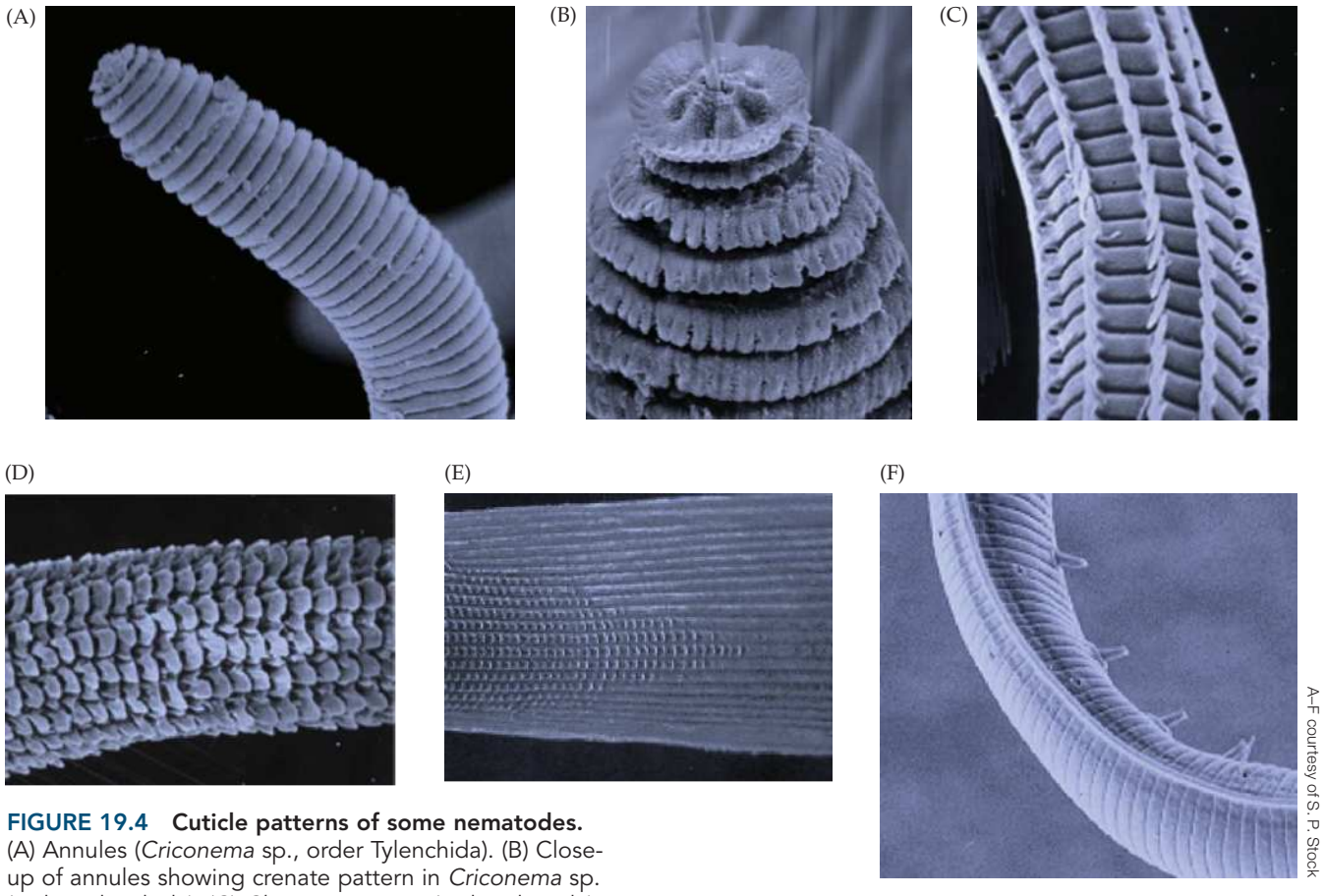

A–F courtesy of S. P. Stock

FIGURE 19.4 Cuticle patterns of some nematodes. (A) Annules (*Criconema* sp., order Tylenchida). (B) Close-up of annules showing crenate pattern in *Criconema* sp. (order Tylenchida). (C) *Chronogaster* sp. (order Plectida). (D) Scalelike ornamentation of annules (criconematid nematode, order Tylenchida). (E) Tessellate pattern and longitudinal striae (*Heterorhabditis* sp., infective juvenile stage, order Rhabditida). (F) Transverse striae and tubular supplement (order Plectida).

epithelium. As in other ecdysozoans, the nematode body is covered by a well-developed and complexly layered cuticle secreted by the epidermis and lacking motile cilia (Figures 19.3 and 19.4). The outermost cuticle layer, the **epicuticle**, secretes a **glycocalyx** surface coating that protects the worm from microbial predators and parasites, and it might facilitate locomotion by lubrication. The cuticle forms a flexible exoskeleton that invaginates at the mouth, cloaca, and rectum as well as at the amphids, phasmids, secretory-excretory pore, and vulva. The cuticle is mainly composed of lipids and proteins associated with mucopolysaccharides. Collagen, a structural protein, is the major component of the cuticle (>80%). Nematodes lack chitin in their cuticle, except for the pharyngeal cuticle of some species (chitin also occurs in the eggshell). As well as serving as an antagonist for the contraction of the longitudinal muscles, the cuticle is semipermeable and plays a role in the secretion-excretion or uptake of substances. The cuticle is also responsible in part for allowing nematodes to live in hostile environments, such as dry terrestrial soils and the digestive tracts of host animals, for it drastically reduces the permeability of the body wall. Predominantly terrestrial or parasitic nematodes usually have a dense, fibrous inner layer of the cuticle, whereas most of the free-living marine and freshwater forms lack this inner layer.

The cuticle is a complex structure, and it is highly variable among nematodes. It may be relatively smooth, or covered with sensory setae and wartlike bumps. The cuticle in many roundworms has rings or **annules**, or it is marked with longitudinal ridges and grooves (Figure 19.4). In many marine forms, it contains radially arranged rods, punctuations, or other inclusions of various shapes. As a nematode grows, it sheds its cuticle and grows a new one through a series of four molts (the first occurs within the egg membrane in some species) during its lifetime. Thus, the intermolt (instar) stages are called J1 through J4, which is followed by the adult. Although molting is likely induced by a steroid hormone, the exact nature of the hormone is not yet known (the steroid ecdysone triggers molting in arthropods). The new, postmolt cuticle commonly has epidermal folds (plicae) over which the new cuticle becomes highly convoluted, enabling the worm to increase in length in an accordionlike manner after ecdysis.

The epidermis (which is sometimes called the "hypodermis") varies among the different taxa, from cellular to syncytial, but is typically thickened into unique dorsal, ventral, and lateral **longitudinal cords** (Figure 19.3A,C). The dorsal and ventral cords house

longitudinal unpaired nerve cords, whereas the lateral thickenings contain excretory canals (when present, as in *Ascaris*) and neurons. Internal to the epidermis is a relatively thick layer of obliquely striated longitudinal muscle arranged in four quadrants. The muscles are connected to the dorsal and ventral nerve cords by unique extensions called **muscle arms** (Figure 19.3A,B). This arrangement is different from the usual neuromuscular junctions in most other animals; in nematodes the connections are made by special extensions of the muscle cells rather than of the neurons. Each neuron can receive many, even hundreds of muscle arms. Oddly, a similar condition apparently exists in some echinoderms and in the cephalochordate *Branchiostoma*, presumably cases of convergent evolution. Also, in some nematomorphs, kinorhynchs, platyhelminths, annelids, and gastrotrichs the longitudinal body wall muscles bear extensions similar to the nematode muscle arms. Whether these are homologous or convergent has not been thoroughly studied. There is no circular muscle layer in nematodes, nor in nematomorphs, a condition viewed as homologous by most workers.

The fluid-filled blastocoelom is not spacious. The apparently large body cavity seen in many laboratory specimens is often an artifact caused by shrinkage of tissues in alcohol. Modern microscopy techniques reveal that the organs of most nematodes occupy nearly all of the internal space, and in very small species the cavity may be entirely obliterated. However, in large species such as *Ascaris* a discernable blastocoel is clearly present. The cuticle provides most of the body support in nematodes. In the absence of circular body wall muscles, some types of locomotion, such as peristaltic burrowing, are impossible. Nematode movements depend on waves of muscle contractions, which travel backward along the body. These movements drive the worm forward, whether it is swimming through water or crawling through soil particles or animal or vegetal tissues. These contractions of the longitudinal muscles produce a whiplike undulatory motion (Figure 19.3E). Among the free-living nematodes this movement pattern relies on contact with environmental substrata, against which the body pushes. The muscles act against the hydrostatic skeleton and the cuticle, which serve as antagonistic forces to the muscle contractions. When placed in a fluid environment and deprived of contact with solid objects, benthic nematodes thrash about rather inefficiently. Some actually do swim (but not very well), and some are able to crawl along using various cuticular spines, grooves, ridges, and glands to gain purchase on the substratum (Figures 19.1E,H and 19.4).

Feeding and Digestion

The vast range of environments inhabited by nematodes is paralleled by the diversity of feeding habits and associated anatomical and behavioral adaptations. Many infaunal nematodes are direct deposit feeders. Others are detritivores or microscavengers, living in or on dead organisms or fecal material. Many of these species apparently do not feed directly on the carcasses they inhabit, but feed on the microorganisms (fungi and bacteria) that grow in the decomposing organic matter. Many free-living nematodes are predatory carnivores, feeding on a variety of other small animals, including other nematodes. Others feed on diatoms and other protists. Plant parasitic nematodes use a specialized oral structure, the **stylet**, to pierce individual root cells and suck out the contents (Figure 19.5F). The high species diversity of nematodes (and other small animals) in the marine meiofaunal habitat has puzzled ecologists for decades. Stable-isotope studies have shown that tidal flat meiofaunal nematodes utilize at least three different trophic levels (from primary to tertiary consumers) and that omnivory and herbivory (mainly on diatoms and dinoflagellates) predominate.

Bacterial symbioses occur in some nematodes. For example, species of *Astomonema* and *Parastomonema* that inhabit sulfur-rich sediments harbor chemoautotrophic bacteria in their highly reduced guts. These worms meet their nutritional requirements by absorbing some of the metabolic products of the bacteria. Some other nematodes (family Stilbonematidae) inhabit sulfide-rich oxygen-poor sediments, where symbiotic bacteria coat their cuticle. These nematodes are able to twist themselves in such a way that they can feed on the bacteria "farmed" on their body surface.

Insect pathogenic nematodes (e.g., Steinernematidae and Heterorhabditidae) carry gram-negative bacteria in their intestines that help them kill their insect hosts. The bacteria, once introduced into the host, grow and reproduce to become food for the nematode, which also grows and reproduces in the insect cadaver.

FIGURE 19.5 Modifications of anterior end among selected nematodes. (A) Frontal view of a generalized nematode. Note basic radial symmetry of the parts. (B) Anterior end (face view) of a typical free-living nematode showing four cephalic papillae and six symmetrical lips each bearing a labial papilla and lateral amphids. (C) Anterior end of *Anaplectus* sp. (order Plectida), a free-living freshwater nematode, showing a circular amphid and the cephalic papillae. (D) Anterior end of *Draconema* sp. (order Desmodorida), a free-living marine nematode showing an amphid and multiple setae. (E) Anterior end of *Cervidellus* sp. (order Rhabditida), a free-living soil nematode, showing probolae (used for sorting of food). (F) Anterior end of *Dorylaimus* sp. (class Dorylaimia), a free-living soil nematode, showing the protruded stylet used to puncture prey. (G) Anterior end of *Ancylostoma caninum* (order Strongylida), a vertebrate parasite, showing cuticular teeth that are used like a lathe on the host's intestine. (H) Anterior end of *Aphanolaimus* sp. (order Areolaimida), a free-living freshwater nematode, showing a large spiral amphid and long cephalic papillae.

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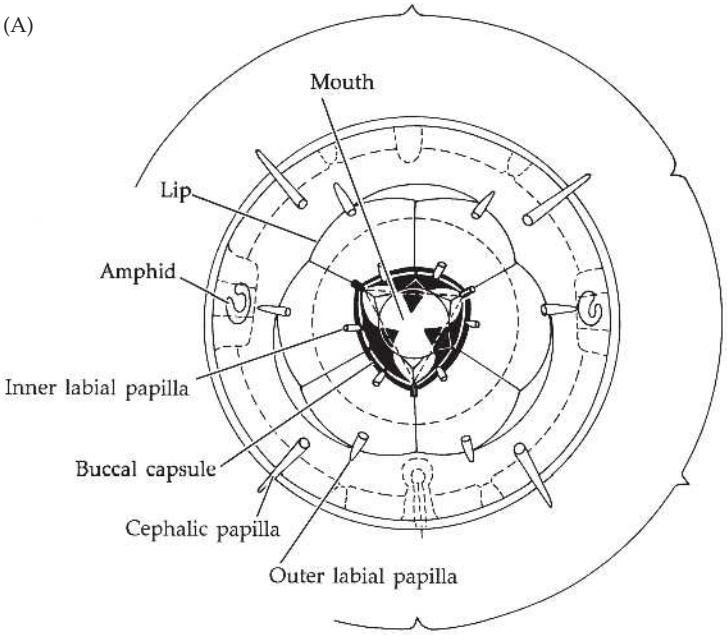

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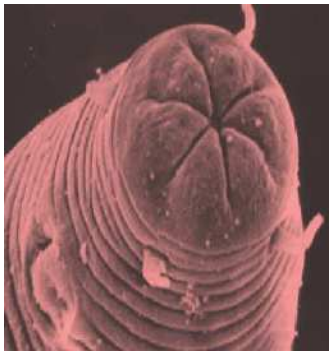

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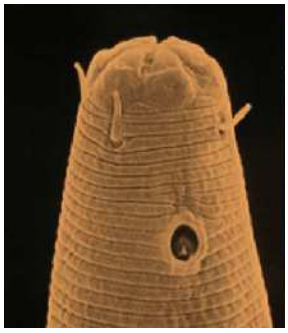

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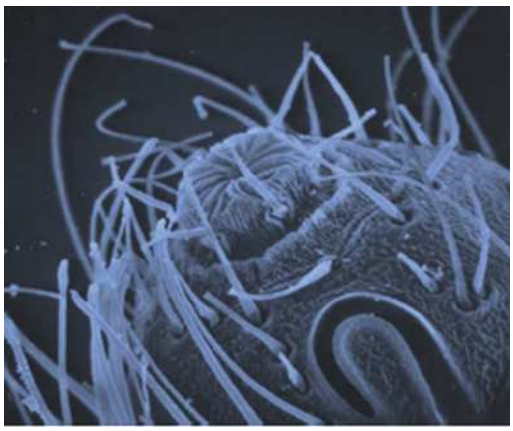

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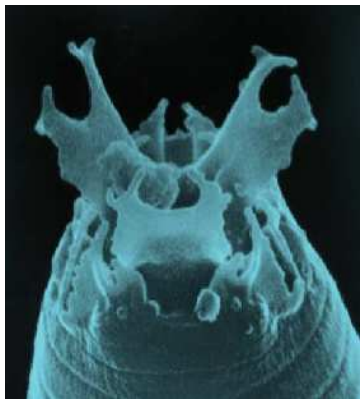

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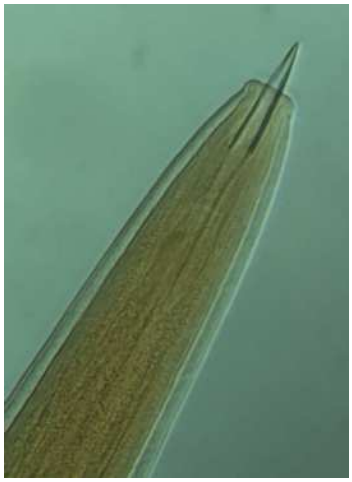

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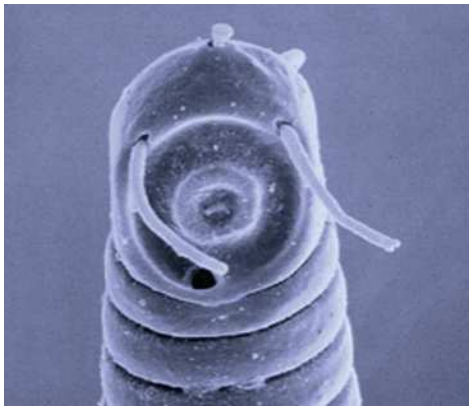

Nematode parasites have been described from every major group of plants and animals, and they have evolved a multitude of life history patterns. In invertebrates and vertebrates (including humans), nematodes subsist on a variety of body fluids and organs, where they can cause extreme tissue damage. The well-known human parasite *Ascaris lumbricoides*, the most common parasitic worm in humans, can grow to 35 cm in length.

Nematode digestive tracts vary greatly in complexity and regional specialization. The anteriorly located mouth is usually surrounded by **lips** (one dorsal and two ventral parts, some or all of which may be fused together and may form elaborate prolongations), with each lip typically bearing a papilla (Figure 19.5). **Labial probolae** are flaplike cuticular processes surrounding the mouth opening in many cephalobid nematodes—there are three flaps, one dorsal and two subventral. **Cephalic probolae** are simple or complex cuticular processes arising from the lips in many cephalobid nematodes; there are six in total—two lateral, two subdorsal, and two subventral. Lips, labial and cephalic probolae, spines, teeth, jaws, and other armature are arranged in radially symmetrical patterns (Figure 19.5). The mouth leads to a buccal cavity or **stoma**, the shape of which is variable depending on the feeding habits of the nematodes. The stoma connects to the muscular pharynx (Figure 19.6).

The basic structural features of the pharynx, sometimes called an esophagus by nematologists, are a triradiate lumen, muscles, one or more valves, and dorsal and ventral glands and neurons. The pharynx is elongate and may be subdivided into distinct muscular and glandular regions, the details of which are of considerable taxonomic importance (Figure 19.6A–G). The muscles of the pharynx pump food material from the buccal cavity into the intestine. The pharyngeal cuticle can have chitin. In most nematodes the intestine is a simple tube composed of a single layer of cells ensheathed by a basal lamina. In some cases it is possible to discern an anterior, middle, and posterior region of the intestine. The posterior portion of the intestine leads to a short proctodeal (i.e., ectodermally derived) rectum and a subterminal anus on the ventral surface of the body (Figure 19.6L). In males the rectum opens up into a cloaca, which also receives products of the reproductive system. The ventral side of a roundworm can be recognized by the presence of the vulva (egg-laying organ) and anus in females or by the cloacal opening in males.

The esophageal glands and the midgut lining secrete digestive enzymes into the intestinal lumen. Initial digestion is extracellular; final intracellular digestion occurs in the intestine, following absorption across the surfaces of the microvilli of the intestinal cells (Figure 19.6K). In mermithid nematodes (most of which are parasites of insects) the pharynx is modified as a **stichosome**, a region of large glandular cells (sometimes called stichocytes) important in protein synthesis. In mermithids, modification of the intestine creates a **trophosome**, a region of enlarged, solid cells that form a closed food storage organ.

FIGURE 19.6 Nematode anatomy. (A–G) Variation in pharynx structure gut anatomy among different nematodes. Note the different degrees of regional specialization. (A) Cylindrical pharynx (*Mononchus*, order Mononchida). (B) Dorylaimoid pharynx (*Dorylaimus*, order Dorylaimida). (C) Bulboid pharynx (*Ethmoliamus*, order Desmodorida). (D) Rhabditoid pharynx (*Rhabditis*, order Rhabditida). (E) Diplogasteroid pharynx (*Diplogaster*, order Rhabditida). (F) Tylenchoid pharynx (*Helicotylenchus*, order Tylenchida). (G) Aphelenchoid pharynx (*Aphelenchus*, order Tylenchida). (H) Anterior end of *Rhabditis* (order Rhabditida), a free-living soil bacterivore showing tubular stoma (lateral view). (I) Anterior end of *Mononchus* (order Mononchida), free-living predatory soil nematode showing cylindrical stoma (lateral view). (J) Anterior end of *Caenorhabditis elegans* (order Rhabditida). (K) Intestinal epithelium of *Ascaris* (order Ascarida). (L) Digestive tract and reproductive system of *Steinernema* female (order Rhabditida).

Circulation, Gas Exchange, Excretion, and Osmoregulation

Nematodes have no specialized circulatory or gas exchange structures. As in many other very small invertebrates, particularly blastocoelomates, diffusion and movement of body cavity fluids accomplish these functions. Some parasitic nematodes possess a form of hemoglobin in these fluids that presumably transports and stores oxygen. Both aerobic and anaerobic metabolic pathways are found among the nematode groups, and many of these worms are able to shift from one mechanism to the other according to environmental oxygen concentrations. Facultative anaerobiosis is surely significant in parasitic nematodes and those that live in other anoxic environments. The blastocoelom serves as a circulatory system, transporting molecules such as CO_2 from the tissues of origin (mostly muscle and reproductive tissue) to the epidermis and intestine for excretion into the environment.

Nematodes have no nephridial structures known to be homologous to those of other metazoans, and soluble waste products are apparently concentrated prior to their elimination. For this purpose they have unique excretory structures, unlike the protonephridia of other protostomes (Figure 19.7). The presumed ancestral condition occurs in certain free-living taxa and has been modified among other groups, especially within specialized parasitic forms. In many free-living threadworms, the system comprises one or two glandular **renette cells** that connect directly to a midventral excretory pore (Figure 19.7A,E,F), and sometimes a third cell forms an ampulla at the opening. Modifications to this system often include

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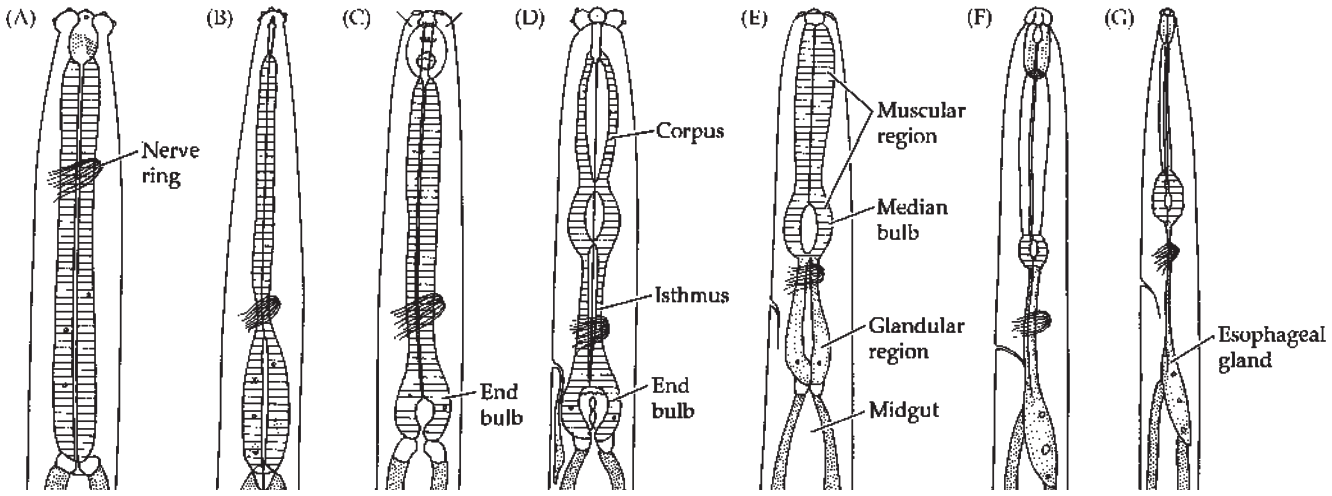

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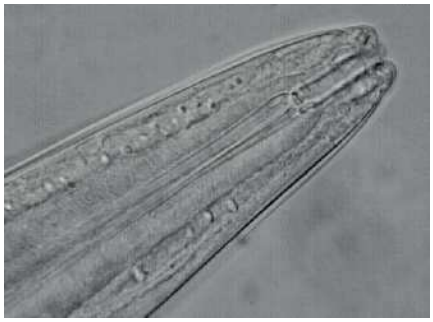

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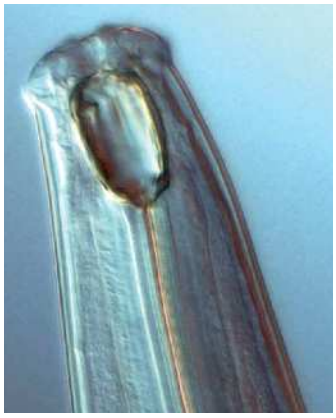

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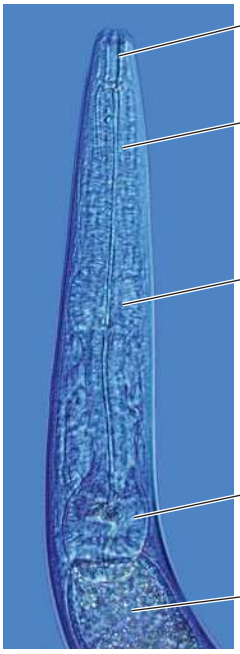

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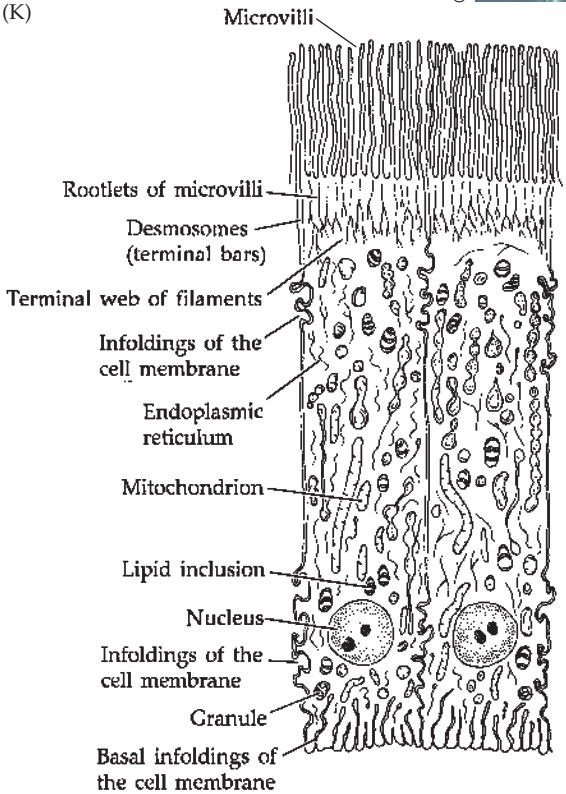

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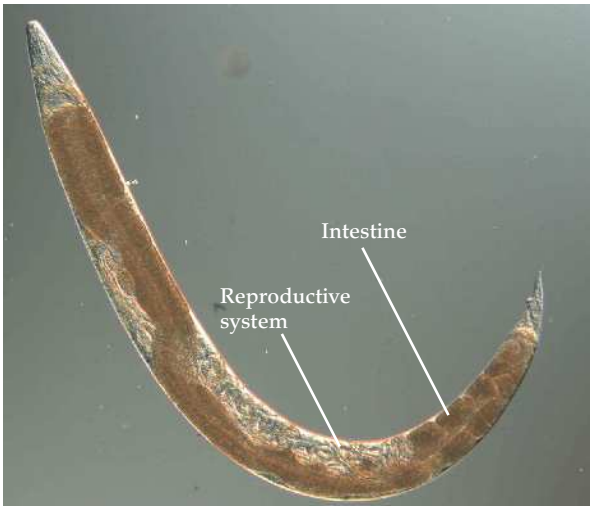

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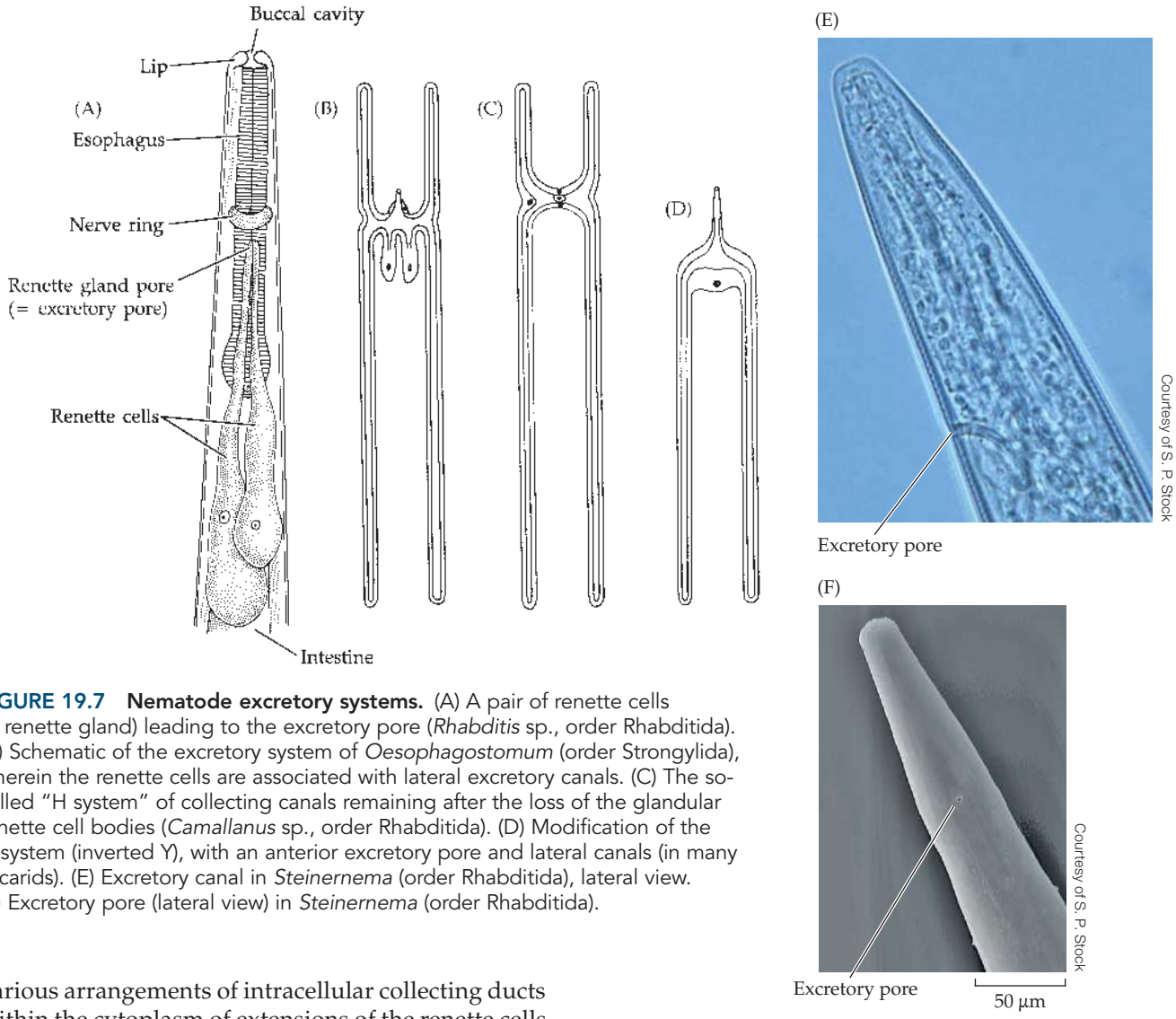

FIGURE 19.7 Nematode excretory systems. (A) A pair of renette cells (= renette gland) leading to the excretory pore (*Rhabditis* sp., order Rhabditida). (B) Schematic of the excretory system of *Oesophagostomum* (order Strongylida), wherein the renette cells are associated with lateral excretory canals. (C) The so-called "H system" of collecting canals remaining after the loss of the glandular renette cell bodies (*Camallanus* sp., order Rhabditida). (D) Modification of the H system (inverted Y), with an anterior excretory pore and lateral canals (in many ascarids). (E) Excretory canal in *Steinernema* (order Rhabditida), lateral view. (F) Excretory pore (lateral view) in *Steinernema* (order Rhabditida).

various arrangements of intracellular collecting ducts within the cytoplasm of extensions of the renette cells (Figure 19.7B). In many parasitic species the renette cell bodies are lost completely, leaving only the system of tubules in an H or inverted Y pattern (Figure 19.7C,D). Many members of the class Enoplia lack renette cells altogether. Instead they have numerous unicellular units distributed along the entire length of the body, each cell opening to the outside via a duct and a pore. It has been suggested that if these ducted cells are excretory in function, they might represent nonciliated protonephridia, but good evidence of this has not been found. In some species the renette cells secrete a substance used by the roundworm to attach to the substrate. In all cases, these excretory structures probably also function in osmoregulation.

Most nematodes are ammonotelic, although some excrete increased amounts of urea when in a hypertonic environment. Apparently much of the loss of nitrogenous wastes is across the wall of the midgut, and the renette cells are primarily osmoregulatory. Water balance is also aided by the activities of other tissues, organs, and structures. In some roundworms, the cuticle is differentially permeable to water in that it allows water to enter but not to leave the body. This condition is advantageous under conditions of potential desiccation, but it presents problems in hypotonic environments where excess water must be eliminated; such elimination is apparently accomplished by the renette cells (when present), by the gut lining, and by the epidermis.

Nervous System and Sense Organs

The classic studies of nematode neuroanatomy were by R. Hesse (1892) and R. Goldschmidt (1908, 1909) who showed that nematodes have 250 to 302 neurons, and their position and structure is roughly the same throughout the phylum (Figures 19.8 and 19.9A,B). Today we know more about the nervous system of *C. elegans* than any other animal, the adult hermaphrodite of this species having exactly 302 neurons, each with a predictable cell lineage. Similarly, *Ascaris suum* females have 298 neurons, also with invariant identity and structure.

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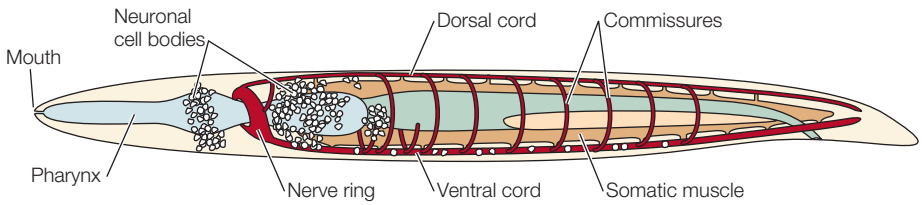

FIGURE 19.8 **The nematode nervous system.**

Nematodes have a simple circumoral nerve ring that encircles the pharynx, composed mainly of axonal and dendritic processes of neurons whose cell bodies lie in bundles anterior and posterior to the ring itself. These bundles are encased in a lamina and often referred to as ganglia, but unlike the ganglia of most other animals, they do not contain a **neuropil** (a network of interwoven nerve fibers and synapses, together with glial filaments, that characterize most bilaterians), only cell bodies. Associated with the nerve ring are longitudinal nerves that extend anteriorly and posteriorly. The anterior nerves (six in total) connect with cephalic sensory organs (sensilla) and labial papillae in the anterior end, arranged in a sixfold symmetry around the mouth. These structures have the nature of mechanoreceptors and chemoreceptors. **Amphids** (= amphid sensilla) are paired organs located laterally on the head. They consist of an external pore leading inward to a short duct and amphidial pouch. The pouch is associated with a unicellular gland and an amphidial nerve from the cerebral nerve ring (Figure 19.9A,B). The receptor sites of amphids are derived from modified cilia, but recall that motile cilia do not occur in nematodes. It is thought that the amphids

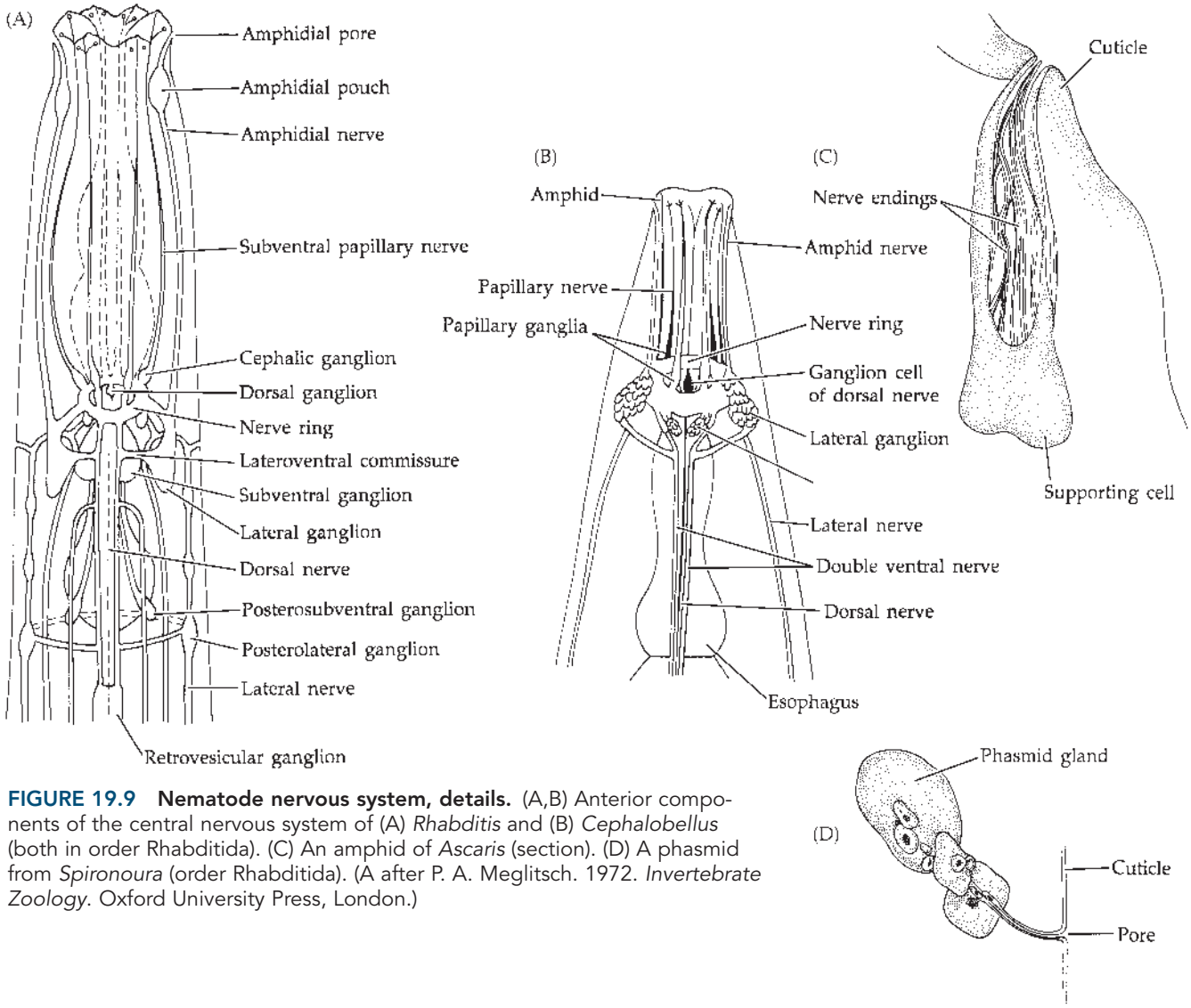

FIGURE 19.9 **Nematode nervous system, details.** (A,B) Anterior components of the central nervous system of (A) *Rhabditis* and (B) *Cephalobellus* (both in order Rhabditida). (C) An amphid of *Ascaris* (section). (D) A phasmid from *Spironoura* (order Rhabditida). (A after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

are polymodal—chemosensory, touch, and osmotic receptors.

Via a series of associated ganglia, longitudinal nerves also extend posteriorly through the epidermal cords (Figure 19.9A). The major nerve trunk is ventral and includes both motor and sensory fibers. It is formed from the union of paired nerve tracts that arise ventrally on the nerve ring and fuse posteriorly, where the main trunk bears ganglia. The dorsal nerve cord is motor, and the less well-developed lateral nerve tracts are predominantly sensory. Lateral commissures connecting some or all of the longitudinal nerves occur in many nematodes. Both the ventral and dorsal nerve cords are closely associated with the epidermis and are separated from the body cavity and somatic musculature by a basal lamina.

Most members of the class Chromadorea possess a posteriorly located pair of glandular structures called **phasmids** (= phasmid sensilla) (Figure 19.9D). These structures are also considered to be chemoreceptors. Some freshwater and marine free-living nematodes in the class Enoplia possess a pair of anterior pigment-cup ocelli as well, and at least some nematodes contain proprioceptor cells in the lateral epidermal cords. These sensory cells contain a fixed cilium and appear to monitor bending of the body during locomotion. A ciliary-type photoreceptor has been reported from only one species, *Oncholaimus vesicarius*. However, even nematodes lacking photoreceptors react to visible and UV light, indicating the presence of dermal light sensitivity (as has been documented in other invertebrate phyla). Recently it was shown that LITE-1, a taste receptor homolog protein known from other invertebrate phyla, mediates UV-light-induced avoidance behavior in *C. elegans*. In this species, the LITE-1 protein serves as a photoreceptor by directly absorbing both UVA and UVB light. Interestingly, LITE-1 shows no sequence homology with the two known metazoan photoreceptor proteins, opsins and cryptochromes, nor any other known photoreceptors in microbes or plants. Evolutionary workarounds for absence of opsins (and opsin photoreceptor genes) in roundworms is also seen in studies of *C. elegans* that found the worms capable of detecting and discriminating colors as a way to avoid toxic microbes in their environment (rotting vegetation). It appears that *C. elegans* may have co-opted a pair of conserved stress-response genes for this purpose, suggesting that a cellular stress response pathway may mediate spectral discrimination by photosensitive cells in these worms.

The most complex behaviors, such as locomotion, navigation, and mating, are mediated by the somatic muscles, which run longitudinally in four bands from head to tail. Nematodes crawl by propagating a wave of muscle contraction along the body in the dorsoventral plane; waves traveling from head to tail result in forward movement, while waves traveling in the opposite direction result in backward movement.

Reproduction, Development, and Life Cycles

Most nematodes are gonochoristic (with males and females) and show some degree of sexual dimorphism (Figure 19.10A,B). The female reproductive system (Figure 19.10A) usually consists of one or two elongate ovaries that gradually hollow as oviducts and then enlarge as uteri (Figure 19.10C–E). The uteri converge to form a short vagina connected to the single gonopore, exiting via the vulva. The female gonopore is completely separate from the anus, opening on the ventral surface near the middle of the body or sometimes just above the anus. However, hermaphroditism (including self-fertilization), parthenogenesis, pseudogamy, and an alternation of hermaphroditism or parthenogenesis with gonochory also occur in various species. And, in some there is a coexistence of males, females, and hermaphrodites (a mode called "trioecy"). In many species, such as *C. elegans*, there are two sexes but these are hermaphrodite and male, the former being viewed as a female that produces a limited number of sperm cells that can reproduce either by self-fertilization or by cross-fertilization involving mating with a male. **Pseudogamy** (also called sperm-dependent parthenogenesis or gynogenesis) is a special type of asexual reproduction in which females use the sperm of males (often from another species) to activate their oocytes. However, the sperm DNA is not used, and the embryos develop only from the maternal DNA to give rise to females. For example, *Mesorhabditis belari* produces only 9% males, whose sperm is necessary to fertilize and activate the eggs. However, most of the fertilized eggs develop without actually using the sperm DNA and so produce only daughters, and only in 9% of the eggs is the male DNA utilized, producing sons.

Males tend to be smaller than females and are often sharply curved posteriorly (leading to the common name "hookworm" for some parasites). The male reproductive system (Figure 19.10B,F) typically includes one (or two) threadlike tubular testes, each of which is regionally differentiated into a distal germinal zone, a middle growth zone, and a proximal maturation zone near the junction with the sperm duct. The sperm duct extends posteriorly, where it enlarges as a seminal vesicle leading to a muscular ejaculatory duct that joins the hindgut near the anus. Some species have prostatic glands that secrete seminal fluid into the ejaculatory duct. Most male nematodes possess a copulatory apparatus, including one or two cuticular **spicules** that transfer sperm (Figure 19.10F). Another structure called the **gubernaculum**, a sclerotized region of the dorsal wall of the cloaca that serves to anchor and guide the spicules during copulation, may be present (Figure 19.10F).

Prior to copulation the males produce sperm and store them in the seminal vesicle, while the females produce eggs that are moved into the uteri. Spermatozoa are aflagellate and lack axonemes; they may be round or elongate depending on the species. Potential mates

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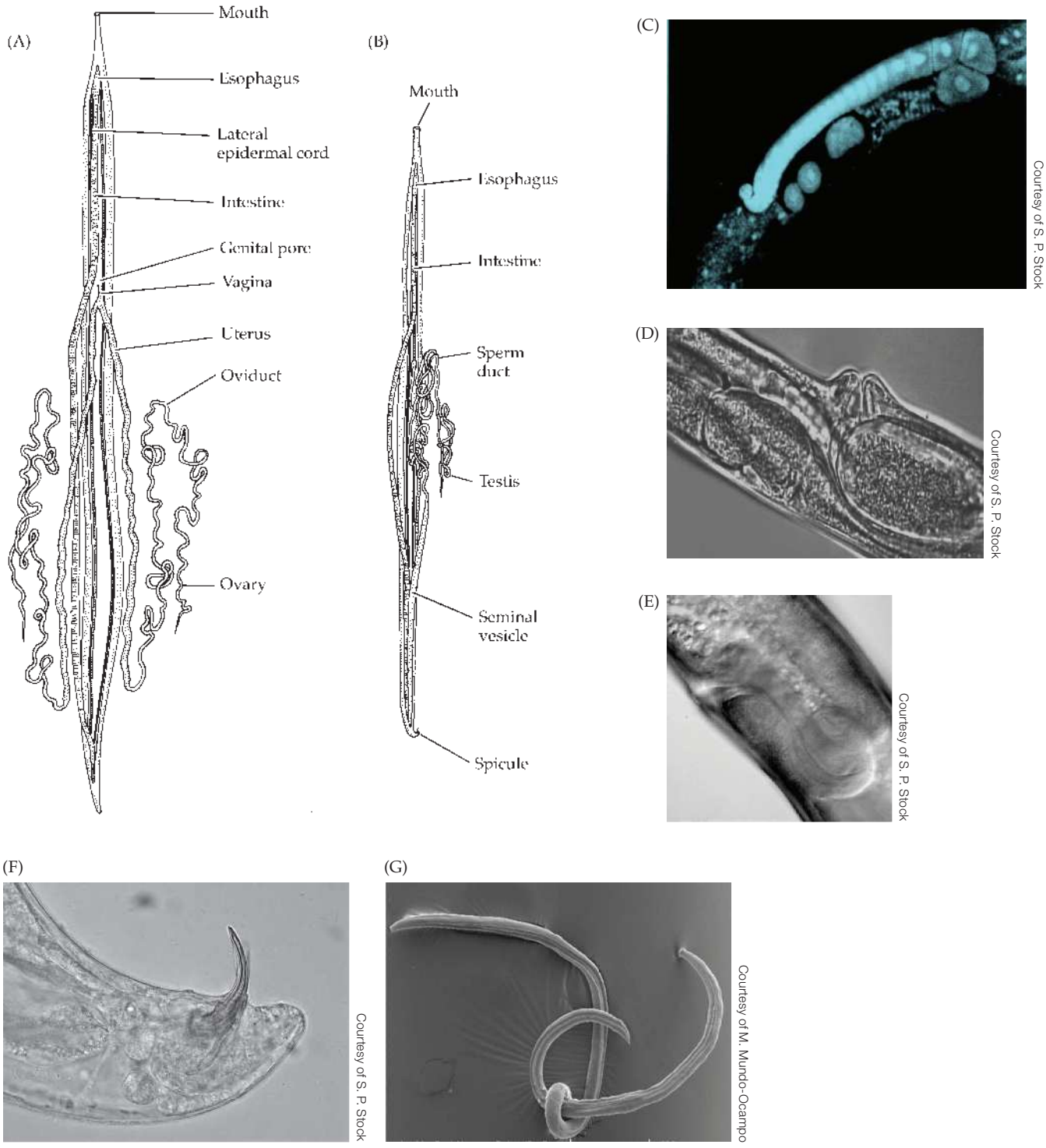

FIGURE 19.10 Nematode reproductive systems. (A,B) Female and male reproductive system of *Ascaris* (dissected). (C) Confocal microscopy image of female ovary of *Heterorhabditis bacteriophora* (an insect pathogen, order Rhabditida). (D) Liplike vulva and vagina of *Plectonchus* sp. (order Rhabditida), a soil microbivore. (E) The insect parasite *Hexamermis* sp. (order Mermithida) has an S-shaped vagina, with the gonopore surrounded by a slightly raised vulva. (F) Spicules and gubernaculum of *Steinernema* sp. (order Rhabditida), an insect pathogen. (G) SEM of male and female *Plectonchus* (order Rhabditida) mating.

make contact (females of some species are known to produce male-attracting pheromones), and the male usually wraps his curved posterior end around the body of the female near her gonopore (Figure 19.10G). Thus positioned, the copulatory structures are inserted into the vagina, and sperm are transferred by contractions of the ejaculatory duct. Fertilization usually occurs within the uterus. A relatively thick double-layered shell, or egg

envelope, forms around each zygote; the inner layer is derived from the fertilization membrane, and the outer layer is produced by the uterine wall. The zygotes are usually deposited in the environment where development takes place. In female (and maternal hermaphrodite) nematodes of many groups (e.g., rhabditids), the zygotes may hatch inside the uterus, a process known as facultative vivipary or **endotokia matricida**, which causes the mother's death (Figure 19.1). The juveniles that hatch within the female remain there, obtaining nutrients from the mother until its body ruptures, liberating the progeny into the environment as infective juveniles. In at least some cases, this phenomenon is promoted by low food supply in the environment, and it thus secures development of juveniles that are well equipped with energy reserves for long-term survival.

In the few known hermaphroditic species, sperm and egg production take place within the same gonad (an ovotestis). Sperm formation precedes egg production, so the animals are technically protandric; but they do not engage in cross-fertilization, as occurs in most sequential hermaphrodites. Rather, the sperm cells are stored until ova are produced, and self-fertilization occurs.

Nematologists typically divide embryogenesis into a "proliferation phase," where nearly all embryonic cell divisions take place and the vast majority of blastomeres are generated, and a "morphogenesis phase," where the ball of cells gradually transfoms into a worm. Interestingly, in *C. elegans* embryogenesis, 113 cells undergo programmed cell death (apoptosis) through a distinct programmed process under the control of over 20 genes. Complete development, from fertilization to hatching, takes 840 minutes in this species.

Development among free-living nematodes is typically direct, although the term "larva" is sometimes used for juvenile stages (something we avoid here). Cleavage is holoblastic and subequal, but the pattern appears to be unique among the Metazoa. The orientation of blastomeres during early cleavage is fairly consistent within those species of nematodes that

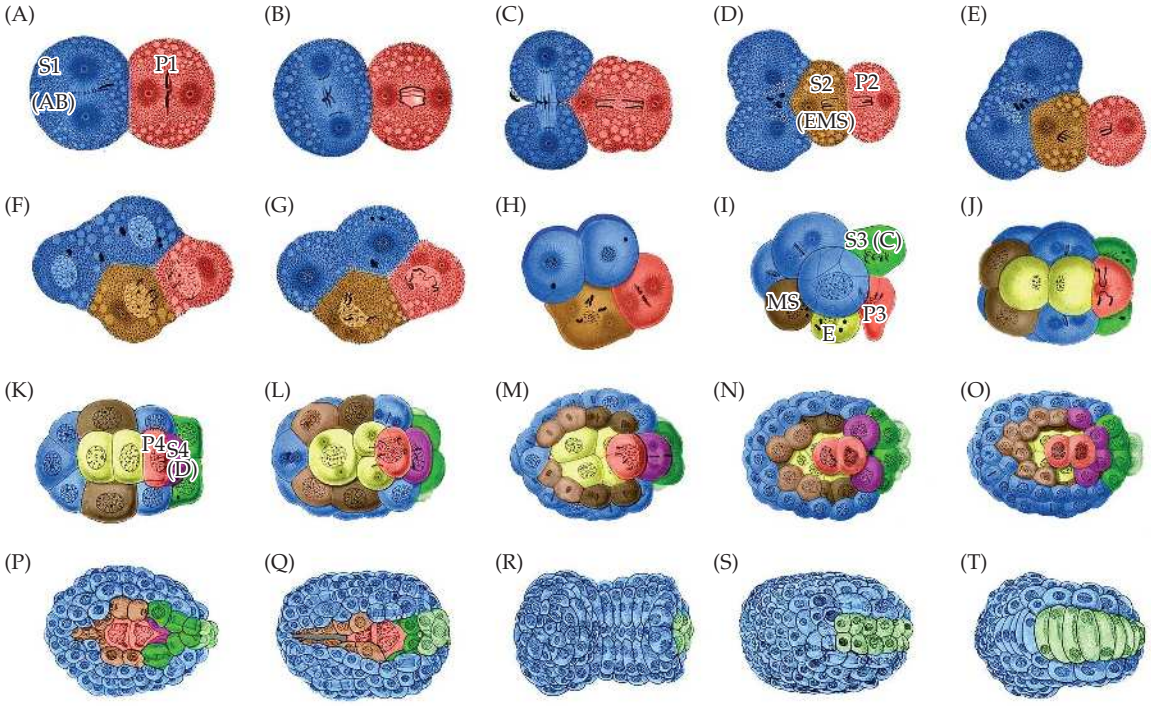

FIGURE 19.11 Embryonic development of *Parascaris equorum*, from the 2-cell stage to early morphogenesis. In nematodes, the early cleavages are typically asymmetric, sequentially separating a small number of somatic lineage founder cells from the germline. (A) The first division of the zygote yields a somatic founder cell S1 (= AB) and P1 cell. In the 2-cell stage, the first somatic founder cell AB divides with a transverse orientation of the cleavage spindle, generating two daughters of equal developmental potential (C). In contrast, its sister, the germline cell P1, undergoes a rotation of the nuclear/centrosome complex leading, first, to a longitudinal orientation of the spindle and, subsequently, to the generation of the somatic cell EMS and a new germline cell P2 (D). Thus, asymmetric divisions of the germline cells (P1–P3) result in somatic founder cells S2–S4 (= EMS, C, D) and the primordial germ cell P4 (= PGC). S2 (= EMS) divides into two daughters (MS and E) with different fates. Somatic founder cells, but not germline cells, pass once through the process of chromatin diminution (indicated by black spots). Gastrulation starts with the translocation of E cells (gut precursors) into the interior while descendants of MS, P4, D, and C temporarily cover the ventral surface (K–O). Eventually, these cells are also internalized (P, Q) and S1 (AB) cells occupy the complete surface of the embryo before morphogenesis begins with a ventral indentation (R). The dorsal view at this stage (S, T) shows those descendants of S3 (C) contributing to posterior hypodermis.

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have been studied, but it cannot be assigned to either a radial or spiral pattern. Early cleavage is asynchronous, unequal, and invariant in *C. elegans*, while it is synchronous, equal, and not invariant in *Enoplus brevis*. Figure 19.11 illustrates this cleavage pattern and some details of cell fates (in *Parascaris equorum*). In most species (e.g., *C. elegans*) the blastomeres are probably fixed early to a specific invariant lineage program, and experimentally eliminated cells are not replaced by others. However, in some species (e.g., *Acrobeloides nanus*) early blastomeres are multipotent and compete for a primary fate, and the loss of one cell may cause a switch in the developmental program of another. Probably in most nematodes (e.g., *C. elegans*) the cells of the four-cell embryo are clustered in a rhombic fashion, but in some (e.g., *Diploscapter coronatus*) the cells of the four-cell embryo are spread out in a linear chain.

A stereoblastula or slightly hollow coeloblastula forms and undergoes gastrulation by epiboly of the presumptive ectoderm combined with an inward movement of presumptive endoderm and mesoderm. After a specific point in development, few nuclear divisions occur, and most subsequent growth, even after hatching, is via the enlargement of existing cells. The gut of *C. elegans* has been shown to derive from all the progeny of the E blastomere, a cell of the eight-cell stage. Most nematodes undergo four postembryonic juvenile stages, separated by molts. In a few, however, such as the diplogastrids, the first of these stages transpires while the nematode is still within the egg membrane, in the embryonic phase, thus they have only three postembryonic juvenile stages.

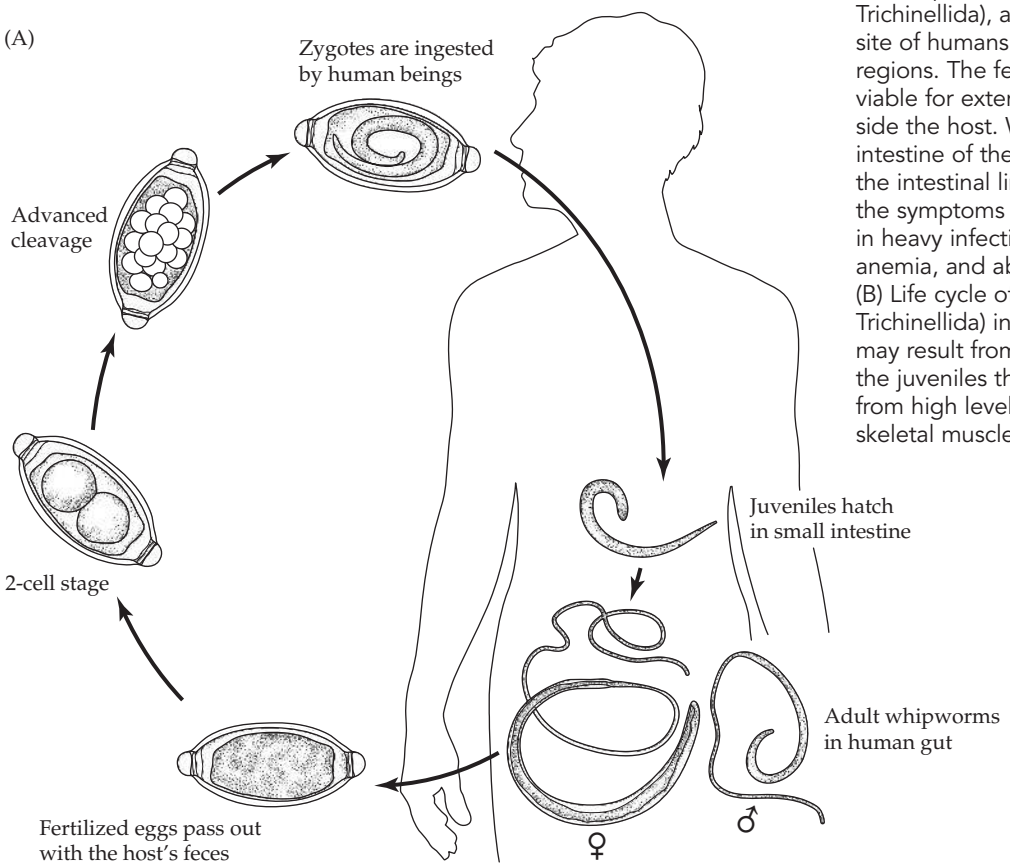
Some groups of roundworms have evolved a strategy to survive adverse environmental conditions by forming a resistant juvenile known as the **dauer stage**, which tolerates different kinds of environmental stress. In *C. elegans*, for example, the second-stage juvenile (J2) can develop either into a normal third-stage juvenile (J3), which molts into an adult, or into a dauer stage. In this species, dauer formation is regulated by at least three environmental cues: starvation, high temperature, and high population density. Nematodes have been kept frozen for over 25 years and then revived. In 2019 a group of Russian scientists published a short note claiming to have revived 41,000-year-old nematodes from Arctic permafrost, but they did not elucidate whether the specimens found were resistant stages or adult worms. And, in 2019 scientists discovered eight species of nematodes living in Mono Lake, California, one of the most inhospitable lakes on Earth for animal life. The lake is three times as salty as the ocean, has a pH of 9–10, and is highly enriched in arsenic. The only other metazoans living in the lake are a brine shrimp and an alkali fly. And, remarkably, the eight nematode species are in different phylogenetic lineages and appear to be the result of several independent colonization events.

Life Cycles of Some Parasitic Nematodes

Plant and animal parasite clades have evolved numerous times among nematodes, and all have a specialized stage for infestation, usually called the infective juvenile (or infective "larva"), which shows striking similarity to the dauer stage of free-living species, and this likely represents an important preadaptation toward parasitism. The study of parasitic nematode life cycles is a field unto itself, and we present only a few illustrative life history cycles here (Figures 19.12 and 19.13). An example of a simple parasitic life cycle is that of the whipworm *Trichuris trichiura* (class Dorylaimia) (Figure 19.12A). These relatively large (3–5 cm long) nematodes reside and mate in the human gut, and the fertilized eggs are passed with the host's feces. Females produce 2,000 to 10,000 eggs per day. Reinfection occurs when another host ingests the embryos. A more complicated life cycle is that of the trichina worm, *Trichinella spiralis*, the causative agent of human trichinosis (Figure 19.12B). This roundworm completes all stages of development in its human (or other carnivorous mammal) host; infective juveniles excyst in the gut, where they mature and reproduce, and the newborn juveniles migrate to the muscles, where they encyst. The parasite is passed by consumption of contaminated muscle tissue (such as when humans consume undercooked pork). Some species of *Trichinella* infest reptiles and birds and do not form encapsulated juveniles. Other important human parasites include two species of hookworms, *Necator americanus* in the New World and *Ancylostoma duodenale* in the Old World. Skin-penetrating nematodes rely on a developmentally arrested infective third-stage juvenile that searches for hosts by a poorly understood process that involves both thermal and olfactory cues.

Most parasites of vertebrates belong to the class Chromadorea, which includes such notables as hookworms, pinworms, ascarid worms, and filariid worms. One of the most dramatic nematode infections in humans is filariasis, caused by any of a number of secernentean nematodes called the filariids. These threadlike parasites require an intermediate host, typically a blood-sucking insect (e.g., fleas, biting flies, mosquitoes). One such filariid is *Wuchereria bancrofti*, whose vector is a mosquito. When present in humans in high numbers, masses of adult *Wuchereria* block lymphatic vessels and cause fluid accumulation (edema) and severe swelling, a condition resulting in grotesque enlargement of body parts and known as lymphatic filariasis, or **elephantiasis**. Such infections often affect the legs and arms, the scrotum in males, and breasts in females. Some 120 million people in 73 countries are infected with lymphatic filariasis.

Onchocerca volvulus, another filariid nematode, is the causative agent of river blindness, transmitted by



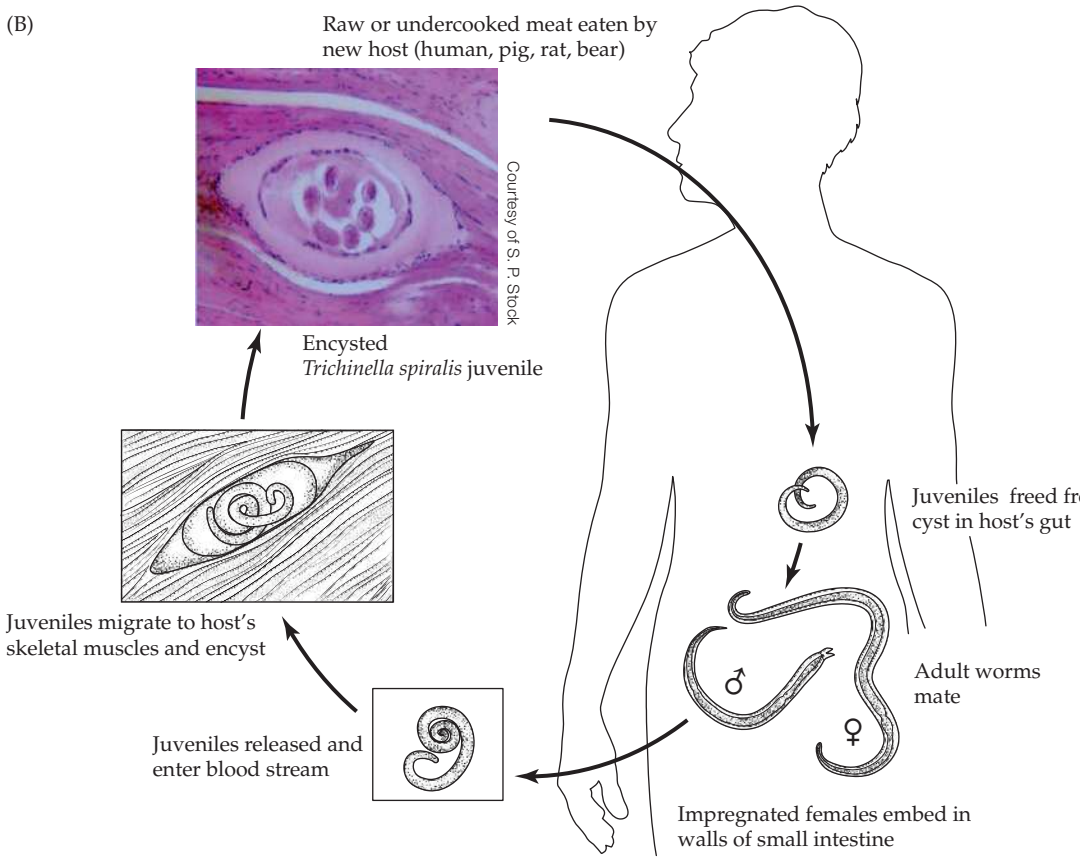


FIGURE 19.12 Life cycles of some parasitic roundworms. (A) Life cycle of the whipworm *Trichuris trichiura* (order Trichinellida), a common intestinal parasite of humans in tropical and subtropical regions. The fertilized eggs can remain viable for extended periods of time outside the host. Whipworms parasitize the intestine of the host and suck blood from the intestinal lining. In low-level infections, the symptoms are minor or absent, but in heavy infections intestinal bleeding, anemia, and abdominal pain can occur. (B) Life cycle of *Trichinella spiralis* (order Trichinellida) in humans; serious symptoms may result from the burrowing activity of the juveniles through the intestinal wall and from high levels of encysted juveniles in skeletal muscle tissue.

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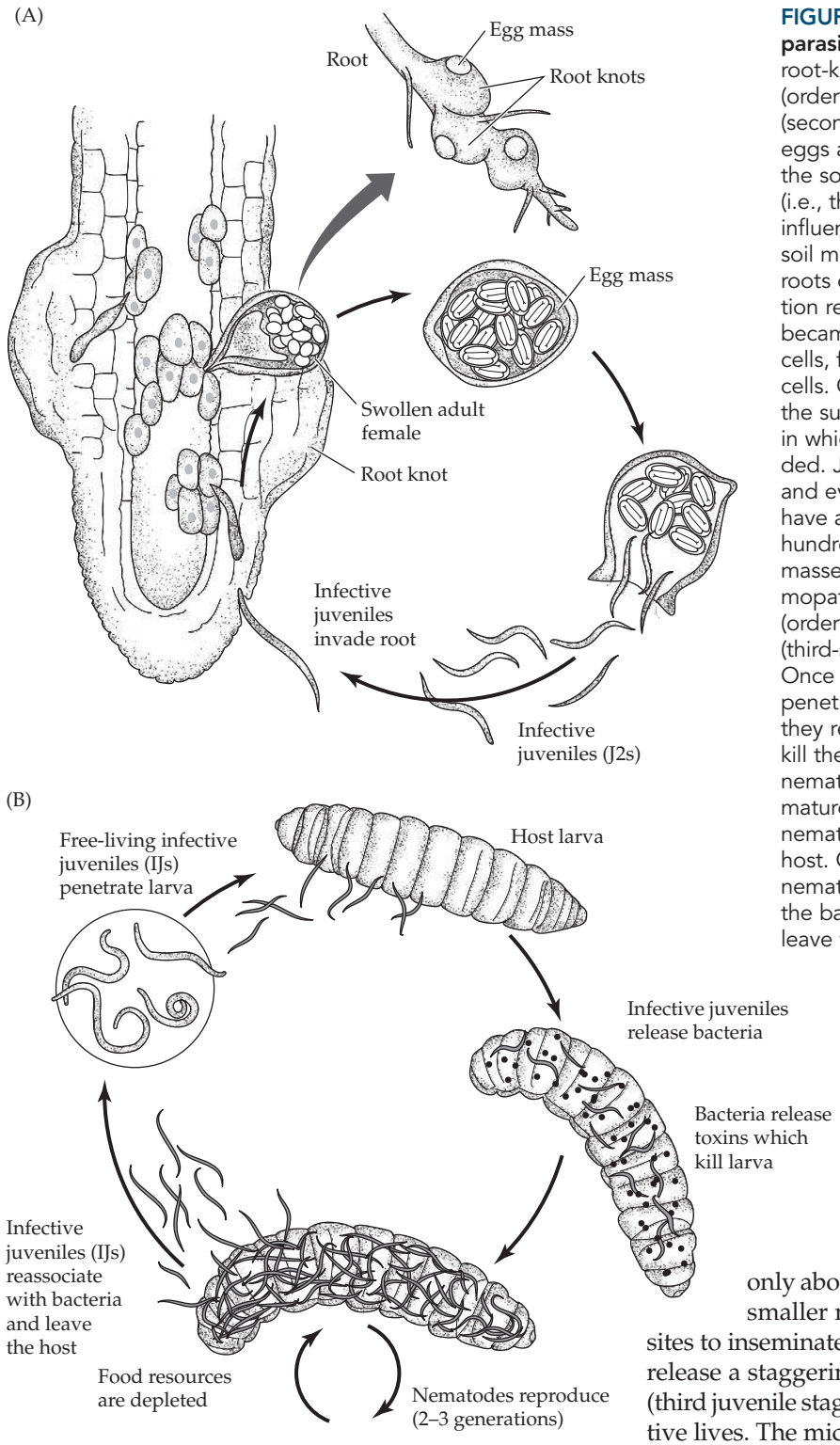

FIGURE 19.13 Life cycles of some parasitic roundworms. (A) Life cycle of the root-knot nematode *Meloidogyne incognita* (order Tylenchida). Infective juvenile stages (second stage juveniles, or J2s) hatch from eggs and have a short free-living stage in the soil, in the rhizosphere of the host plants (i.e., the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms). J2s may reinvade the roots of the host plants in the root elongation region and migrate in the root until they became sedentary. J2s feed on parenchyma cells, forming feeding sites known as giant cells. Concomitant with giant cell formation, the surrounding root tissue gives rise to a gall in which the developing juvenile is embedded. J2s undergo morphological changes and eventually become adults. Females have a saccate shape and produce many hundreds of eggs that they lay in gelatinous masses. (B) Generalized life cycle of an entomopathogenic nematode, *Steinernema* sp. (order Rhabditida). Free-living infective stages (third-stage juveniles, or IJs) live in the soil. Once they encounter a suitable host, they penetrate it and release symbiotic bacteria as they reach the host's body cavity. The bacteria kill the host by septicemia and reproduce. The nematodes then feed on the bacteria as they mature and grow into adults. Two to three nematode generations can develop inside the host. Once food resources are depleted, the nematodes become IJs and reassociate with the bacteria in a mutualistic manner until they leave the cadaver in search of a new host.

bites from certain black fly species (Simuliidae). The disease (and the parasite) comes out of Africa, where it is endemic in 27 countries, but it also occurs in 6 Latin American countries as a result of the slave trade. If left to run its course, river blindness is a disease for life. Adult worms can live 12 to 15 years and be sexually active for 9 to 11 years. Adults live in large nodules under the skin—a telltale diagnostic feature. Each nodule harbors 2 to 3 female individuals measuring up to 50 cm in length (but only about 0.5 mm in diameter), and the much smaller males (to 4 cm long) migrate to these sites to inseminate the females. Once fertilized, females release a staggering 1,300 to 1,900 microfilarial worms (third juvenile stage) per day throughout their reproductive lives. The microfilariae are also the infective stages in this disease. It is the microfilarial stage that is transmitted to humans by the biting black flies. Once in the blood stream, these tiny (250–300 μm long) microfilariae circulate throughout the host's body, some eventually arriving in the eyes, where they infest the vitreous chamber, retina, and optic nerve. Here, when the microfilariae die, they cause scarification, leading to visual impairment and eventually blindness. It is estimated that 37 million people in Africa have onchocerciasis, hundreds of thousands of them eventually becoming blind.

In the 1970s, the drug avermictin (Ivermectin) was developed from a bacterium (*Streptomyces avermectinius*) found on a golf course in Japan. The drug kills or permanently sterilizes many adult filariid worms, with few side effects to the host animal. At first this drug was broadly developed for use on husbandry animals, cats, and dogs, but in 1996 the FDA approved its use in humans. Recent studies have shown that a large part of the pathogenicity of filarial worms is due to immune response of the host toward the nematode's naturally occurring *Wolbachia* bacterial symbionts. Also, it has been demonstrated that elimination of *Wolbachia* from the worms generally results in either their death or sterility. Consequently, current strategies for control of filarial nematode diseases include elimination of *Wolbachia* via administration of antibiotics such as doxycycline, which are more effective and less harmful than most antinematode medications.

Plant parasitic nematodes annually cause billions of dollars in crop losses worldwide. Some of the most damaging and widely distributed plant parasites are root-knot nematodes (*Meloidogyne*) and root-cyst nematodes (e.g., *Heterodera, Globodera*). In the soil, root-knot nematode eggs develop into nonmotile first-stage juveniles (J1) that reside inside the translucent egg case, where they molt into a motile J2 stage. The J2 can infect plants by attacking the root tips and moving to the area of cell elongation, where they initiate a feeding site by injecting esophageal gland sections into the cells. The secretions cause dramatic physiological changes to the root cells, transforming them into giant syncytial cells that die when the nematode dies. Figure 19.13A shows the life cycle of a root-knot nematode that attaches to the roots of a host tomato plant. However, other species can cause damage to the aerial parts of the plants, including leaves, stem, flowers, and seeds. Some species transmit plant pathogens (viruses and bacteria) through their feeding activity on roots. For example, *Xiphinema index* acts as a vector for the grapevine fan-leaf virus, an important disease of grapes. Some species, such as the pine wood nematode *Bursaphelenchus xylophilus*, are important forestry parasites worldwide.

Many nematodes parasitize invertebrates in both aquatic and terrestrial ecosystems. One of the most interesting groups is the so-called insect-pathogenic (or entomopathogenic) nematodes. Many of these nematodes associate (mutualistic symbiosis) with certain gram-negative bacteria, which they harbor in their intestines. Once the nematodes enter a suitable host, they release the bacteria, which kill the insect host by a massive septicemia in 24 to 48 hours. The bacteria then become the nematode's food, allowing them to mature and reproduce in the insect cadaver. Figure 19.13B shows a generalized entomopathogenic life cycle. These nematodes have been successfully used in the control of many agricultural insect pests. The worms with their symbiotic bacteria are raised and sold worldwide as biological control agents. Some of the more interesting symbiotic nematodes are those that, during their dauer stage, inhabit the reproductive tract of a solitary bee and then, as adults, inhabit the bee's brood cells, where they feed on the fungi and bacteria growing in their host's brood chambers.

Phylum Nematomorpha: Horsehair Worms and Their Kin

The Nematomorpha comprises a small group of long worms. There are about 365 described species of nematomorphs (Greek *nema*, "thread"; *morph*, "shape"), commonly called the hair, horsehair, or gordian worms. The phylum name (and the common name of hair and horsehair worms) derives from the threadlike shape of these animals (Figure 19.14) and from the belief held for some time after their discovery in the fourteenth century that they actually arose from the hairs of horses' tails. They are generally from 1 to 3 mm in diameter and up to 1 m in length. Many of the highly elongate forms tend to twist and turn upon themselves in such a way as to give the appearance of complicated knots, hence the name gordian worms. In the American Midwest large clumps of intertwined groups of *Gordius difficilis* are commonly found in cold, spring-fed habitats. Most species occur in fresh water, but five marine species have also been described. Characteristics of this phylum are listed in Box 19B.

BOX 19B Characteristics of the Phylum Nematomorpha

1. Triploblastic, bilaterally symmetrical, unsegmented, vermiform; body long and very thin
2. Body cavity largely obliterated by mesenchyme and organs
3. Cuticle well developed, with a single cuticular molt reported in some species
4. Body without functional cilia or flagella
5. Body wall containing only longitudinal muscles (no circular muscles)
6. Gut reduced to various degrees
7. With an aquatic larva and a unique juvenile stage that is parasitic in terrestrial arthropods
8. Epidermis forming longitudinal cords housing longitudinal nerves
9. Without special excretory, circulatory, or gas exchange organs
10. Gonochoristic; at least one known parthenogenetic species
11. With unique cleavage pattern
12. Adults mostly found in fresh water and wet terrestrial habitats, with five known marine pelagic species; all parasitic during the juvenile phase but free-living as adults

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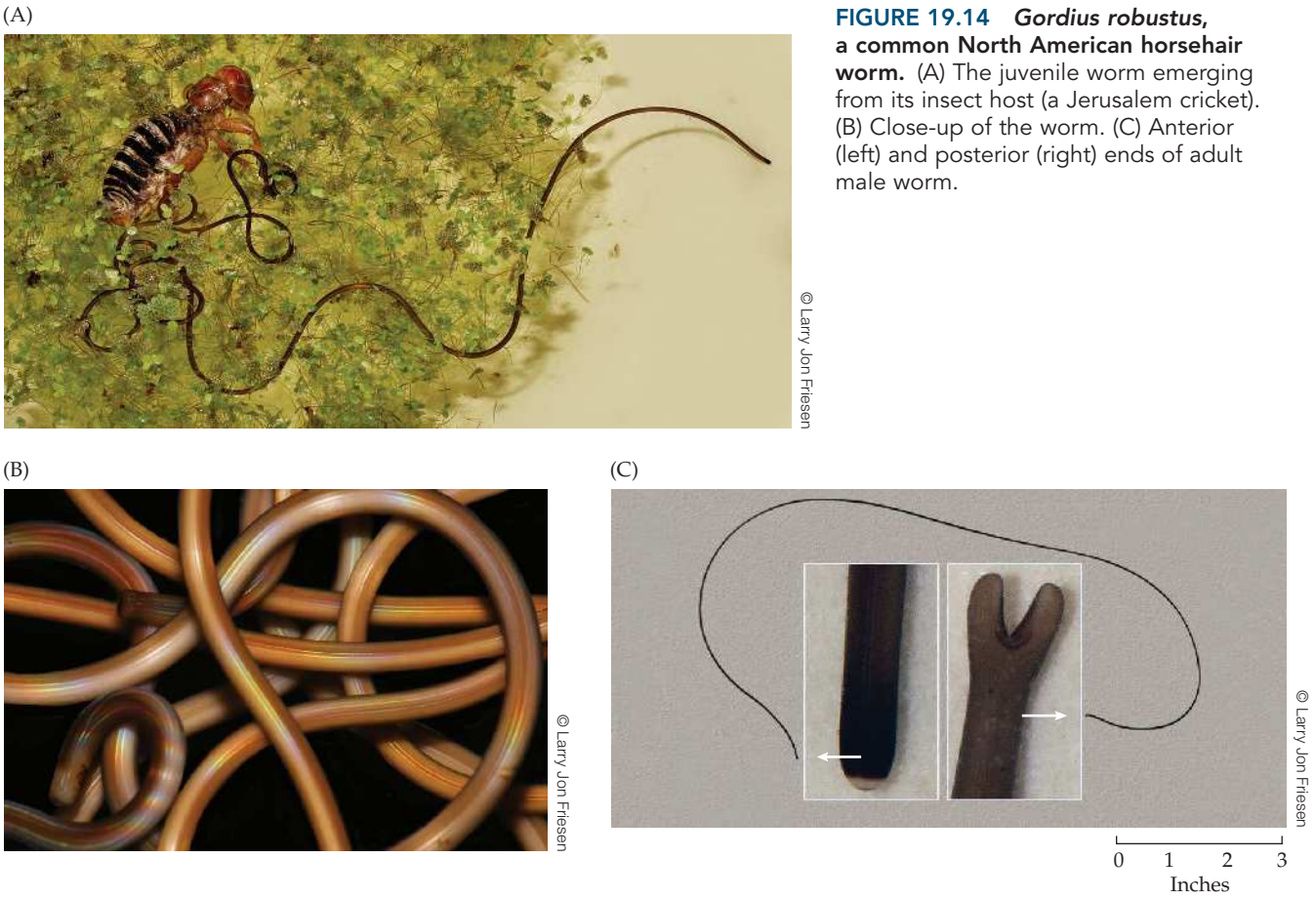

FIGURE 19.14 ***Gordius robustus*, a common North American horsehair worm.** (A) The juvenile worm emerging from its insect host (a Jerusalem cricket). (B) Close-up of the worm. (C) Anterior (left) and posterior (right) ends of adult male worm.

Nematomorphs were once thought to have a persistent blastocoelom, but recent work has shown most of these spaces to be artifacts—thus these worms are generally now regarded as acoelomates. The embryological blastocoel (the coeloblastula) is largely or fully obliterated by the invasion of mesenchyme and organs during development, and neither larvae nor adults have a significant body cavity (although some tiny fluid-filled spaces may remain in some cases, and these might represent remnants of the blastocoelom). In mature animals, the gonads become very spacious and occupy a large volume of the body. The digestive tract is largely nonfunctional, and nematomorphs appear to lack any structural excretory mechanisms. Like nematodes, nematomorphs possess only longitudinal (and no circular) body wall musculature—in contrast, the closely related ecdysozoan phyla Kinorhyncha, Priapula, and Loricifera have both longitudinal and circular musculature in the body wall. There are no functional cilia in these animals.

The larvae of nematomorphs, in both marine and continental species, parasitize mainly arthropods. After emerging from their final host, most adults live in fresh water, among litter and algal mats near the edges of ponds and streams, or in the case of the genus *Nectonema*, are pelagic in coastal marine environments.

NEMATOMORPHA CLASSIFICATION

ORDER NECTONEMATOIDEA Marine, pelagic; with a double row of natatory setae along each side of body; with dorsal and ventral longitudinal epidermal cords and integrated dorsal and ventral nerve cords; small body spaces may be evident, though fluid filled; gonads single; larva parasitizes decapod crustaceans. Monogeneric: *Nectonema* (5 known species).

ORDER GORDIOIDEA Without lateral rows of setae; with a single, ventral epidermal cord in a submuscular position, including the single nerve cord; body cavity largely filled with mesenchyme; older individuals develop spacious gonads; gonads paired. The larva parasitizes aquatic intermediate hosts (primarily arthropods and molluscs), while final hosts are mainly terrestrial arthropods; free-living aquatic adult may be short-lived. About 360 known species. *Chordodes, Gordius, Paragordius*, etc.

The Nematomorph Body Plan

Body Wall, Support, and Locomotion

The general organization of the body wall of nematomorphs is similar in many aspects to that of the nematodes (Figure 19.15A–C). The cuticle of adult specimens, secreted by the epidermis, is very thick (especially in the gordioids) and comprises an outer homogeneous

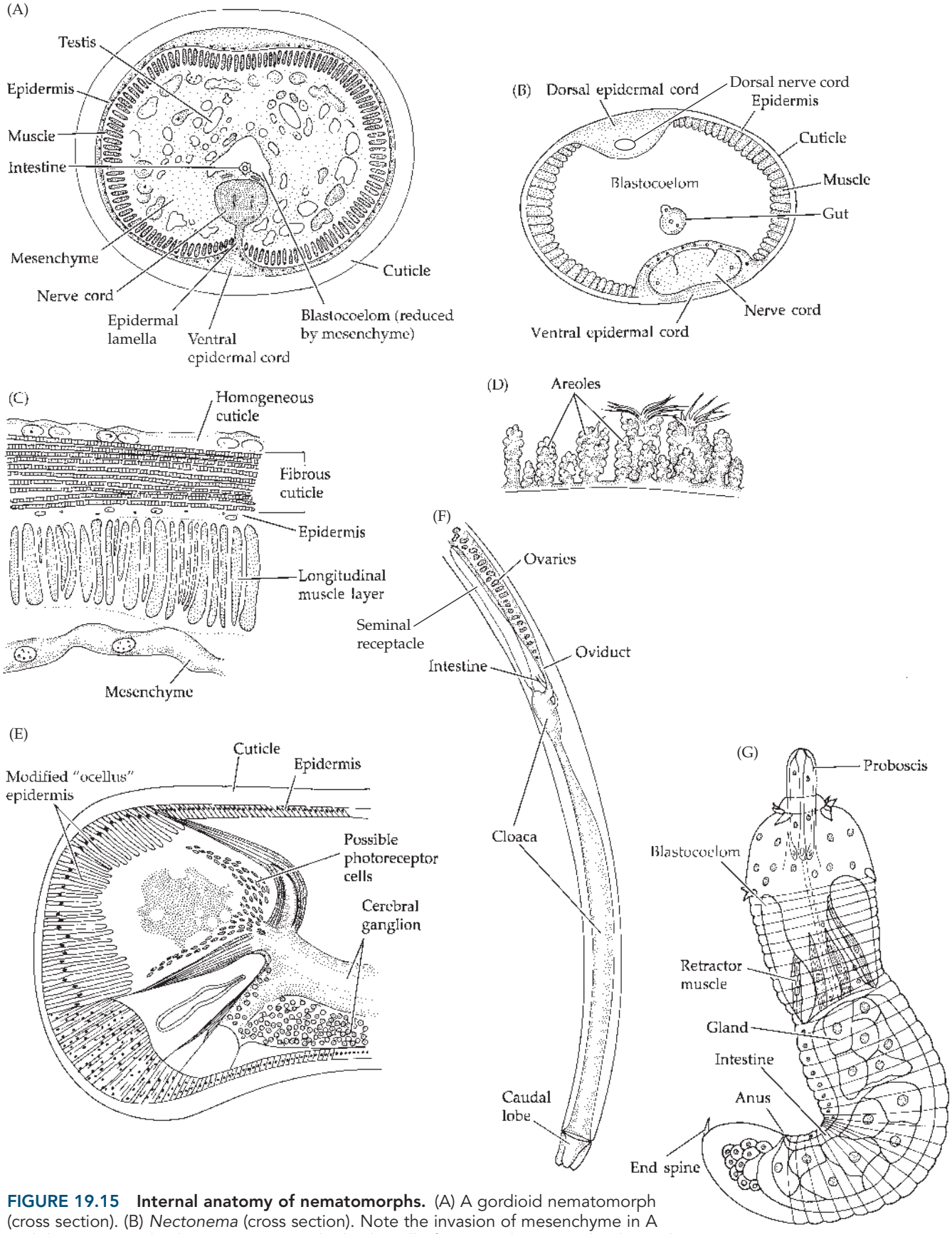

FIGURE 19.15 Internal anatomy of nematomorphs. (A) A gordioid nematomorph (cross section). (B) *Nectonema* (cross section). Note the invasion of mesenchyme in A and the persisting body cavity in B. (C) The body wall of *Paragordius*, a gordioid. (D) The ornate areoles of *Chordotes*, a gordioid. (E) The anterior end of *Paragordius* (sagittal section). Note the elements of the nervous system and the suspected photoreceptor units. (F) The female reproductive system of *Paragordius*. (G) A nematomorph larva. (G after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

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layer and an inner, lamellate, fibrous layer. The homogeneous layer often forms bumps, warts, or papillae (collectively called **areoles**; Figure 19.15D), some of which bear apical spines or pores. The function of the areoles is unknown, but spined ones may be touch sensitive, and pore-bearing ones may produce a lubricant. Some species have two or three caudal lobes at the posterior end, and these can be sexually dimorphic.

The unciliated epidermis covers the entire body and rests upon a thin basal lamina. The epidermis forms ventral (Gordioidea) or dorsal and ventral (Nectonematoidea) epidermal cords containing longitudinal nerve tracts. In Gordioidea the ventral cord is in a submuscular position and connected to the epidermis by a thin lamella. Beneath the epidermis is a single layer of longitudinal muscle cells; as in nematodes, there is no layer of circular muscle in the body wall.

The body cavity of nematomorphs is very small and filled with fluid (e.g., *Nectonema*) or altogether absent and filled with mesenchyme (Figure 19.15A,B). Body support comes mainly from the well-developed cuticle. Locomotion in the pelagic *Nectonema* is by undulatory swimming using the body wall muscles and the natatory bristles (Figure 19.16E) or by passive flotation in nearshore currents, aided by the bristles, which provide resistance to sinking. Freshwater nematomorphs use their longitudinal muscles to move by undulations or by coiling and uncoiling movements.

Feeding and Digestion

Nematomorphs might feed only during the parasitic juvenile stage, when they absorb nutrients across their thin body wall from the host's tissue and fluids, leaving adults to rely entirely on nutrients stored during the juvenile parasitic life. There is some evidence that adults of a few species might take in nutrients by absorbing small organic molecules across the body wall, but this seems a remote possibility due to the thickness of the adult cuticle and the reduced state of the intestine. There is growing evidence that parasitism by nematomorphs in insects can alter the host's behavior in ways that cause the insect to ultimately position itself near or in standing water, ensuring that the adults emerge in an appropriate habitat.

The digestive tract of nematomorphs is a simple elongate tube running the length of the body (Figure 19.15A,F,G). In juveniles, the gut is actively involved with uptake and storage of nutrients, transported across the body wall (although possible nutrient uptake through the mouth cannot be excluded). The intestine (midgut) is a thin-walled tube and may serve an excretory function as well as a digestive one. The hindgut is proctodeal (ectodermally derived), functions as a cloaca, and receives the reproductive ducts. In *Nectonema* a tiny mouth leads to a midgut that deteriorates posteriorly and is not connected to the genital opening.

Circulation, Gas Exchange, Excretion, and Osmoregulation

Very little is known about the physiology of nematomorphs. Internal transport is undoubtedly by diffusion through body fluids and mesenchyme and is probably aided by body movement. In the free-living stage gordian worms are presumably obligate aerobes as adults and are restricted to moist environments with ample available oxygen. The threadlike body results in short diffusion distances between the environment and the body organs and tissues.

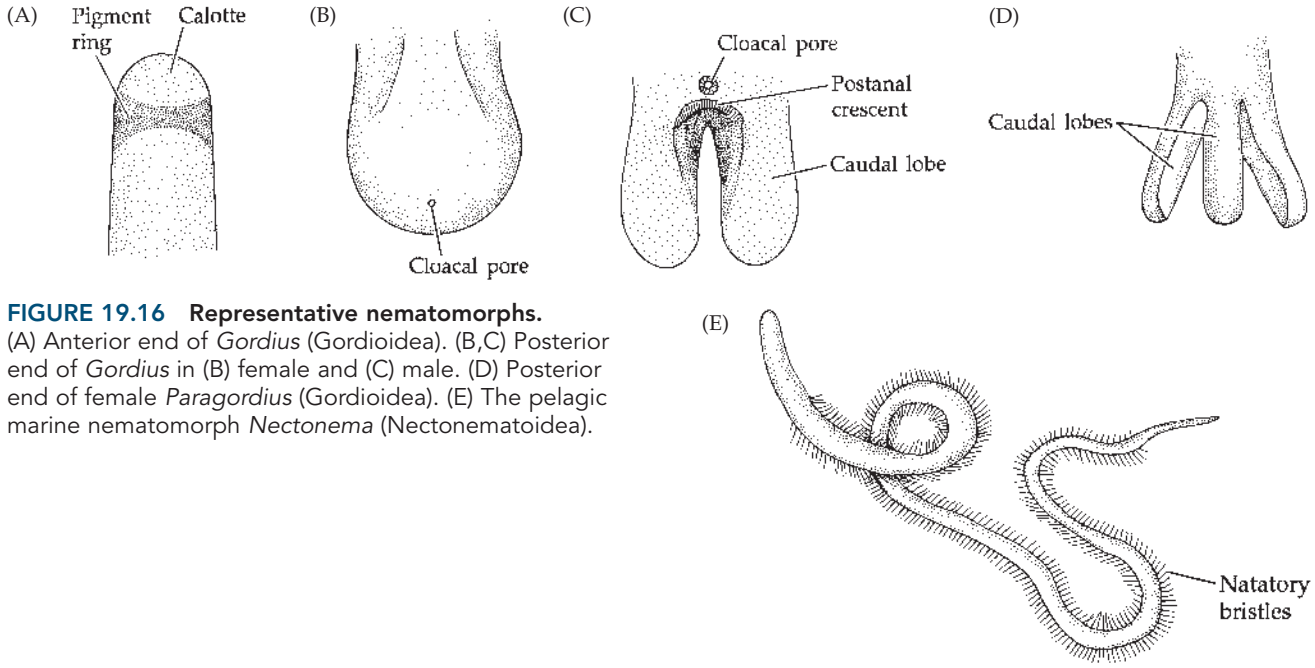

FIGURE 19.16 Representative nematomorphs. (A) Anterior end of *Gordius* (Gordioidea). (B,C) Posterior end of *Gordius* in (B) female and (C) male. (D) Posterior end of female *Paragordius* (Gordioidea). (E) The pelagic marine nematomorph *Nectonema* (Nectonematoidea).

Excretory and osmoregulatory functions probably operate on a strictly cellular level, as there are no protonephridia or other known special structures for these functions. Some workers, however, have speculated that the cells of the midgut may function in the excretion of metabolic wastes and that they may have a structure similar to the Malpighian tubules of insects.

Nervous System and Sense Organs

Like the nervous systems of nematodes and some other small Metazoa, the nervous system of nematomorphs is closely associated with the epidermis. The cerebral ganglion forms a circumesophageal mass of nervous tissue that is mainly subesophageal in gordioids but mainly dorsal in *Nectonema*. This connects to a ventral, longitudinal nerve cord in gordioids but to both dorsal and ventral, intraepidermal cords in *Nectonema* (Figure 19.15A,B). The nerve cords generally extend the length of the body and are attached to the epidermis by a tissue connection called the epidermal lamella (Figure 19.15A,B).

All nematomorphs are touch sensitive, and some are apparently chemosensitive. Adult males are able to detect and track mature females from a distance. However, the structures associated with these sensory functions are a matter of speculation. Presumably, some of the cuticular areoles are tactile, and perhaps others are chemoreceptive. Members of the genus *Paragordius* possess modified epidermal cells in the head region that contain pigment and may be photoreceptors (Figure 19.15E), although this function has not been confirmed. Other possible sensory structures are four "giant cells" near the cerebral ganglion in *Nectonema*.

Reproduction and Development

Nematomorphs are gonochoristic and display some sexual dimorphism (Figure 19.16B–D). The African species *Paragordius obamai* is a notable exception and has been shown to be parthenogenetic in culture. The male reproductive system includes one (in *Nectonema*) or two (in gordioids) testes (Figure 19.15A). Each testis opens to the cloaca via a short sperm duct. The reproductive system of female gordioids is not completely understood. They possess a pair of elongate ovaries with repeated pouches. A seminal receptacle as an extension of the cloaca is present. *Nectonema* contains no discrete ovary; instead, the germinal cells occur as scattered oocytes in the body cavity.

Mating has been studied in some gordioids. The females remain relatively inactive, but males become highly motile during the breeding season and respond to the presence of potential mates in their environment. Once a male locates a receptive female, he wraps his body around her and deposits a drop of sperm near her cloacal pore. The sperm find their way into the seminal receptacle and are stored while the ova mature. The eggs are fertilized internally and laid in gelatinous strings.

Early development has been studied in only a few species of gordioid nematomorphs. Cleavage is holoblastic, but not spiral or radial. A coeloblastula forms, then gastrulates by invagination of the presumptive endoderm. Mesodermal cells proliferate into the blastocoel from the area around the blastopore and in most cases appear to obliterate it. The anus and cloacal chamber also form from the area of the blastopore.

The life cycles of nematomorphs are not fully understood and may differ among species. A nematomorph larva develops and emerges from its egg case. In most cases, the new larva parasitizes an aquatic intermediate (paratenic) host, usually an arthropod or mollusc, and encysts in the host's tissues. Although transmission between intermediate and final host is not well understood, it is suspected that the final host (e.g., grasshopper, cricket, beetle, mantid, occasionally a myriapod or arachnid) consumes the intermediate host, whereupon the larva excysts and becomes a parasitic juvenile. The free-living aquatic adult may be short-lived.

It is likely that metamorphosing insects with aquatic larvae play the most important role as intermediate hosts. Within the definitive host's hemocoel, the larva grows into a juvenile nematomorph, which emerges from the host when it is mature. A single cuticular molt has been reported in some species, taking place shortly before the young worm emerges. Juveniles are nearly full size when they leave their host and do not grow much as adults. For most of the two dozen or so horsehair worms of North America, the hosts are not known.

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Chapter Summary

This chapter introduced you to two groups of worms—phyla Nematoda (roundworms, threadworms) and Nematomorpha (horsehair, or gordian, worms)—that constitute a well-supported clade called Nematoida. Nematoida is one of the main lineages of Ecdysozoa (the molting animals), the others being Panarthropoda and Scalidophora, although the latter may also be a grade. The unique cuticle of adult nematoid worms is unusual in lacking chitin, the body is acoelic or blastocoelic, the body wall lacks circular muscles but has two to four unique epidermal cords that carry longitudinal nerves, there are no cilia, and the sperm are aflagellate. The adult stage of all nematomorphs is endoparasitic in pancrustaceans, and many nematodes are endoparasites of plants and animals. The largest species in both phyla can exceed a meter in length, though most species are very small (measured in millimeters). Nematodes are ubiquitous, being found in almost every habitat on Earth—freshwater, marine, terrestrial—on every continent. They have a unique secretory-excretory system composed of one or two renette cells or a bundle of collecting tubules. The cleavage pattern of nematodes is unique (neither radial nor spiral), and they do not produce a larva, but a series of juvenile stages looking like smaller adults. One of the 27,000 species of known nematodes, the tiny (1 mm long) *Caenorhabditis elegans* has been adopted as a model organism in many fields, including neurobiology, developmental biology, toxicology, and genetics, and is perhaps the best-known animal. Human nematode parasites include the whipworm (*Trichuris trichiura*), trichina worm (*Trichinella spiralis*), the filariid worm *Wuchereria bancrofti* (causative agent of elephantiasis), and the filariid worm *Onchocerca volvulus* (which causes river blindness). About 365 species of Nematomorpha have been described from freshwater habitats (and five from the marine environment). Most nematomorph life cycles include a minute, parasitic larva that grows to a large size and lives for a long period once it reaches a definitive host, but reproductive adults are free-living. Future research topics on nematodes and nematomorphs include clarifying their phylogenetic relationships relative to other ecdysozoans, developing better preventives for human and crop-related nematode infections, and better understanding the life cycles of many species with complex life histories. In addition, the field of nematology is in urgent need of a new phylogenetic system, given the conflict between the traditional taxonomy of the group and the phylogenetic history of the clade, making many traditional groups, including the famous Rhabditida, obsolete.

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CHAPTER 20

Panarthropoda and the Emergence of the Arthropods

Tardigrades, Onychophorans, and the Arthropod Body Plan

The clade Panarthropoda comprises three phyla: Arthropoda, Onychophora, and Tardigrada. Arthropoda is the largest phylum in the clade Ecdysozoa (and the largest phylum of Metazoa). In fact, with an estimated 1,196,521 named species (995,521 hexapods, 113,000 chelicerates, 72,000 crustaceans, 16,000 myriapods), arthropods are about 82% of all described living animal species. They are so abundant and so diverse and play such vital roles in all of Earth's environments that we devote five chapters to them. The present chapter is divided into four parts. First we introduce two close relatives of the arthropods, the phyla Tardigrada (water bears; 1,300 species) and Onychophora (velvet worms; 200 species). Then we introduce the phylum Arthropoda itself, exploring its general body plan and basic unifying features and how this combination of attributes has led to its preeminent success. Finally, we provide a brief overview of arthropod evolution. Detailed treatments of the living arthropod subphyla—Crustacea and Hexapoda (together, forming the clade Pancrustacea), Myriapoda, Chelicerata—are provided in Chapters 21, 22, 23, and 24.

The close relationship among Tardigrada, Onychophora, and Arthropoda has rarely been questioned—except for a few molecular studies that placed tardigrades with nematodes and/or nematomorphs. Stem group Panarthropoda probably arose in ancient Precambrian seas, as estimated by molecular data, and the phylum Arthropoda in particular has undergone a tremendous evolutionary radiation since its origins in the Fortunian Age of the lowermost Cambrian. For years it was thought that tardigrades were the sister group to the Arthropoda, but recent molecular phylogenies suggest that onychophorans hold that role, and Tardigrada is the sister group to that pairing. The terrestrial subphyla Hexapoda, Arachnida,

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

and Myriapoda probably all emerged from the sea between the Cambrian and the Silurian.

Defining Panarthropoda morphologically is less straightforward than one might think, as most characters typically used in textbooks are absent in one of the three phyla (Table 20.1). However, they all have muscles isolated in bands, although only weakly so in the tardigrades and onychophorans. They also all have paired ventrolateral segmental appendages with terminal "claws," but the nature of these appendages differs among them. But only the phylum Arthropoda has undergone a full "arthropodization" process, with both the body segmented (and with segmental sclerites) and the appendages segmented (divided into segmental podomeres/articles separated by arthrodial membranes and intrinsic muscles). Onychophorans and arthropods share the same general pattern of gap gene expression along the proximodistal axis of the appendages (these data are not yet known for tardigrades). All three groups have a ganglionic supraesophageal brain, but that of tardigrades is composed of a single ganglion pair, and that of onychophorans is composed of two (protocerebrum and deutocerebrum), while Arthropoda have three (protocerebrum, deutocerebrum, tritocerebrum). The ventral nerve cords of these three groups also differ, with a paired ganglionated nerve cord in tardigrades and arthropods versus a lack of segmental ganglia in onychophorans. Similarly, onychophorans do not express external segments but show an annulated cuticle. Nevertheless, the segment polarity transcription factor protein engrailed is expressed in the posterior ectoderm of developing segments in each of these panarthropod groups, suggesting that it plays a common role in establishing segmental boundaries in the three phyla. While a segmented mesoderm and a mixocoel have been suggested as synapomorphies for Panarthropoda, these are not seen in tardigrades (where they may have been secondarily lost).

FIGURE 20.1 Examples of the Panarthropoda. (A) Phylum Tardigrada; a water bear with developing oocytes. (B) Phylum Onychophora; a velvet worm. (C,D) Phylum Arthropoda, subphylum Crustacea. (C) An oceanic shrimp, *Sicyonia ingentis*. (D) A clam shrimp (order Diplostraca). (E) Phylum Arthropoda, subphylum Trilobita. (F–H) Phylum Arthropoda, subphylum Chelicerata. (F) A horseshoe crab, *Limulus polyphemus* (class Merostomata). (G) An orchard spider, *Leucauge* (a long-jawed orb weaver; class Arachnida). (H) A pycnogonid (class Pycnogonida). (I) Phylum Arthropoda, subphylum Myriapoda. A lithobiomorphan centipede. (J) Phylum Arthropoda, subphylum Hexapoda. A horse lubber grasshopper (*Taeniopoda eques*) from Arizona.

Today, arthropods occur in virtually every environment on Earth, exploiting every imaginable lifestyle (Figure 20.1C–J). Modern forms range in size from microscopic mites and crustaceans less than 1 mm long to Japanese spider crabs (*Macrocheira kaempferi*) with leg spans that reach nearly 4 m. Our inadequate knowledge of Earth's biodiversity is apparent when we consider the estimates of numbers of *undescribed species* of arthropods, which range from 3 million to over 100 million species. Most of this undiscovered diversity resides among the insects and mites on land and the crustaceans in the sea. Whether we lean toward the conservative or the liberal estimates, we are struck by the reality that no other phylum approaches the magnitude of species richness seen in arthropods. One might say, the modern world belongs to the arthropods. Yet, despite their overwhelming diversity, arthropods do share a suite of fundamental similarities and a distinct unifying

TABLE 20.1 A Comparison of the Panarthropod Phyla

Phylum/ subphylum	Number of described species	With segmental mesoderm and a mixocoel	Malpighian tubules	Muscles isolated as bands	Jointed legs	Compound eyes	With arthrodial membranes
Tardigrada	1,200	No	Present; endodermally derived	To some degree	No	No	No
Onychophora	200	Yes	Absent	Partly	No	No	No
Arthropoda: Crustacea	72,000	Yes	Absent	Strongly	Yes	Yes	Yes
Arthropoda: Hexapoda	941,054	Yes	Present; ectodermally derived	Strongly	Yes	Yes	Yes
Arthropoda: Myriapoda	16,000	Yes	Present: ectodermally derived	Strongly	Yes	Yes	Yes
Arthropoda: Chelicerata	113,000	Yes	Present; endodermally derived	Strongly	Yes	Yes	Yes
Trilobita (extinct)	>15,000	Unknown	Unknown	Strongly	Yes	Yes	Yes

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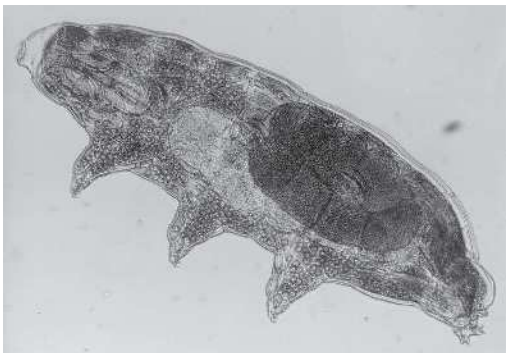

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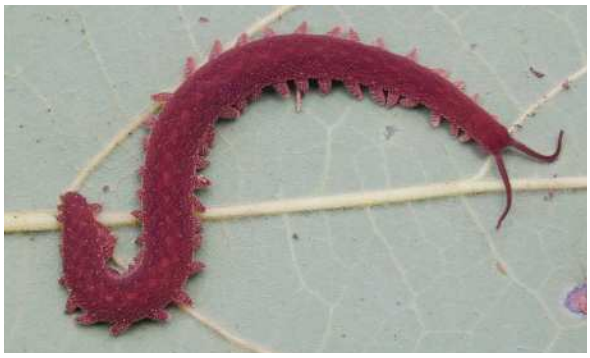

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(J)

Courtesy of R. Brusca

body plan that we describe later in this chapter. But first, we begin our discussion with the less diverse, but equally charismatic relatives of the arthropods—the water bears and velvet worms.

Phylum Tardigrada

The first recorded observation of a tardigrade was by Polish theologian Johann Conrad Eichhorn in 1767. Since then, about 1,300 species have been described. Fossil tardigrades are very rare; they include specimens from the middle Cambrian of Siberia with "Orsten"-type preservation, having only three pairs of legs (Box 20A), from North American Cretaceous amber—*Milnesium swolenskyi* from the Late Cretaceous of New Jersey (USA), *Beorn leggi* from the Late Cretaceous of Manitoba (Canada), and *Paradoryphoribius chronocaribbeus* from Miocene age Dominican amber. More recently, rock fossil tardigrades have been discovered from the lower Cambrian Chengjiang deposits of China, but these remain unpublished.

Phylogenomic analyses, as well as neuroanatomical studies, support the traditional view that tardigrades are part of the Panarthropoda clade. Although the phylogenetic position of tardigrades relative to Onychophora is still debated, the most recent evidence suggests Onychophora is the sister group to Arthropoda, while Tardigrada is the sister group to that clade.

Most living tardigrade species are found in semiaquatic habitats, such as the water films on mosses, lichens, liverworts, and certain angiosperms, or in soil and forest litter. Others live in various freshwater and marine benthic habitats, both deep and shallow, often interstitially or among shore algae. A few very interesting species have been reported from hot springs. Some marine species are commensals on the pleopods of isopods or the gills of mussels; others are ectoparasites on the epidermis of holothurians or barnacles. Tardigrades occasionally occur in high densities, up to 300,000 per square meter in soil and more than 2,000,000 per square meter in moss. All are small, usually on the order of 0.1–0.5 mm in length, although some l.3 mm giants have been reported.

Under the microscope, tardigrades resemble miniature eight-legged bears, especially as they move with a lumbering, ursine gait—hence the name Tardigrada (Latin *tardus*, "slow"; *gradus*, "step"). Their locomotion, paunchy body, and clawed legs have earned them the nickname "water bears" (Figures 20.1A and 20.2–20.11).

Most terrestrial tardigrade species are widespread, and many might be cosmopolitan. A major factor in their wide distribution is probably the fact that their eggs, cysts, and tuns are resistant and light enough to be carried great distances either by winds or on soil clinging to insects, birds, and other animals. The minute sizes and precarious habitats of water bears have resulted in numerous traits also seen in some blastocoelomate groups that live in similar habitats.

Tardigrades are well known for their remarkable powers of **anabiosis** (a state of dormancy that involves greatly reduced metabolic activity during unfavorable environmental conditions) and **cryptobiosis** (an extreme state of anabiosis in which all external signs of metabolic activity are absent). Soil and freshwater tardigrades, during dry periods when the ponds or vegetation they inhabit become desiccated, encyst by pulling in their legs, losing body water, and secreting a double-walled cuticular envelope around the shriveled body. Such anabiotic cysts maintain a very low basal metabolism. Further reorganization (or "deorganization") of the body can result in a single-walled **tun** stage, in which body metabolism is undetectable (a cryptobiotic state). The extreme expression of cryptobiosis is the **anhydrobiosis** state, in which terrestrial tardigrades can survive as dry tuns for many years.

The resistant qualities of tardigrade tuns in anhydrobiosis have been demonstrated by experiments in which individuals have recovered after immersion in extremely toxic compounds such as brine, ether,

BOX 20A Characteristics of the Phylum Tardigrada

1. With modified or nonteloblastic segmentation; living species with 4 pairs of legs
2. Malpighian tubules without cuticle (i.e., endodermally derived)
3. With nonjointed, telescopic legs lacking intrinsic musculature
4. With a unique nerve connection between the first brain lobe and first ventral trunk ganglion
5. All sensory structures—cirri (mechanoreceptors) and clavae (chemoreceptors)—similar to those of arthropods
6. Body coelom greatly reduced and functioning as a hemocoel (defined coelomic compartments absent or restricted to gonadal cavities)
7. With thin, uncalcified cuticle, but always very complex—in all heterotardigrades with an outer honeycomb layer, followed with pillars and finally with a procuticle containing α-chitin
8. Muscles in isolated bands; body wall without sheetlike circular muscle layer
9. Cross-striated muscles in the stylet muscles of all tardigrades; cross-striated muscles in all muscles of all arthrotardigrades
10. Mouth terminal or ventral
11. Without circulatory system, gas exchange structures, or metanephridia
12. Cyclomorphosis is known in several marine eutardigrades
13. Capable of pronounced anabiosis/cryptobiosis

The section on Tardigrada was revised by Reinhardt Møbjerg Kristensen.

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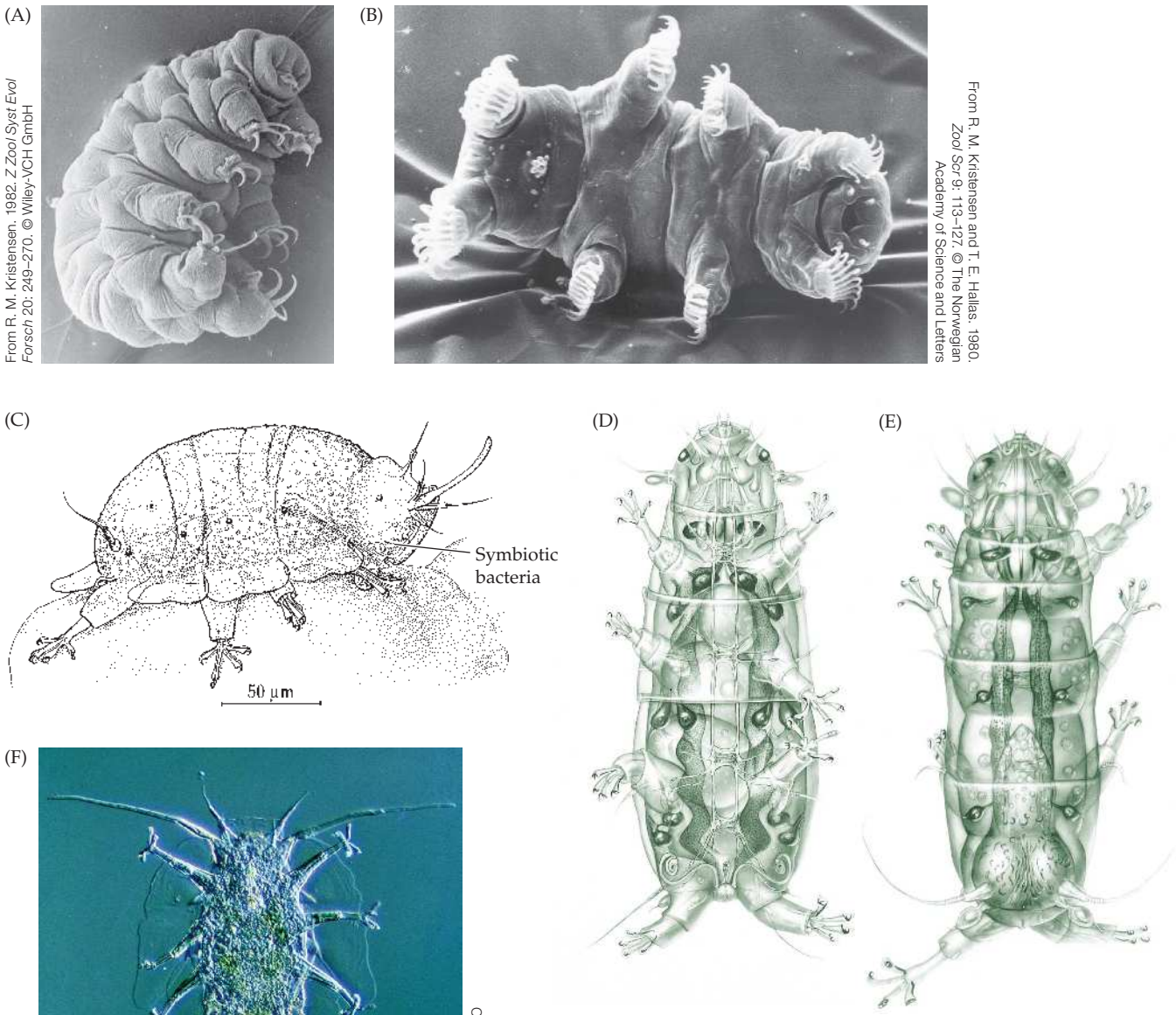
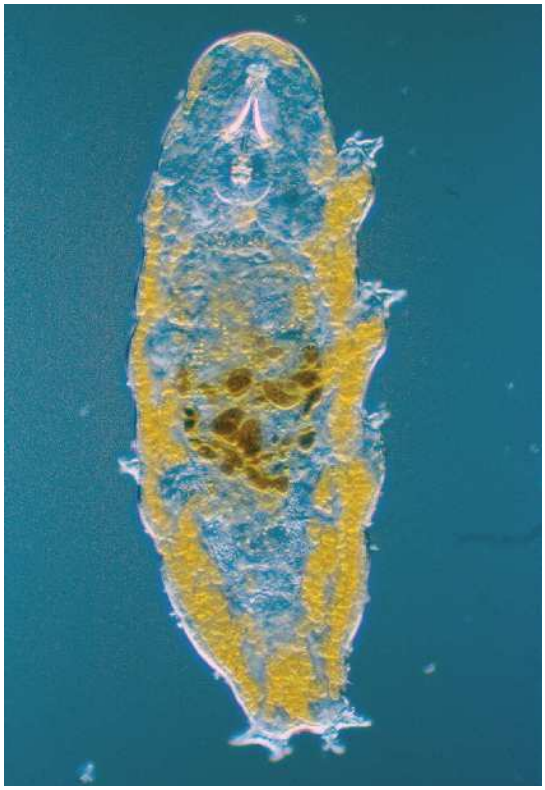


FIGURE 20.2 Representatives of the phylum Tardigrada. (A) *Halobiotus crispae*, a marine species common on brown algae in Greenland. This species undergoes a yearly cyclomorphosis involving a special hibernation stage (the pseudosimplex) during which it overwinters in the icy Greenland littoral zone. (B) *Echiniscoides sigismundi* (ventral view), a littoral species from Denmark. (C) *Wingstrandarctus corallinus* from the Coral Sea (which has symbiotic bacteria in its head). (D,E) *Styraconyx qivitoq* (ventral and dorsal views), a tardigrade that lives on ectoprocts and has been collected only in Greenland. (F) A marine water bear, *Florarctus heimi* (Arthrotardigrada), from coal sand at Heron Island, Australia. A male with extremely long primary clavae (chemoreceptors).

absolute alcohol, and even liquid helium. They have survived temperatures ranging from +149°C to –272°C, on the brink of absolute zero. They have also survived high vacuum, intense ionizing radiation, and long periods with no environmental oxygen whatsoever. Following desiccation, when water is again available, the animals swell and become active within a few hours. Many rotifers, nematodes, mites, and a few insects are also known for their anabiotic powers, and these groups often occur together in the surface water films of plants such as mosses and lichens. Tardigrades are also found on the Greenland ice sheet, in the so-called cryoconite holes formed by stardust and dark terrestrial material such as soot and volcanic dust, where few other metazoans can survive. Experiments with tardigrades in anhydrobiosis have demonstrated they can even survive at least several months in outer space. The BIOPAN 6 experiment in 2007 showed that tardigrades from mosses (Figure 20.3) could survive outside the spacecraft in anhydrobiosis for several months. In the most extreme case, embryos of *Milnesium tardigradum*



Courtesy of R. M. Kristensen

FIGURE 20.3 The giant eutardigrade *Richtersius coronifer*. From moss on the Swedish island of Öland. The cryptobiotic tun of this species survived experiments in outer space.

kept for three months in an outer space hatch had 100% survival after rehydration. And in 2019 an Israeli spacecraft carrying tardigrades crash-landed on the moon, leaving them stranded in a state of anhydrobiosis on that satellite's surface.

One marine tardigrade genus (*Echiniscoides*) survives quite well with a life cycle that regularly alternates between active (Figure 20.2B) and tun stages, and it can even survive an experimentally induced cycle forcing it to undergo cryptobiosis every six hours! Evidence indicates that the tardigrade aging process largely ceases during cryptobiosis and that by alternating active and cryptobiotic periods, tardigrades may extend their life spans to several decades. One rather sensational report described a dried Italian museum specimen of moss that yielded living tardigrades when moistened after 120 years on the shelf! However, the tardigrades died shortly later.

Early genomic analyses of tardigrades indicated that this group had incorporated a huge number of foreign genes into its own genome, by way of horizontal gene transfer, from various Eubacteria, Archaea, and even plants and fungi. These adopted genes, which comprised as much as 17.5% of the tardigrades' DNA, were thought to play a role in the ability of water bears to withstand extreme stresses. But this was later shown to be the result of contamination, and although subsequent genome resequencing showed some level of horizontal gene transfer, this was in the order of 1%–2%, similar to many other animals.

In certain areas of extreme environmental conditions, marine tardigrades may undergo an annual cycle of **cyclomorphosis** (rather than the cryptobiosis typical of terrestrial and freshwater forms). During cyclomorphosis, two distinct morphologies alternate. For example, *Halobiotus crispae*, a littoral species first found in Greenland (Figures 20.2A and 20.4), has a summer morph and a winter morph. The latter is a special hibernation stage called the **pseudosimplex** that is resistant to freezing temperatures and perhaps low salinities. In contrast to cryptobiotic tuns, the pseudosimplex is active and motile. Cyclomorphosis is coupled with gonadal development, and in Greenland only the summer morph is sexually mature.

Currently the phylum Tardigrada comprises 31 families in three classes: Heterotardigrada, Apotardigrada, and Eutardigrada. The classes are defined largely on the basis of the details of the head appendages, the nature of the leg claws, and the presence or absence of Malpighian tubules. The former monotypic class Mesotardigrada includes the single species *Thermozodium esakii*, known only from the hot springs of Unzen Park, near Nagasaki, Japan, but it has not been found since the end of the Second World War. Recently, a team of experts looked for this species but could not rediscover it, therefore leaving *T. esakii* a nomen dubium. Heterotardigrades include the orders Arthrotardigrada (nearly all marine) and Echiniscoidea (marine, freshwater, and terrestrial); however, the arthrotardigrades are clearly paraphyletic with respect

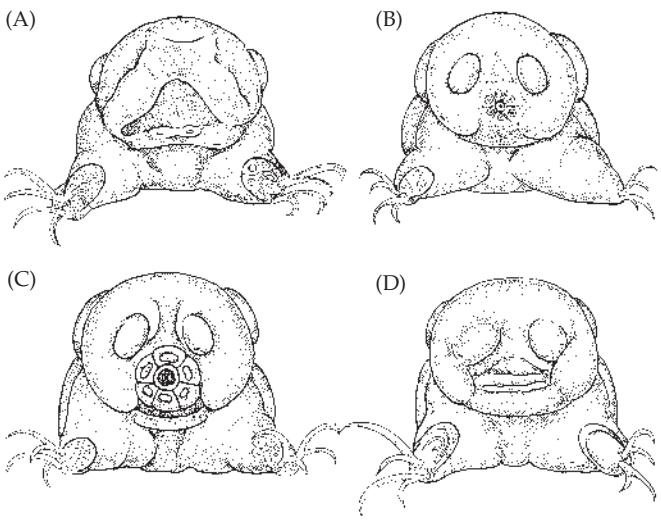


FIGURE 20.4 Cyclomorphosis in a marine tardigrade, *Halobiotus crispae*, from Greenland; frontal views. (A) The hibernation stage, pseudosimplex 1 (winter form, with double cuticle). (B) Pseudosimplex 2 (spring form, with thin cuticle and small claws). (C) The sexually mature stage (summer form, with large claws). (D) The molting (simplex) stage, with closed mouth opening (molting animals can be found year round).

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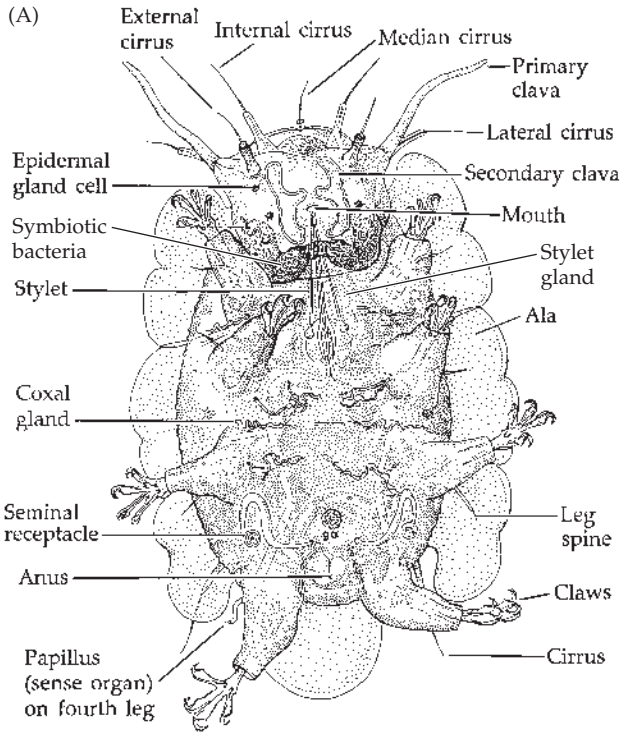
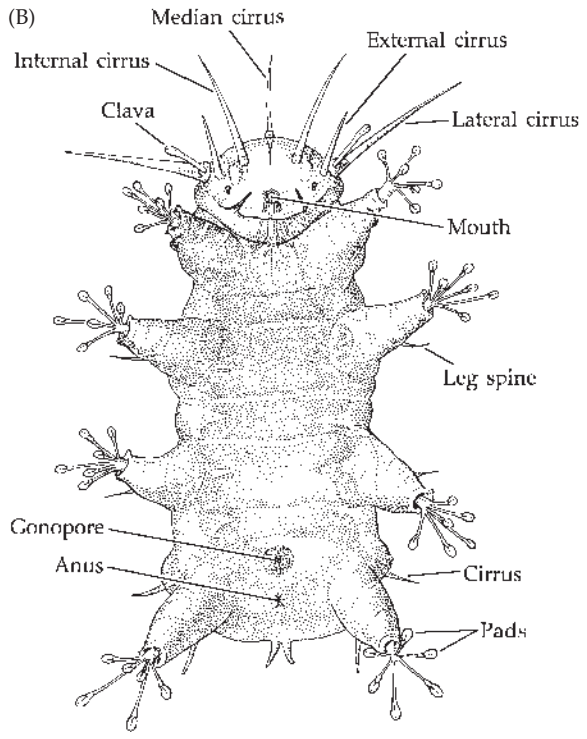
to the echiniscoids. Apotardigrada and Eutardigrada are freshwater-terrestrial, except for two secondarily marine genera of eutardigrades.

The Tardigrade Body Plan

Tardigrades have four pairs of ventrolateral legs (Figures 20.2, 20.3, 20.4, 20.5, and 20.6). The legs of eutardigrades (Figure 20.2A) are short, hollow extensions of the body wall, essentially lobopodal in design, and similar to the lobopodal legs of onychophorans. Each leg terminates in one or as many as a dozen or so "claws" (Figures 20.4, 20.5, 20.6, and 20.7). The claws may be modified as adhesive pads or discs, or the claws may resemble those of onychophorans. In the marine arthrotardigrades (Figures 20.2C and 20.5A), the legs are telescopic and each consists of a so-called coxa, femur, tibia, and tarsus; however, there is no evidence that these leg "segments" are homologous with those of arthropod legs.

As in onychophorans, the body is covered by a thin, unmineralized cuticle that is periodically molted. It is often ornamented and occasionally divided into symmetrically arranged dorsal and lateral (rarely ventral) plates (Figures 20.2 and 20.5C). These plates may be homologous with the sclerites of arthropods, but this is not certain. The cuticle shares some features with both onychophorans and arthropods, but it is also unique in certain ways—for example, the epicuticle often has support pillars (Figure 20.8). Elsewhere the cuticle comprises up to seven distinguishable layers and contains various sclerotized ("tanned") proteins and always chitin in the procuticle, and it lines the foregut and rectum. The cuticle is secreted by an underlying epidermis, which is composed of a constant cell number in many (but not all) species. Such cell constancy and the phenomenon of eutely are common in minute metazoans, and we have noted several other examples among the blastocoelomate phyla (e.g., some rotifers and nematodes). Growth in tardigrades proceeds by





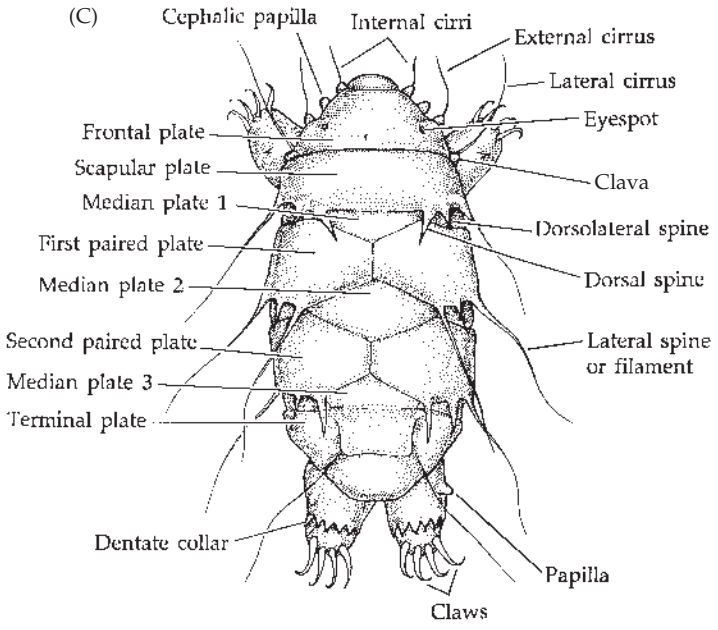
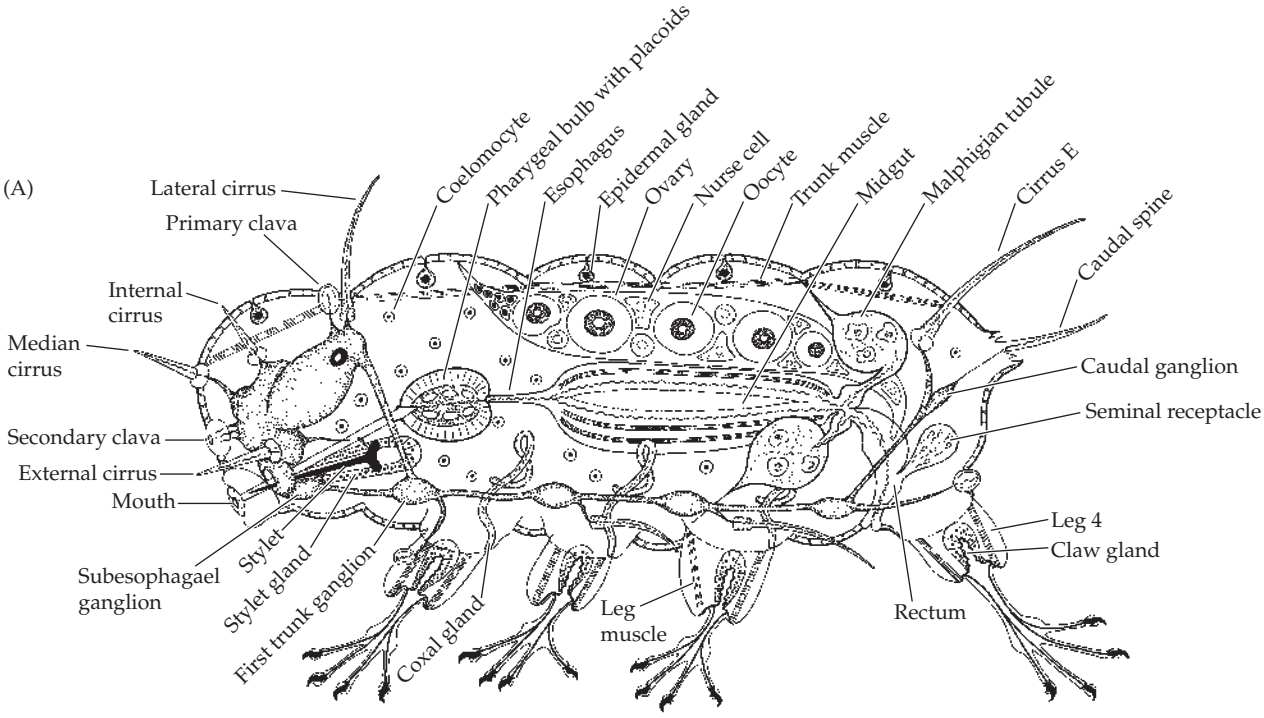
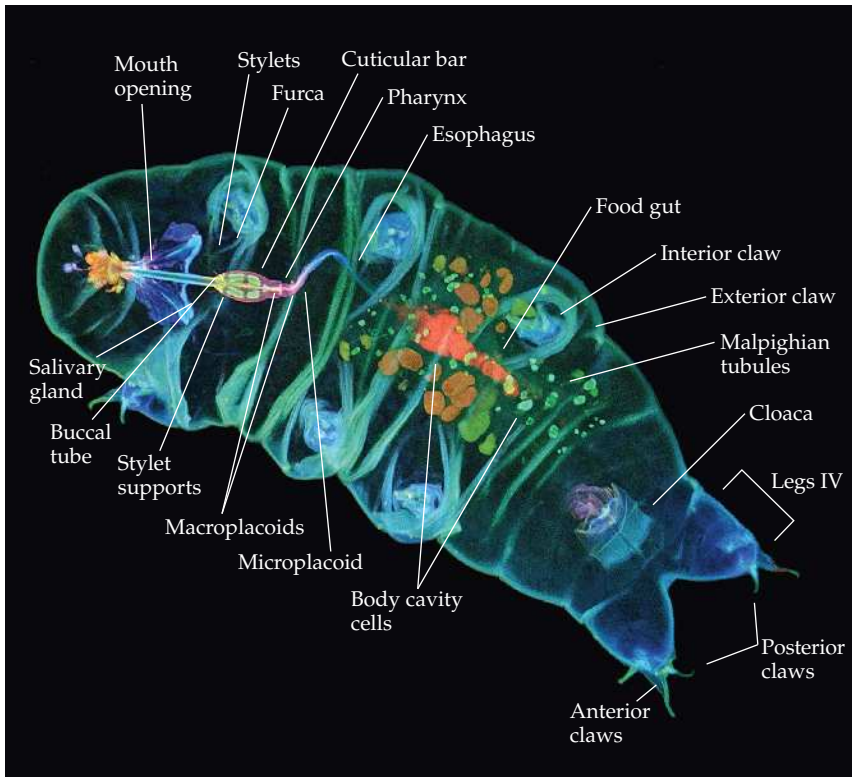


FIGURE 20.5 Tardigrade anatomy. (A) *Wingstrandarctus corallinus* (ventral view), an inhabitant of shallow, sandy marine habitats in Australia and Florida. (B) *Batillipes noerrevangi* (ventral view). (C) Generalized *Echiniscus* (dorsal view).

molts, as in onychophorans and arthropods, with sexual maturity being attained after three to six instars. Not only is the cuticle molted—the buccal canal, the two stylets, the two stylet supports, and the distal part of legs with claws or toes are also re-formed during ecdysis. Both the claws and the stylets are formed in special glands—called **stylet** and **claw glands** (Figures 20.5A and 20.6). During ecdysis the animal cannot eat, and the mouth opening is closed. This stage is called the **simplex stage**.





Courtesy of Tagide deCarvalho and William Miller

FIGURE 20.6 More tardigrade anatomy. (A) Body plan of a generalized tardigrade. (B) The tardigrade *Hypsibius exemplaris*. This beautiful confocal micrograph was accomplished by the use of fluorescent dyes. *Hypsibius exemplaris* is a European species kept in cultures around the world and emerging as a "model organism."

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The body is quite short, segmentation is homonomous, and tardigrades are rather weakly cephalized. Such a compact body seems to be derived from a loss of most of the trunk region, making the tardigrade body basically homologous with the arthropod head. Nonmarine tardigrades are often colorful animals, exhibiting shades of pink, purple, green, red, yellow, gray, and black. Color is determined by cuticular pigments, the color of the food in the gut, or the presence of granular bodies with carotene in the coelomocytes suspended in the hemocoel.

Like the coelom of arthropods and onychophorans, the adult coelom of tardigrades is either greatly reduced and confined largely to the gonadal cavities or absent altogether, depending on the interpretation. The main body cavity is thus a hemocoel, and the colorless body fluid directly bathes the internal organs and body musculature. Furthermore, all Eutardigrada and Apotardigrada have many coelomocytes in this body fluid. The coelomocytes provide nutrition to all the organs in the body. In the Arthrotardigrada the situation is very different, as there is clearly no body cavity (thus they are acoelomate) and the coelomocytes are fixed (e.g., to the brain). Here the coelomocytes are called "amebocytes."

The musculature of tardigrades is quite different from that of onychophorans, in which the body wall muscles are in sheetlike layers; in tardigrades there is no circular muscle layer in the body wall, and the muscles occur in separate bands extending between subcuticular attachment points, as they do in arthropods (Figure 20.6).

It was long thought that tardigrades possessed only smooth muscle, in contrast to the striated muscles of arthropods, and in the past this feature was used as an argument against a close relationship between these two phyla. However, we now know that both smooth and striated muscles occur in all tardigrades, the latter predominantly in the order Arthrotardigrada. The striated muscles are of the arthropod type, being cross-striated rather than obliquely-striated like those of onychophorans. Numerous fine structural details of the muscle attachment regions are also shared between tardigrades and arthropods. Furthermore, in all tardigrades the stylet muscles always are cross-striated. It has been suggested that a partial shift from arthropod-like striated muscle to smooth muscle in some tardigrades might have accompanied a transition from the marine to the terrestrial environment, and it might be functionally tied to the phenomenon of cryptobiosis. Furthermore, both slow and fast nerve fibers occur in tardigrades, the former predominating in the somatic musculature and the latter in the leg musculature. However, the leg musculature appears to be entirely extrinsic, like that of onychophorans, with one muscle attachment near the tip of the leg and the other within the body proper. Many of the muscle bands in tardigrades consist of only a single muscle cell or a few large muscle cells each.

Locomotion

The concentration of muscles as discrete units and the thick cuticle in tardigrades demand a different locomotory strategy than the primarily hydrostatic system seen in onychophorans. Instead, tardigrades use a step-by-step gait controlled by independent antagonistic sets of muscles or by flexor muscles that work against hemocoelic pressure. The claws, pads, or discs at the ends of the legs are used for purchase and for clinging to objects, such as strands of vegetation or sediment particles (Figure 20.7). And, at least one marine species, *Tholoarctus natans*, is capable of limited jellyfish-like swimming by use of a bell-shaped expansion of the cuticle margin to keep it suspended just above the sediment.

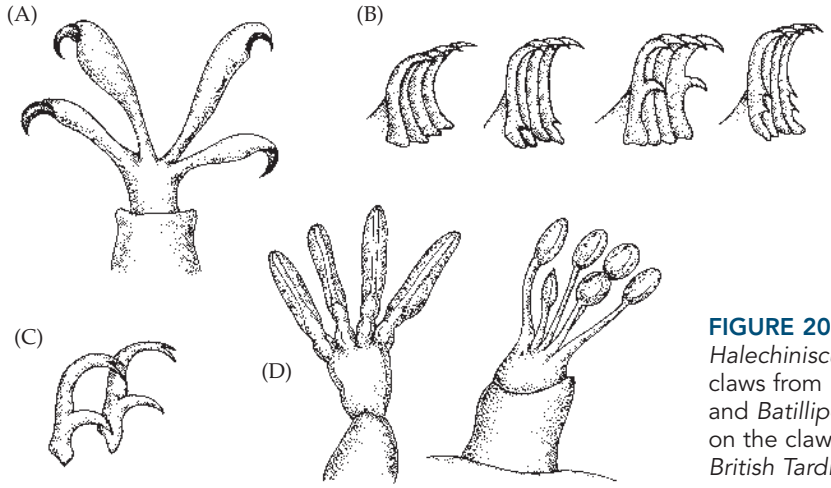

FIGURE 20.7 Tardigrade feet. (A) The foot of *Halechiniscus*. (B) Claw types from *Echiniscus*. (C) Typical claws from *Macrobiotus*. (D) The feet of *Orzeliscus* (left) and *Batillipes* (right), showing adhesive discs or pads on the claws. (After C. I. Morgan and P. E. King. 1976. *British Tardigrades*. Academic Press, London.)

Feeding, Digestion, and Excretion

Tardigrades usually feed on the fluids inside plant or animal cells by piercing the cell walls with a pair of **oral stylets**. Soil-dwelling species feed on bacteria, algae, and decaying plant matter or are predators on small invertebrates. Carnivorous and omnivorous tardigrades have a terminal mouth; herbivorous and detritivorous ones have a ventral mouth.

The mouth opens into a short stomodeal buccal tube, which leads to a bulbous, muscular pharynx (Figure 20.6). A pair of large salivary glands flank the esophagus and produce digestive secretions that empty into the mouth cavity; these glands also are responsible for the production of a new pair of oral stylets with each molt, hence they are often referred to as **stylet glands** (Figures 20.5A and 20.6). The muscular pharynx produces suction that attaches the mouth tightly to a prey item during feeding and pumps the cell fluids out of the prey and into the gut. In many species there is a characteristic arrangement of chitinous rods, or **placoids**, within an expanded region of the pharynx. These rods provide support for the musculature of that region and may contribute to masticating action. The pharynx empties into an esophagus, which in turn opens into a large intestine (midgut), where digestion and absorption take place. The short hindgut (the cloaca or rectum) leads to a terminal anus. In some species defecation accompanies molting, with the feces and cuticle being abandoned together. Several marine arthrotardigrades have symbiotic bacteria in cephalic vesicles (Figures 20.2C and 20.5A). In *Wingstrandarctus* these bacteria may be used when the tardigrades are starving. The vesicles can be empty when the tardigrades have a full, green gut content, indicating they have been feeding on plant material.

At the intestine-hindgut junction in freshwater and terrestrial species of eutardigrades there are three large glandular structures called **Malpighian tubules** (Figure 20.6), each consisting of only about nine cells. The precise nature of these organs is not well understood, but they are probably not homologous with the Malpighian tubules of arthropods. In at least one marine eutardigrade genus (*Halobiotus*), the Malpighian tubules are greatly enlarged and have an osmoregulatory function. It is probable that some excretory products are absorbed through the gut wall and eliminated with the feces; other waste products may be deposited in the old cuticle prior to molting. In terrestrial heterotardigrades, excretory and ion/osmoregulatory structures are found between the second and third pairs of legs. However, in several marine arthrotardigrades segmental trunk glands open at the base of the legs and a single pair of these segmental glands is located in the head. These glands may be homologous with the coxal glands of arthropods.

Circulation and Gas Exchange

Perhaps because of their small size and moist habitats, tardigrades have no traces of discrete blood vessels, gas exchange structures, or metanephridia; consequently, they rely on diffusion through the body wall and the extensive body cavity. The body fluid contains numerous cells (sometimes called coelomocytes) credited with a storage function.

Nervous System and Sense Organs

The nervous system of tardigrades is built on the arthropod plan and is distinctly metameric. A large dorsal cerebral ganglion is connected to a subpharyngeal ganglion by a pair of commissures surrounding the buccal tube (Figure 20.6). From the subpharyngeal ganglion, a pair of ventral nerve cords extends posteriorly, connecting a chain of four pairs of ganglia that serve the four pairs of legs. As a unique apomorphy for all tardigrades, there exists a nerve connective between the first brain lobe and the first ventral trunk ganglion. Sensory bristles or spines occur on the body, particularly in the anterior and ventral region and on the legs. The structure of these bristles is essentially homologous with that of arthropod setae (Figure 20.8). A pair of sensory eyespots is often present inside the dorsal brain. Each eyespot consists of five cells, one of which

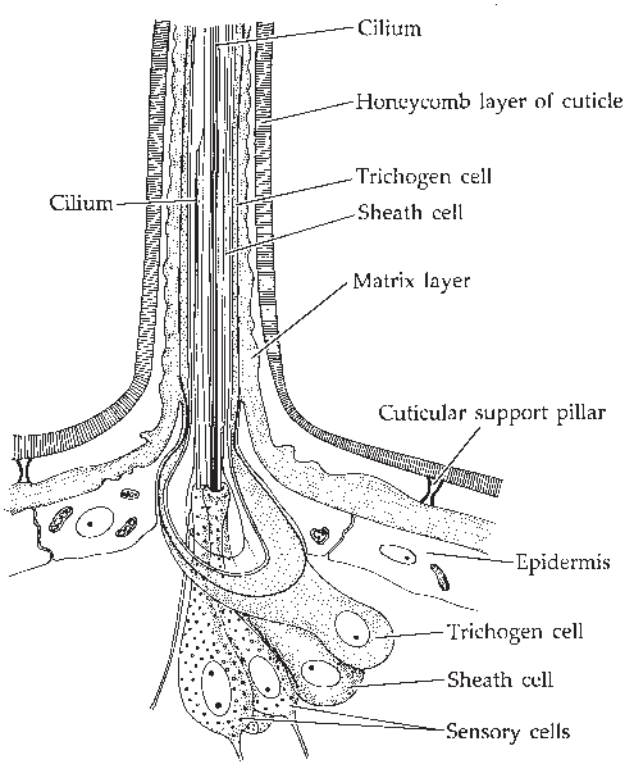

FIGURE 20.8 **Base of an external bristle of *Batillipes noerrevangi* (longitudinal section), showing the relationship between the various cells and the cuticle.**

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is a pigmented light-sensitive cell with both microvilli and modified ciliary structure.

The anterior end of many heterotardigrades bears long sensory **cirri**, and most of these species also have one to three pairs of hollow anterior sensory structures called **clavae** that are probably chemosensory in nature (Figures 20.2C and 20.5). The clava appears structurally similar to the olfactory seta of many arthropods. Many males have longer clavae than females.

Reproduction and Development

Many tardigrades are gonochoristic, with both sexes possessing a single saclike gonad lying above the gut. In males, the gonad terminates as two sperm ducts, suggesting that the single gonad is derived from an ancestral paired condition (Figure 20.9). The ducts extend to a single gonopore, which opens just in front of the anus or into the rectum. In females a single oviduct (right or left) opens either through a gonopore anterior to the anus or into the rectum (which in this case is called a cloaca) (Figure 20.6). There are two complex seminal receptacles (e.g., Arthrotardigrada) that open separately (Figure 20.5A) or a single small seminal receptacle (e.g., some Eutardigrada) that opens into the rectum near the cloaca (Figure 20.6).

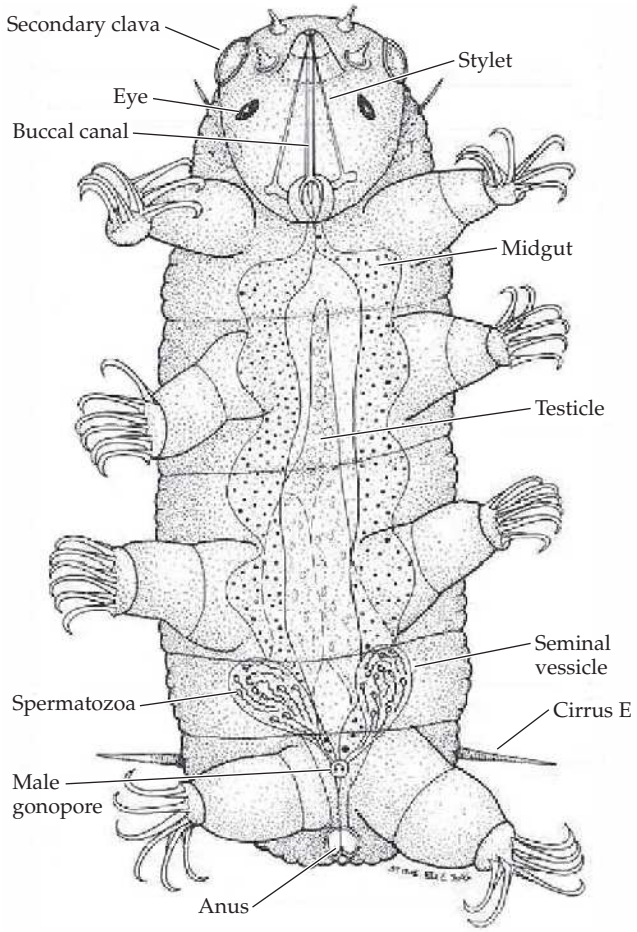


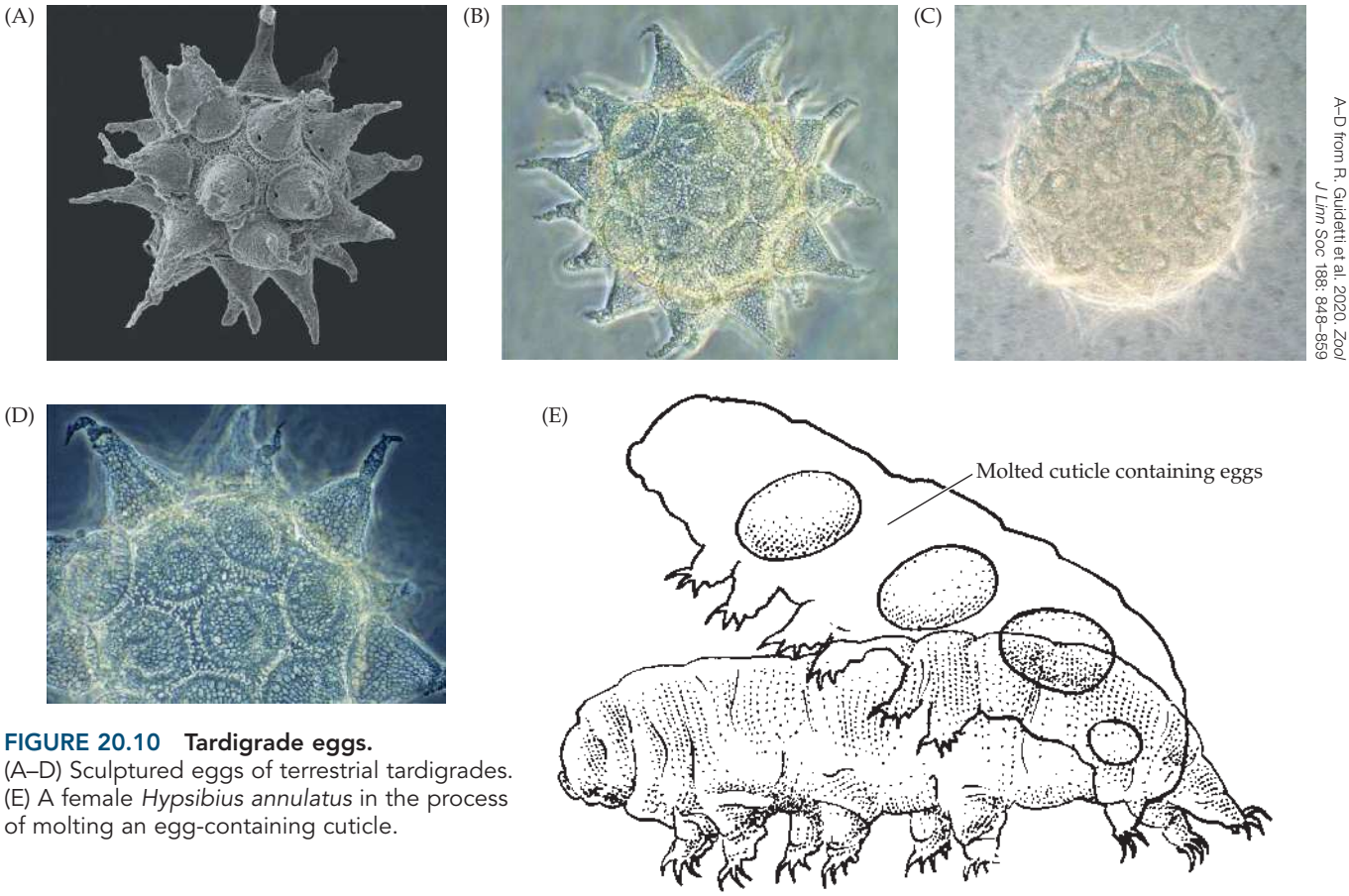
FIGURE 20.9 Reproductive system of a male tardigrade. Ventral drawing of *Isoechiniscoides sifae*, a marine heterotardigrade with six claws on each leg. (Illustration by Stine B. Elle from N. Møbjerg et al. 2016. *Zool J Linn Soc* 178: 804–818.)

Males are unknown in some terrestrial genera, but most tardigrades that have been studied copulate and lay eggs, and copulation is amazingly diverse among these little water bears. Parthenogenesis may be common in some terrestrial species, notably those in which males are unknown. Hermaphroditism has also been reported in a few genera. Dwarf males have been recently discovered in several marine genera. In some tardigrades the male deposits sperm directly into the female's seminal receptacles (or cloaca) or into the body cavity by cuticular penetration. In the latter case fertilization takes place in the ovary. In other tardigrades, a wonderfully curious form of indirect fertilization takes place: the male deposits sperm beneath the cuticle of the female prior to her molt, and fertilization occurs when she later deposits eggs in the shed cuticular cast (Figure 20.10). Several studies have shown tardigrade sperm to be uniflagellate. In at least a few marine species, a primitive courtship behavior exists, wherein the male strokes the female with his cirri. Thus stimulated, the female deposits her eggs on a sand grain, upon which the male then spreads his sperm.

Females lay from 1 to 30 eggs at a time, depending on the species. In strictly aquatic species the fertilized eggs are either left in the shed cuticle or glued to a submerged object. The eggs of many terrestrial species bear thick, sculptured shells that resist drying (Figures 20.10 and 20.11). Some species alternate between thin-walled and thick-walled eggs, depending on environmental conditions.

There have been only a few studies on tardigrade embryology. Development appears to be direct and rapid, but indeterminate. Cleavage has been described as holoblastic and always radial. A blastula develops, with a small blastocoel; eventually it proliferates an inner mass of endoderm that later hollows to form the archenteron. Stomodeal and proctodeal invaginations develop, completing the digestive tube. Subsequent to gut formation, five pairs of archenteric coelomic pouches are said to appear off the gut, reminiscent of the enterocoelic development of many deuterostomes. The first pair arises from the stomodeum (ectoderm) and forms the stylet glands and stylets, and the last four pairs from the midgut (endoderm). The two posterior pouches fuse to form the gonad; the others disappear as their cells disperse to form the body musculature.

Tardigrades were long thought to have typical teloblastic segmentation, a type of development where there is a growth zone from which the new body segments arise. However, recent work has shown that



A–D from R. Guidetti et al. 2020. *Zool J Linn Soc* 188: 848–859

FIGURE 20.10 Tardigrade eggs.
(A–D) Sculptured eggs of terrestrial tardigrades. (E) A female *Hypsibius annulatus* in the process of molting an egg-containing cuticle.

tardigrades develop all four pairs of legs and the coelomic pouches very early in embryogenesis, and the legs are present when they hatch. So, teloblastic segmentation may be modified in living species. However, extinct Cambrian tardigrades from Siberian limestone may have had teloblastic growth—the smallest specimens have only three pairs of legs, and larger specimens have limb buds for the fourth pair of legs. Development in living species is typically completed in 14 days or less, whereupon the young use their stylets to break out of the shell (Figure 20.11C).

Juveniles lack adult coloration, have fewer lateral and dorsal spines and cirri, and may have reduced numbers of claws, when compared to adults. At birth, the number of cells in the body is relatively fixed, and growth is primarily by increases in cell size rather than in cell number. In nature, these remarkable animals may live only a few months or may survive for a great many years.

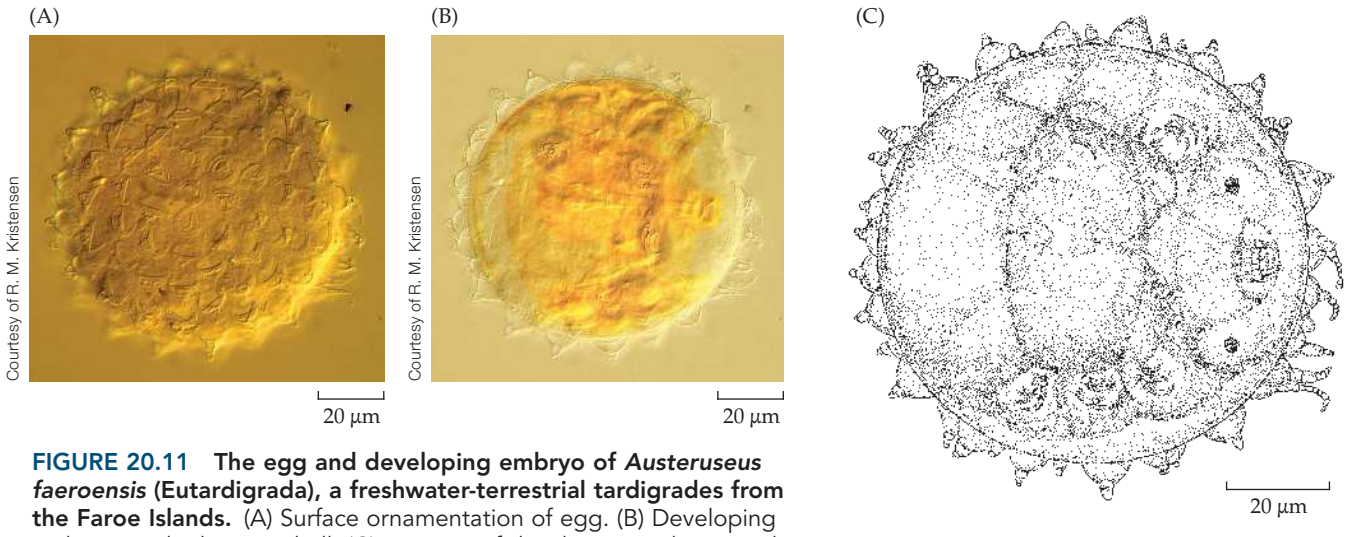


FIGURE 20.11 The egg and developing embryo of *Austeruseus faeroensis* (Eutardigrada), a freshwater-terrestrial tardigrades from the Faroe Islands. (A) Surface ornamentation of egg. (B) Developing embryo inside the egg shell. (C) Drawing of developing embryo inside the egg shell.

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Phylum Onychophora

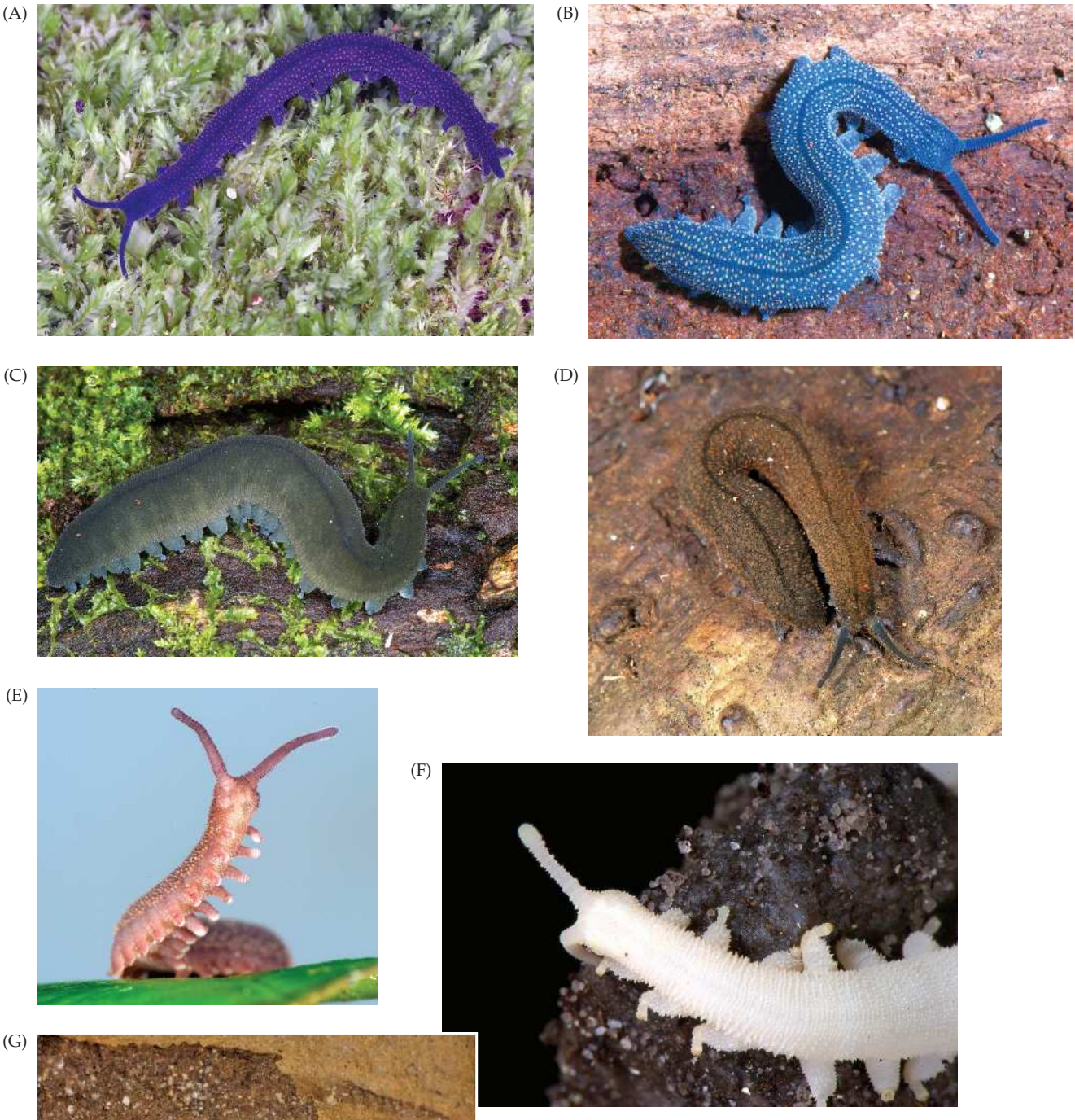
The first living onychophoran (Greek *onycho*, "talon"; *phora*, "bearer") was described by the Reverend Lansdown Guilding in 1826 as a leg-bearing slug (a mollusc). Since that initial discovery, 220 or so species of onychophorans have been described, 200 of which are considered valid, and probably at least that many more remain to be discovered (Figures 20.1B and 20.12). All the living species are terrestrial, constituting the only animal phylum that is entirely land-bound. We now know that onychophoran relatives, probably part of the stem group, known as lobopodians, were part of the explosive marine diversification in the lower Cambrian (see Chapter 1). Their fossils have been found in middle Cambrian marine faunas at several localities (e.g., *Aysheaia pedunculata* from the famous middle Cambrian Burgess Shale deposits of British Columbia, Canada, and *Aysheaia prolata* from a similar deposit in Utah), in the remarkable Chengjiang lower Cambrian (520–530 Ma) deposits of China, and in the equally stunning Swedish upper Cambrian Orsten fauna. Perhaps the most famous lobopodian fossil is the Cambrian genus *Hallucigenia*, long a mystery because it was originally interpreted in an upside-down orientation but later turned right side up and discovered to possess long dorsal spines (Figure 20.13A). The fossil record of crown group Onychophora is, however, restricted to a Carboniferous deposit from the Stephanian deposits of Montceau-les-Mines (France) (Figure 20.12G) and to a few amber deposits from the Cretaceous of Myanmar (Figure 20.13E).

Onychophora constitutes an old group that has changed very little over the past 310 million years. At some point in its long history, prior to the Carboniferous Period (when the first unambiguous crown-group onychophorans appear in the fossil record), they successfully invaded the terrestrial environment. Like arthropods and tardigrades, onychophorans are segmented animals, and they have features that are somewhat intermediate between those of tardigrades and arthropods. The three phyla together comprise the clade called Panarthropoda. Due to their special type of segmentation, in the past, workers regarded onychophorans as "living fossils," or "missing links" between other segmented soft-bodied animals, such as annelids, and the arthropods. However, molecular phylogenetic studies now place the annelids in the Spiralia, quite distant from the Panarthropoda, which are ecdysozoans. Their close relationship to arthropods has triggered a great deal of research on onychophorans, aimed at understanding the early steps in the evolution of Earth's most diverse animal phylum. Indeed, research on velvet worms has undergone a revival in the twenty-first century with a plethora of studies focusing on their development, the nervous system, and segmentation, as well as taxonomic and biogeographic treatments.

Living onychophorans comprise two families, Peripatidae and Peripatopsidae (Figure 20.12). The former is circumtropical in distribution (with multiple species in the Neotropics, one in western Africa, and a few in Southeast Asia), whereas the latter is circumaustral (confined to the more temperate Southern Hemisphere), with species in Chile, South Africa, New Zealand, and Tasmania but also in the tropical regions of New Guinea and Australia. During dry periods, velvet worms retire to protective burrows or other retreats where they can preserve moisture and become inactive. During wet periods they can be found actively hunting at night, inside damp fallen tree logs, or in leaf litter. Onychophorans live for several years, during which time periodic molting takes place, as often as every two weeks in some species (Box 20B).

BOX 20B Characteristics of the Phylum Onychophora

1. Segmentation probably teloblastic; 13–43 pairs of legs
2. Muscles in isolated bands
3. With superficially annulated, nonjointed, telescopic, lobopodal legs lacking intrinsic musculature; legs with terminal claw (or hooks)
4. Cerebral ganglion (brain) lying dorsal to pharynx, probably with only two pairs of ganglia; protocerebrum innervating eyes and antennae; deutocerebrum innervating jaws
5. With jaws, probably homologous with chelicerae of Chelicerata, or antennae of myriapods and hexapods (first antennae of crustaceans)
6. Paired ventral nerve cords different from those of tardigrades and arthropods, with no relationship between arrangement of median or ring commissures and position of legs; cell bodies of serotonergic neurons not arranged in the segmentally repeated and bilaterally symmetrical pattern characteristic of arthropods (instead, scattered in an apparently random fashion along the length of the nerve cord)
7. With slime papillae, possibly from modified nephridia (innervated by ventral nerve cords)
8. Embryonic coelomic cavities fused with spaces of primary body cavity (blastocoel); adult body thus a mixocoel/hemocoel; with unique subcutaneous vascular channels (hemal channels)
9. Body wall with sheetlike muscle layer
10. Gas exchange by tracheae and spiracles (probably not homologous with arthropod trachea)
11. Gonochoristic



A–G courtesy of G. Giribet

FIGURE 20.12 Some onychophorans. (A) *Peripatoides* sp. from Waikato, North Island, New Zealand. (B) *Peripatoides aurorbis*, Kahurango National Park, North Island, New Zealand. (C) *Peripatopsis moseleyi*, Karkloof Nature Reserve East, Kwazulu-Natal, South Africa. (D) *Peripatopsis capensis*, Marloth Nature Reserve, South Africa. (E) Unidentified Peripatidae from the Central Amazon Conservation Complex, Roraima, Brazil. (F) *Peripatopsis alba*, Wynberg Cave, Table Mountain National Park, South Africa. (G) The fossil onychophoran *Antennipatus montceauensis* from the Stephanian deposits of the Montceau-les-Mines Lagerstätte, Late Carboniferous of France.

CLASSIFICATION OF ONYCHOPHORA

FAMILY PERIPATIDAE 19 to 43 leg pairs, genital opening between the penultimate pair of legs; with a diastema on the inner blades of the jaws. Tropical distribution, 75 species in 10 genera: *Eoperipatus* and *Typhloperipatus* (Southeast Asia), *Mesoperipatus* (West Africa), and a series of poorly characterized genera from the Neotropics, e.g., *Epiperipatus*, *Heteroperipatus*, *Macroperipatus*, *Oroperipatus*, *Peripatus*, *Plicatoperipatus*.

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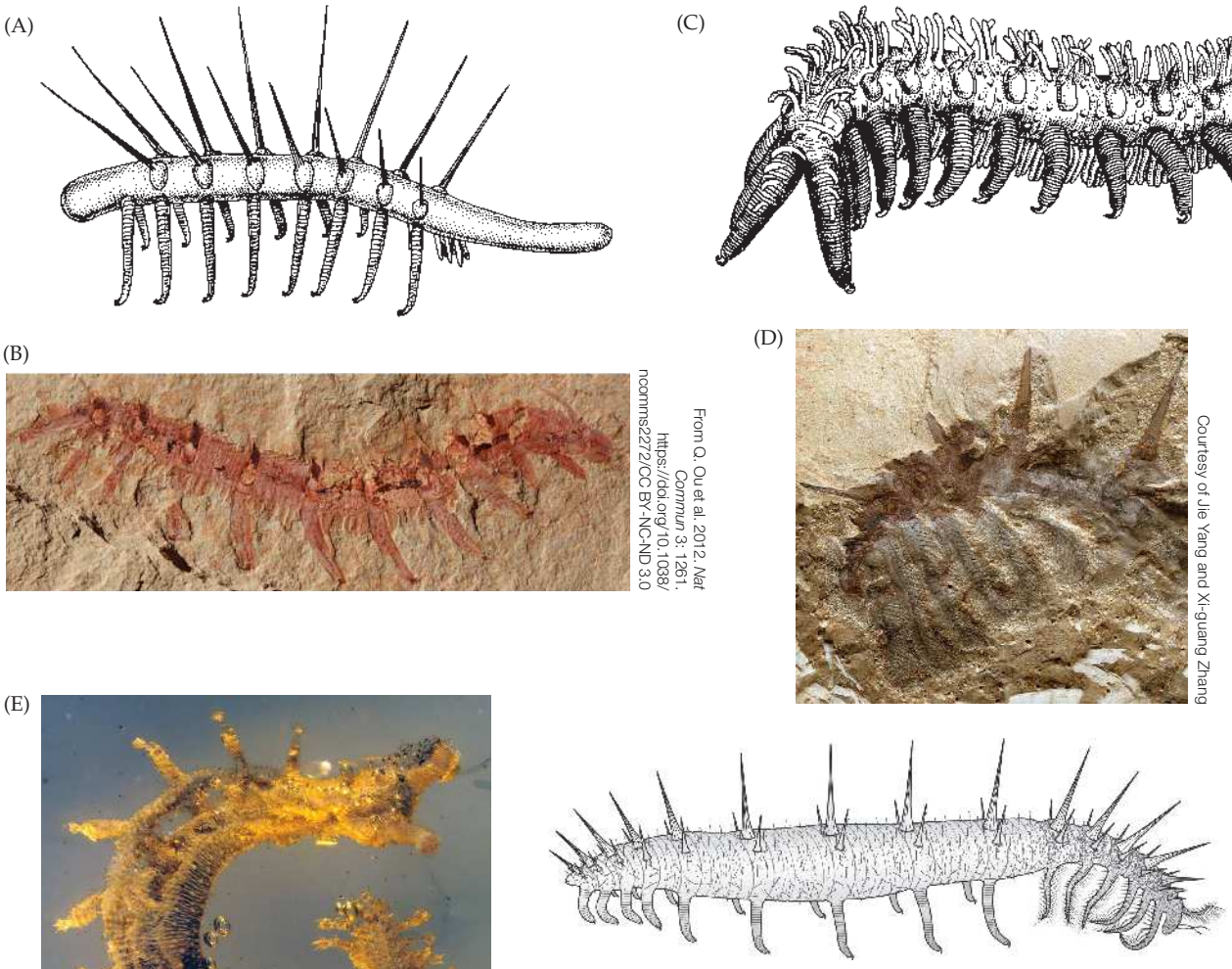

FIGURE 20.13 Reconstructions of Cambrian marine lobopodians and a fossil crown group onychophoran. (A) The enigmatic *Hallucigenia sparsa*, with two rows of long dorsal spines. (B) *Onychodictyon ferox* from the lower Cambrian Chengjiang deposits of China, with dorsal spines and papillae. (C) *Aysheaia pedunculata*, from middle Cambrian Burgess Shale deposits. (D, photo and drawing) In 2015 the remarkable lobopodian fossil *Collinsium ciliosum* was described from the Cambrian Xiaoshiba deposit in southern China (not far from the famous Chengjiang deposit). Like *Hallucigenia*, its dorsum is covered with long hard spines, but with many more than seen in *Hallucigenia*—up to 72 in fact. It also differs from *Hallucigenia* in having distinctly different anterior and posterior legs; the front legs being brushlike and probably functioning as feeding appendages, the rear legs being clawed and likely adapted for clinging to a sponge or cnidarian or other substratum. Being one of the earliest animals to develop armor, and reaching lengths of nearly 10 cm, this species would have been a striking and formidable Cambrian marine creature. It is further evidence that the ancestors to modern Onychophora were far more morphologically and ecologically diverse than today's velvet worms. A reconstruction of *C. ciliosum* is shown below the photograph of the actual fossil. (E) *Cretoperipatus burmiticus*, in amber, from the Cretaceous of Myanmar. (A,C after L. Ramsköld and X.-G. Hou. 1991. *Nature* 351: 225–228. https://www.nature.com/articles/351225a0)

FAMILY PERIPATOPSIDAE 13 to 29 leg pairs, genital opening between the last pair of legs; without a diastema on the inner blades of the jaws. Temperate to tropical in the Southern Hemisphere, 125 species in 39 genera, e.g., *Austroperipatus*, *Cephalofovea*, *Euperipatoides*, *Kumbadjena*, *Nodocapitus*, *Occiperipatoides*, *Ooperipatellus*, *Ooperipatus*, *Opisthopatus*, *Paraperipatus*, *Peripatoides*, *Peripatopsis*, *Phallocephale*, *Planipapillus*, *Tasmanipatus*.

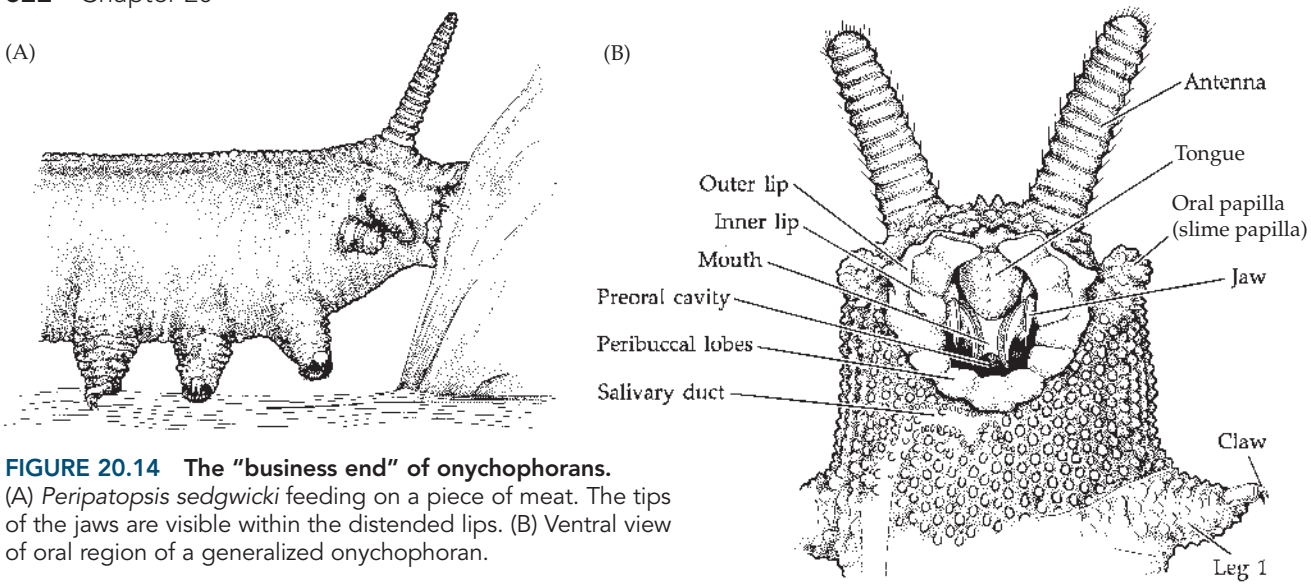

FIGURE 20.14 The "business end" of onychophorans. (A) *Peripatopsis sedgwicki* feeding on a piece of meat. The tips of the jaws are visible within the distended lips. (B) Ventral view of oral region of a generalized onychophoran.

The Onychophoran Body Plan

Modern onychophorans loosely resemble caterpillars, ranging from 5 mm to 15 cm in adult length. Within a given species, males are smaller than females and normally have fewer legs. Little cephalization is externally visible, and body segmentation is homonomous, where all legs differ little. Three paired appendages are found on the head: one pair of fleshy annulated antennae, a single pair of jaws, and a pair of fleshy **oral papillae** ("**slime papillae**"), resembling a small leg, lying posterior to the mouth (Figure 20.14). Circular lips surround the jaws. Beady eyes are located at the base of the antennae in most species (Figure 20.15), but a few species are eyeless (Figure 20.12F). The anterior head appendages are followed by 13–43 pairs of simple **lobopodal (saclike) walking legs**. A series of **ventral and preventral organs** is common among onychophorans and serves as an attachment site for segmental limb depressor muscles. The origin of these structures can be traced back in the embryo as lateroventral segmental, ectodermal thickenings *not* associated with the development of the nervous system. Although the head appendages and lobopods are superficially annulated, they are not jointed or segmented, nor do they possess intrinsic musculature (i.e., all appendage muscles attach at one end to the body proper).

The homology of onychophoran head structures with those of arthropods has long been a matter of debate, but the issue now seems resolved, in part thanks to the use of DNA labeling, immunocytochemistry, and neuronal tracing techniques in developing embryos. The eyes and antennae are innervated by the protocerebrum, unlike in any living arthropod, where the protocerebrum innervates only the eyes. The jaws are homologous with the chelicerae of chelicerates, or to the (first) antennae of myriapods, crustaceans, and hexapods, and are innervated by the deutocerebrum. Although the slime papillae align with the pedipalps of chelicerates and the second antennae of crustaceans, they are innervated by the ventral nerve cords, and not by the tritocerebrum as in arthropods, as the brain of velvet worms seems to comprise only two pairs of ganglia.

Similarly, the paired ventral nerve cords are very different from those of tardigrades and arthropods, as there is no relationship between the arrangement of median or ring commissures and the position of the legs. In addition, the cell bodies of serotonergic neurons are not arranged in the segmentally repeated and bilaterally symmetrical pattern characteristic of arthropods. Rather, these neurons are scattered in an apparently random fashion along the length of the onychophoran nerve cord. In summary, the overall arrangement of nerve pathways in the onychophoran nerve cord differs markedly from the rope-ladder arrangement in arthropods. In fact, it is more similar to the arrangement of orthogonally crossing nerve pathways found in the nervous systems of various wormlike protostomes than to those of tardigrades or arthropods.

Externally, the unjointed, fleshy nature of the head appendages, the structure of the jaws, and the legs appear quite different from those of arthropods. The serially arranged, clawed lobopodal appendages of onychophorans (including certain enigmatic fossil forms) have no clear counterpart in the animal kingdom.

The body is covered by a thin chitinous cuticle (containing α-chitin, as in arthropods) that is molted, as is in all other ecdysozoans. However, unlike that of arthropods, the cuticle of onychophorans is soft, thin, flexible, very permeable, and not divided into articulating plates or sclerites, but instead annulated like that of priapulans, and exhibiting multiple plicae per segment. Beneath the cuticle is a thin epidermis, which overlies a connective tissue dermis and layers of circular, diagonal, and longitudinal muscles (Figure 20.16). The body surface of onychophorans is covered with wartlike papillae of multiple kinds, usually arranged in rings or bands around

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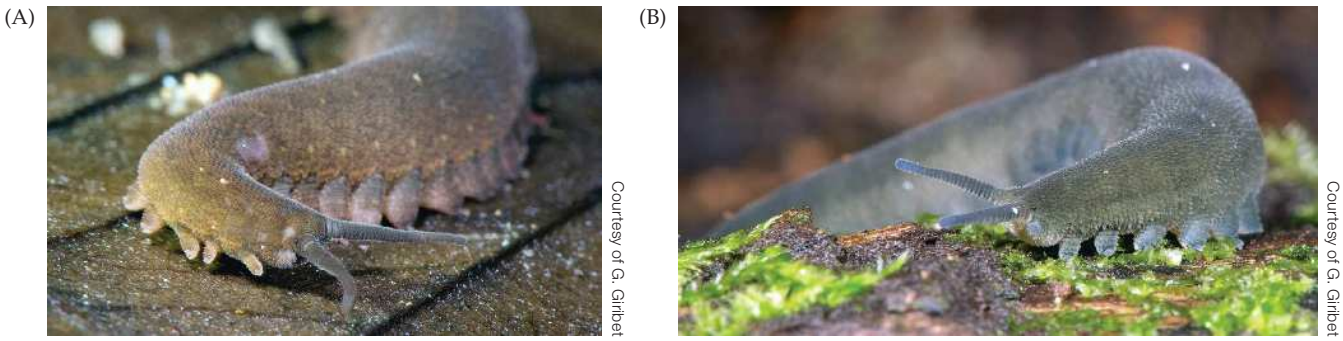

FIGURE 20.15 Although a few species of onychophorans are blind, most have small beady eyes that are homologous with the simple eyes of arthropods. (A) *Peripatus* sp. from Reserva Ducke, Manaus, Amazonia, Brazil. (B) *Peripatopsis moseleyi*, Karkloof Nature Reserve, Kwazulu-Natal, South Africa.

the trunk and appendages. These are classified as primary and secondary papillae, and they are of taxonomic importance. The papillae are covered with minute scales. Most onychophorans are distinctly colored blue, green, orange, or black, and the papillae, sometimes quite colorful, and scales give the body surface a velvety sheen—hence the common name "velvet worms."

The coelom formation in relation to that of arthropods has received considerable attention and is restricted almost entirely to the gonadal cavities in the adult onychophoran. In the Neotropical species *Epiperipatus biolleyi* the fate of the embryonic coelomic cavities has been studied in detail, providing evidence that embryonic coelomic cavities fuse with spaces of the primary body cavity (blastocoel). During embryogenesis, the somatic and splanchnic portions of the mesoderm separate, and the former coelomic linings are transformed into mesenchymatous tissue. The resulting body cavity therefore represents a mixture of primary and secondary (coelomic) body cavities, that is, the "mixocoel," but the homology of the segmental coeloms and nephridia in onychophorans and arthropods is not supported from the point of view of comparative anatomy. The hemocoel is also arthropod-like, being partitioned into sinuses, including a dorsal pericardial sinus.

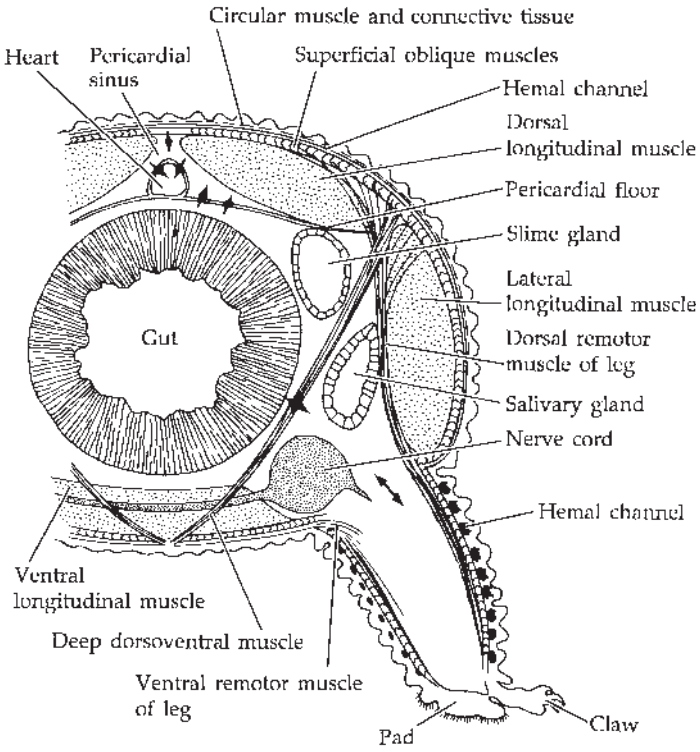

FIGURE 20.16 Body segment and leg of Peripatopsis (transverse section). Arrows indicate direction of blood flow.

Locomotion

The segmentally paired walking legs of onychophorans are conical, unjointed, ventrolateral lobes with a multispined terminal claw (sometimes called hooks). When the animal is standing or walking, each leg rests on three to six distal transverse pads (Figure 20.16). These lobopodal legs are filled with hemocoelic fluid and contain only extrinsic muscle insertions. Walking is accomplished by leg mechanics governed by a complex interplay of 15 muscles, including one promotor, one remotor, one levator, one retractor, two depressors, two rotators, one flexor, and two constrictors, as well as muscles for stabilization and by hydrostatic forces exerted via the hemocoel. Waves of contraction pass from anterior to posterior. When a segment is elongated, the legs are lifted from the ground and moved forward. When a segment contracts, a pulling force is exerted and the more anterior legs are held against the substratum. The overall effect is reminiscent of some types of annelid locomotion, wherein the parapodia are used mainly for purchase rather than as legs or paddles.

The body muscles are a combination of smooth and obliquely striated fibers and are arranged similarly to those of annelids. The thin cuticle, soft body, and hydrostatic body plan allow

onychophorans to crawl and force their way through narrow passages in their environment. As we saw in the annelids, the efficiency of a hydrostatic skeleton is enhanced by internal longitudinal communication of body fluids. The ancestors of the onychophorans apparently expanded the blood vascular system to achieve a hemocoelic hydrostatic skeleton.

Feeding and Digestion

Onychophorans occupy a niche similar to that of medium-sized centipedes. They are carnivores that prey on small invertebrates such as snails, worms, termites, and other insects, which they pursue into cracks and crevices. Special **slime glands**, thought to be modified nephridia, open at the ends of the oral papillae (Figure 20.18); through these openings an adhesive is discharged in two powerful disorganized jets, sometimes to a distance of 30 cm. The glue hardens quickly, entangling prey (or would-be predators) for subsequent leisurely dining.

The jaws are used to grasp and cut up prey. Paired salivary glands, also thought to be modified nephridia, open into a median dorsal groove on the jaws (Figure 20.14). Salivary secretions pass into the body of the prey and partly digest it; onychophorans then suck the semiliquid tissues into their mouth, after they ingest their own glue. The mouth opens into a chitin-lined foregut, composed of a pharynx and esophagus. A large, straight intestine is the principal site of digestion and absorption. The hindgut (rectum) usually loops forward over the intestine before passing posteriorly to the anus, which is located ventrally or terminally on the last body segment.

Circulation and Gas Exchange

The circulatory system of onychophorans is arthropod-like and linked to their hemocoelic body plan. A tubular heart is open at each end and bears a pair of lateral ostia in each segment. The heart lies within a pericardial sinus. Blood leaves the heart anteriorly and then flows posteriorly within the large hemocoel via body sinuses, eventually reentering the heart by way of the ostia. The blood is colorless, containing no oxygen-binding pigments. Onychophorans possess a unique system of subcutaneous vascular channels, called **hemal channels** (Figure 20.16 and 20.17C). These channels are situated beneath the transverse rings, or ridges, of the cuticle. A bulge in the layer of circular

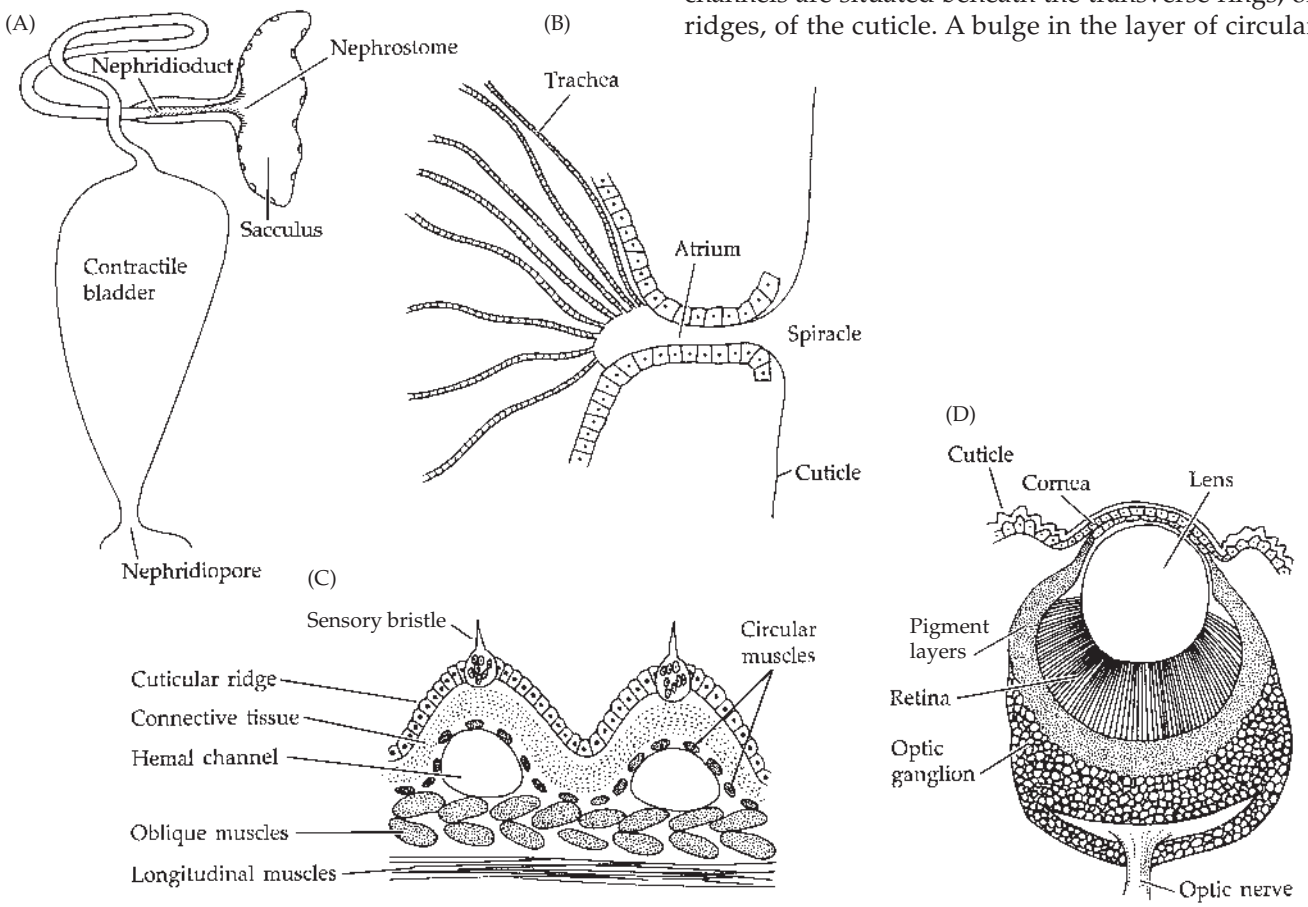

FIGURE 20.17 Some onychophoran anatomy. (A) Nephridium of *Peripatopsis capensis*. (B) A tracheal unit of *P. capensis* (cross section). (C) The body wall of *Peripatopsis moseleyi* (section). Note the hemal channels internal to each annular ridge. The ridges bear papillae surmounted by sensory bristles. (D) The eye of an onychophoran (longitudinal section). (A,B after L. A. Borradaile and F. A. Potts. 1961. *The Invertebrata, a Manual for the Use of Students*, 4th ed. Cambridge University Press, London.)

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muscle forms the outer wall of each channel, and the oblique muscle layer forms the inner wall. The hemal channels may be important in the functioning of the hydrostatic skeleton. Thus the superficial annulations of the onychophoran body are external manifestations of the subcutaneous hemal channels, as may be true of some Cambrian lobopodians.

Gas exchange is by tracheae that open to the outside through the many small spiracles located between the bands of body papillae. Each tracheal unit is small and supplies only the immediate tissue near its spiracle (Figure 20.17B). Anatomical data suggest that the tracheal system is not homologous with those of insects, arachnids, or terrestrial isopods but has been independently derived in each of these terrestrial groups, including in Onychophora.

Excretion and Osmoregulation

A pair of nephridia lies in each leg-bearing body segment, except the one possessing the genital opening (Figures 20.17A and 20.18). The nephridiopores are situated next to the base of each leg, except at the fourth and fifth legs, where the nephridia open through distal nephridiopores on the transverse pads of the legs

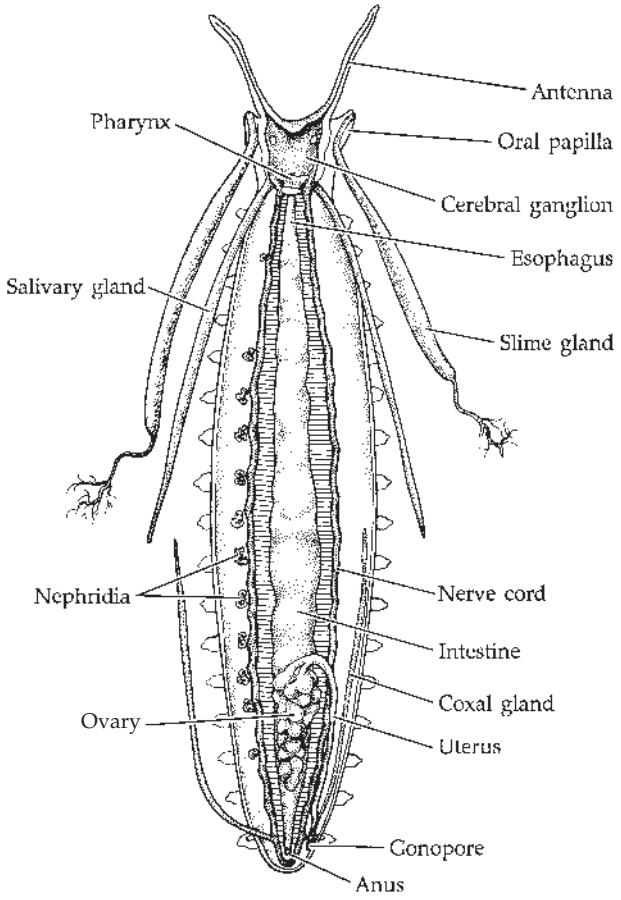

FIGURE 20.18 Internal anatomy of a generalized onychophoran.

themselves. The nephridial anlagen develops by reorganization of the lateral portion of the embryonic coelomic wall that initially gives rise to a ciliated canal. All other structural components, including the **sacculus**, merge after the nephridial anlagen has been separated from the remaining mesodermal tissue. The nephridial sacculus thus does not represent a persisting coelomic cavity, as previously thought, since it arises de novo during embryogenesis. There is no evidence for "nephridioblast" cells participating in the nephridiogenesis of Onychophora, which is in contrast to the general mode of nephridial formation in Annelida. Each set of sacculus + nephridioduct together is called a **segmental gland**. The nephridioduct, or tubule, enlarges to form a contractile bladder just before opening to the outside via the nephridiopore. The nature of the excretory wastes is not known. The anterior nephridia are thought to be modified as the salivary glands and slime glands, in addition to the nephridial anlagen in the antennal segment, and the posterior ones form the gonoducts in females.

The legs of some onychophorans, such as *Peripatus*, bear thin-walled eversible sacs or vesicles that open to the exterior near the nephridiopores by way of minute pores or slits. These vesicles may function in taking up moisture, as do the coxal glands of many myriapods, hexapods, and arachnids. They are everted by hemocoelic pressure and pulled back into the body by retractor muscles.

Nervous System, Sense Organs, and Behavior

The nervous system of onychophorans is ladderlike in structure but differs considerably from that of arthropods and tardigrades. A large bilobed cerebral ganglion ("brain") lies dorsal to the pharynx. A pair of ventral nerve cords, without segmental ganglia, is connected by nonsegmental ring commissures, which are also connected to multiple longitudinal nerve tracts. The protocerebrum innervates the eyes and antennae; the deutocerebrum innervates the jaws. The paired leg nerves are the only segmental structures in the onychophoran nerve cords, and the somata of serotonin-like immunoreactive neurons do not show any ordered arrangement but are instead scattered throughout the entire length of each nerve cord, showing neither a serially iterated nor a bilaterally symmetric pattern, in contrast to the strictly segmental arrangement of serotonergic neurons in arthropods (Figure 20.19). The general body surface, especially the larger papillae, is supplied with sensillae that might be homologous with those of tardigrades and arthropods.

Onychophorans are nocturnal animals and photophobic. With the exception of some cave-adapted species, there is a small dorsolateral eye at the base of each antenna. The eyes are of the direct rhabdomeric type, with a large chitinous lens and a relatively well-developed retinal layer (Figure 20.17D).

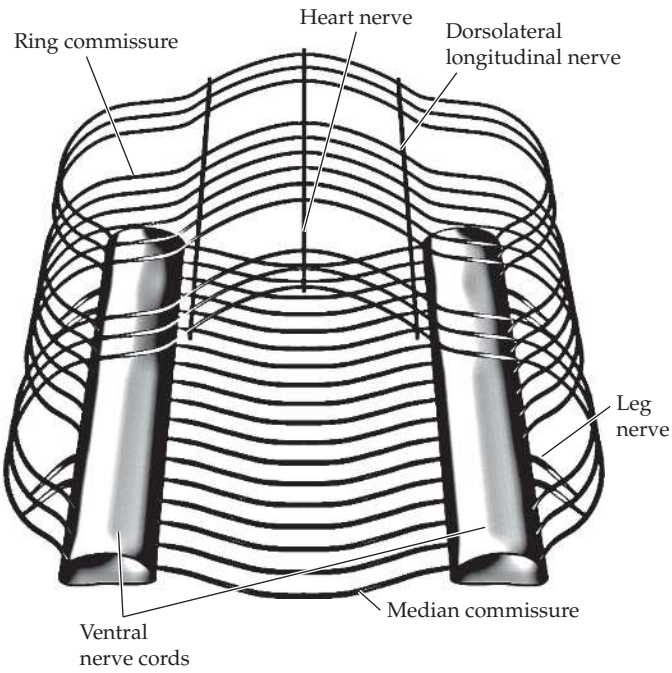

FIGURE 20.19 Schematic diagram of the arrangement of the main serotonin-like immunoreactive nerve tracts in the onychophoran trunk. Innervation of gut, various fiber networks, nephridial nerves, and ventral and lateral branches contributing to the subepidermal network are not shown.

The presence in onychophorans of only one optic neuropil and the development of the eye from an ectodermal groove correspond with the median ocelli rather than the compound eyes of arthropods. In addition, there are some parallels in innervation patterns between onychophoran eyes and the median ocelli of arthropods, since both are associated with the central (rather than lateral) part of the brain. These similarities have been interpreted to mean that there may be particular correspondences between the eyes of Onychophora, median ocelli of Chelicerata, and nauplius eyes of Malacostraca since in all these taxa there is a visual input to the central body.

Males of onychophorans have segmental **crural glands**, a type of exocrine gland that opens on the ventral surface at the base of the legs. These glands have been shown to secrete a pheromone that attracts conspecific females.

Reproduction and Development

With the exception of one known parthenogenetic population from Trinidad (often assigned to the mainland species *Epiperipatus imthurni*), all onychophorans are gonochoristic. Most females have a pair of largely fused ovaries in the posterior region of the body (Figure 20.18). Each ovary connects to a gonoduct (oviduct), and each gonoduct to a uterus. The uteri open through a posteroventral gonopore. Males are smaller than females and have a pair of elongate, separate testes. Paired sperm ducts join to form a single tube in which sperm are packaged into spermatophores up to 1 mm in length. The male gonopore is also located posteroventrally.

Copulation has been observed in a few onychophorans. In the South African genus *Peripatopsis* the male deposits spermatophores seemingly at random on the general body surface of the female (Figure 20.15B). The presence of the spermatophores stimulates special amebocytes in her blood to bring about a localized breakdown of the integument beneath the spermatophore. Sperm then pass from her body surface into her hemolymph, through which they eventually reach the ovaries, where fertilization takes place. In some onychophorans a portion of the uterus is expanded as a seminal receptacle, but sperm transfer in these species is not well understood. Insemination can also be vaginal or facultative between vaginal and dermal. Several Eastern Australian species present a diversity of male extragenital sexual structures in the form of organs on the dorsal surface of the head, which are highly elaborate in some species and may be involved in the mechanics of sperm transfer.

Embryological work on onychophorans has revealed some unusual features. For example, onychophorans may be oviparous, viviparous, or ovoviviparous. Females of oviparous species (e.g., *Ooperipatus*) have an ovipositor and produce large, oval, yolky eggs with chitinous shells. It is believed that this is the primitive onychophoran condition, even though living oviparous species are rare and deeply nested in the phylogeny of the group. The eggs of oviparous onychophorans contain so much yolk that early, superficial, intralecithal cleavage takes place, with the eventual formation of a germinal disc similar to that seen in many terrestrial arthropods. Most living onychophorans, however, are viviparous and have evolved a highly specialized mode of development associated with small, spherical, nonyolky eggs. Interestingly, most Old World viviparous species, although developing at the expense of maternal nutrients, lack a placenta, whereas most New World viviparous species have a placental attachment to the oviducal wall (Figure 20.20A). Placental development is viewed as the most advanced condition in onychophorans.

The yolky eggs of lecithotrophic species have a typical centrolecithal organization. Cleavage is by intralecithal nuclear divisions, similar to that seen in many groups of arthropods. Some of the nuclei migrate to the surface and form a small disc of blastomeres that eventually spreads to cover the embryo as a blastoderm, thus producing a periblastula. Simultaneously, the yolk mass divides into a number of anucleate "yolk spheres" (Figure 20.20B–D).

Nonyolky and yolk-poor eggs are initially spherical, but once within the oviduct, they swell to become ovate. As cleavage ensues, the cytoplasm breaks up into a number of spheres. The nucleate spheres are the blastomeres, and the anucleate ones are called

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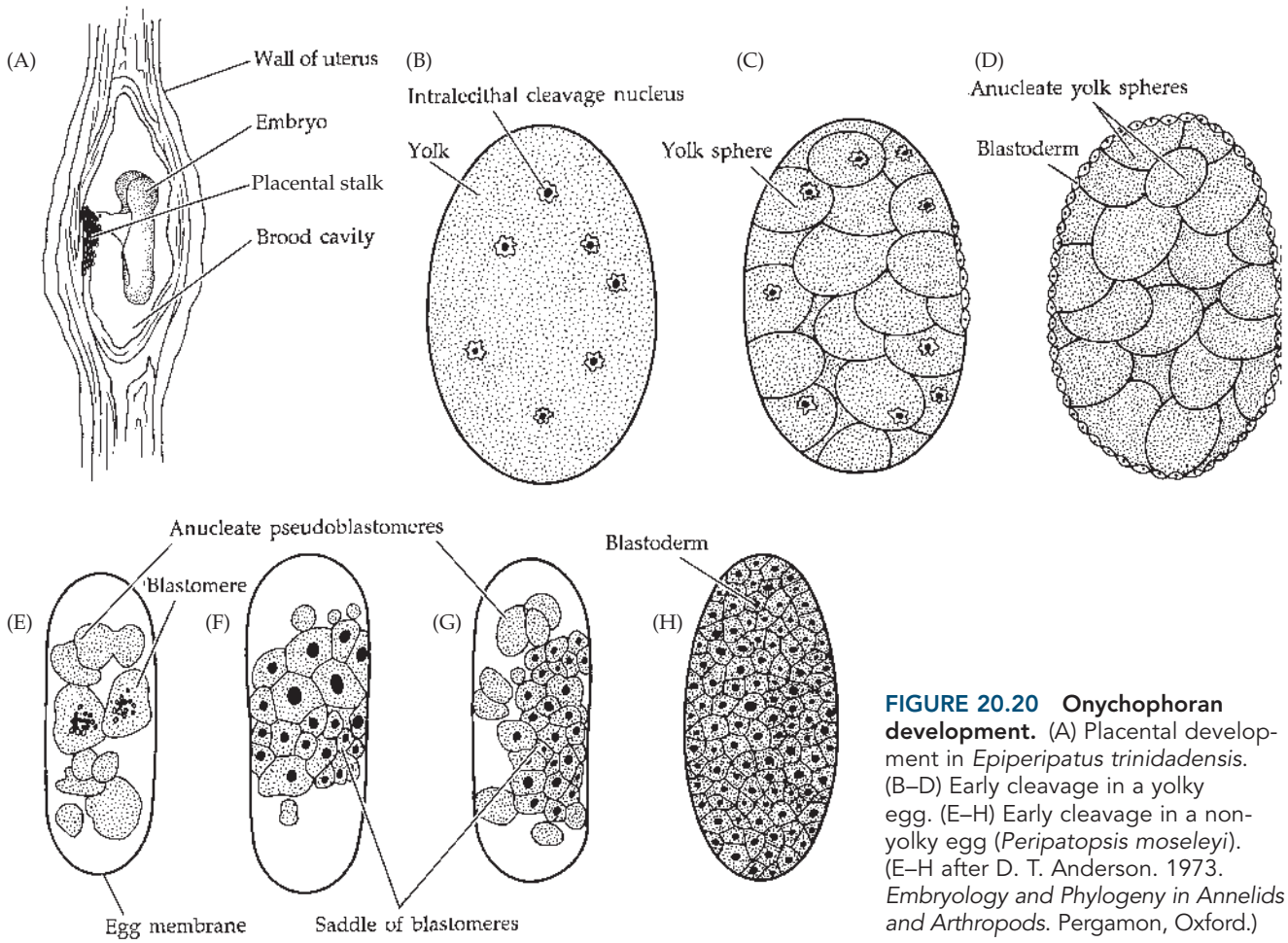

FIGURE 20.20 Onychophoran development. (A) Placental development in *Epiperipatus trinidadensis*. (B–D) Early cleavage in a yolky egg. (E–H) Early cleavage in a nonyolky egg (*Peripatopsis moseleyi*). (E–H after D. T. Anderson. 1973. *Embryology and Phylogeny in Annelids and Arthropods*. Pergamon, Oxford.)

pseudoblastomeres (Figure 20.20E–G). The blastomeres divide and form a saddle of cells on one side of the embryo (Figure 20.20G). The pseudoblastomeres disintegrate and are absorbed by the dividing blastomeres. The saddle expands to cover the embryo with a one-cell-thick blastoderm around a fluid-filled center.

Placental oviparous species have even smaller eggs than do nonplacental species, and the eggs do not swell after release from the ovary. Further, these eggs are not enclosed in membranes. Cleavage is total and equal, yielding a coeloblastula. The embryo then attaches to the oviducal wall and proliferates as a flat placental plate. As development proceeds, the embryo moves progressively down the oviduct and eventually attaches in the uterus. Sperm can remain motile in the seminal receptacle for up to 6 months. Gestation may be quite long, up to 15 months, and the oviduct/uterus often contains a series of developing embryos of different ages. Although gastrulation is still not fully understood in onychophorans, in several species a slitlike ventral furrow has been seen to form on the anterior–posterior axis. It was long thought that this slit underwent a median closure; the remaining ends giving rise to the mouth and anus. However, gene expression studies in *Euperipatoides kanangrensis* suggest that this groove does not correspond to the blastopore, even though both the mouth and anus do develop from it. Rather, a posterior pit on the developing embryo appears to be the blastopore; the posterior of the ventral groove at some point fuses with it to form the definitive anus. This has been called a case of "concealed" deuterostomy.

Development after the formation of the blastula is remarkably similar among the few species of onychophorans that have been studied. Gastrulation in onychophorans involves very little actual cell migration. Cells of the presumptive areas undergo immediate organogenesis by direct proliferation. This process involves the proliferation of small cells into the interior of the embryo through and around the yolk mass or fluid-filled center and the production by surface cells of the germinal centers of limb buds and other external structures. All onychophorans have direct development. In all species that have been studied, the full complement of segments and adult organ systems is attained before they hatch.

Onychophorans are also unusual in that neither a presegmental acron nor a postsegmental pygidium or telson can be distinguished. In onychophorans, even though growth is teloblastic, the growth zone from which the

trunk segments arise appears to be postanal. When the last mesoderm has been formed, the growth-zone ectoderm apparently develops directly into the anal somite with no postsegmental ectoderm remaining. Onychophorans thus have the last pair of legs in subterminal position, as opposed to tardigrades, with the fourth pair of legs being terminal—a character that seems to differentiate them from the Cambrian lobopodians.

Systematics and Biogeography

The phylogenetic relationships of onychophorans have received recent attention, when the use of DNA sequence data has been generalized and used in many evolutionary studies at multiple hierarchical levels, illustrating in several cases the existence of cryptic species. DNA markers have shown strong evidence for the division of Onychophora into Peripatidae and Peripatopsidae, with both families diverging around the Carboniferous–Permian Periods, before the breakup of Pangaea. Peripatidae, with their tropical distribution, have a species-poor lineage in Southeast Asia, a monotypic genus in western Africa, and most of their diversity in the Neotropics, including many Caribbean islands (this Neotropical clade is called Neopatida). Peripatidae has been diversifying since around the Triassic Period. Peripatopsidae, restricted to the former circum-Antarctic Gondwanan landmasses, divides into a South African/Chilean clade (West Gondwana) and into an Australian/New Guinea/New Zealand clade (East Gondwana), diversifying initially around the Jurassic Period, long after its divergence from Peripatidae.

An Introduction to the Phylum Arthropoda

With over a million described living species, and 3–100 times that many estimated still to be described, the phylum Arthropoda is unprecedented in its diversity. There are four clearly distinguished groups of extant arthropods, which are usually recognized as subphyla: Crustacea (crabs, shrimps, etc.), Hexapoda (insects and their kin), Myriapoda (centipedes, millipedes, etc.), and Chelicerata (horseshoe crabs, arachnids, and pycnogonids). However, we now know that the hexapods arose from among the Crustacea, leaving the latter as a paraphyletic taxon (the two groups together comprise the clade Pancrustacea). Among the several lineages of fossil arthropods that have been identified are the Trilobita (trilobites and their kin), which have left a fossil record from the early Cambrian to the end of the Permian. After 150 years of debate over the evolutionary relationships of arthropods, molecular systematics has finally allowed us to largely resolve the phylogeny among these groups (see Figure 20.39). We now know with a high degree of certainty, based on genomic and transcriptomic analyses, that extant arthropods split into two clades, chelicerates and mandibulates, the latter comprising the myriapods and the pancrustaceans (Crustacea + Hexapoda). The basic features of the arthropod body plan are listed in Box 20C. Some of these features are unique to the phylum Arthropoda and thus represent defining synapomorphies; others also occur in closely related taxa, such as the onychophorans and tardigrades.

BOX 20C Characteristics of the Phylum Arthropoda

1. Body segmented, both internally and externally; segments arising by teloblastic growth (showing *engrailed* gene expression)
2. Minimally, body divided into head (cephalon) and trunk; commonly with further regional body specialization or tagmosis; typically with a head shield or carapace covering fused head segments
3. Head with labrum (or clypeolabrum) (showing *Distal-less* gene expression) and with presegmental acron
4. Cuticle forming well-developed exoskeleton, generally with thick sclerotized plates (sclerites) consisting of dorsal tergites, lateral pleurites, and ventral sternites; cuticle of exoskeleton consists of chitin and protein (including resilin), with or without varying degrees of calcification; without collagen
5. Each true body segment primitively with a pair of segmented (jointed), ventrally attached appendages, showing a great range of specialization among the various taxa; appendages composed of a proximal protopod and a distal telopod (both multiarticulate); some protopodal articles bearing medial endites or lateral exites
6. Cephalon with a pair of lateral faceted (compound) eyes and one to several simple median ocelli; compound eyes, ocelli, or both lost in several groups
7. Coelom reduced to portions of the reproductive and excretory systems; main body cavity an open hemocoel (= mixocoel); circulatory system largely open; dorsal heart a muscular pump with lateral ostia for blood return
8. Gut complex and highly regionalized, with well-developed stomodeum and proctodeum; digestive material (and often also the feces) encapsulated in a chitinous peritrophic membrane
9. Nervous system with dorsal (supraenteric) ganglia (= cerebral ganglia), circumenteric (circumesophageal) connectives, and paired, ganglionated ventral nerve cords, the latter often fused to some extent
10. Growth by ecdysone-mediated molting (ecdysis); with cephalic ecdysial glands
11. Muscles metamerically arranged, striated, and grouped in isolated, intersegmental bands; dorsal and ventral longitudinal muscles present; intersegmental tendon system present; without circular somatic musculature
12. Most gonochoristic, with direct, indirect, or mixed development; some species parthenogenetic

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Taxonomic History and Classification

The great Swedish naturalist Carl Linnaeus, in the first half of the eighteenth century, recognized six major groups of animals (Vermes, Insecta, Pisces, Amphibia, Aves, Mammalia), placing all of the invertebrates except the insects in Vermes. In the early nineteenth century, such famous zoologists as Lamarck and Cuvier presented substantial reorganizations of Linnaeus's earlier scheme, and it was during this period that the various arthropod taxa began to emerge. Lamarck recognized four basic arthropod groups: Cirripedia (barnacles), Crustacea, Arachnida, and Insecta. He placed the ostracods with the brachiopods and, of course, did not realize the crustacean nature of the barnacles. Cuvier joined the arthropods and annelids in his Articulata (referring to the segmented nature of these animals), and Lankester also classified them together with rotifers in his Appendiculata. The great zoologists Hatschek, Haeckel, Beklemishev, Snodgrass, Tiegs, Sharov, and Remane all viewed the Articulata as a discrete phylum, including in it at various times the groups Echiura, Sipuncula, Onychophora, Tardigrada, and Pentastomida. It was Leuckart who, in 1848, separated out the arthropods as the distinct phylum we recognize today; Von Siebold coined the name Arthropoda in the same year, noting the jointed legs (Greek *arthro*, "jointed"; *pod*, "foot") as the group's principal distinguishing attribute, but he also included Tardigrada as mites. Haeckel published the first evolutionary tree of the arthropods in 1866. And, beginning in 1997 with the benchmark study by Anna Marie Aguinaldo and colleagues, molecular phylogenetics began to reveal that annelids and arthropods are not at all as closely related as long thought, the former now being placed in the clade Spiralia, with arthropods being in the clade Ecdysozoa. Brief diagnoses of the four living arthropod subphyla are provided below, and detailed treatments of these groups are presented in Chapters 21, 22, 23, and 24.

It is important to offer a word of caution about the use of terminology among the various groups of arthropods. Because the lineage of Arthropoda is so vast and diverse, specialists usually concentrate on only one or a few subgroups. Thus, over time, slightly different terminologies have evolved. Students sometimes feel overwhelmed by arthropod terminology—for example, the hindmost region of the body may be called an abdomen or pleon (as in insects and crustaceans), an opisthosoma (in chelicerates), or a pygidium (in trilobites). But there is a greater, though more subtle danger to this mixed terminology. Different terms for similar parts or regions in different taxa do not necessarily imply nonhomology; conversely, the same term applied to similar parts of different arthropods does not always imply homology. To deal with these problems in this text, we have made an effort to achieve consistency in terminology as much as possible, to simplify word use and spelling, and to indicate homologies (and nonhomologies) where known.

Of all fossil invertebrates, trilobites are perhaps the most symbolic of ancient and exotic faunas. The subphylum Trilobita, or Trilobitomorpha (Latin *trilobito*, "three-lobed"; Greek *morph*, "form"), includes over 20,000 species of arthropods known only from the fossil record (see Figures 20.37 and 20.38. They were restricted to (and characteristic of) Paleozoic seas. Trilobites dominate the fossil record of the Cambrian and Ordovician Periods (541 to 443.8 Ma) and continued to be important components of marine communities until the Permo-Triassic mass extinction that marked the end of the Paleozoic Era. Because of their hard molting exoskeletons (made of chitin and calcium carbonate, as in modern crustaceans and horseshoe crabs), great abundances, and broad distributions, the trilobites left a rich fossil record, and more is known about them than about most other extinct taxa. Most of the present world's land areas were submerged during various parts of the Paleozoic, so trilobite fossils are found in marine sedimentary rocks worldwide.

The trilobite body was divided into three tagmata: cephalon, thorax, and pygidium (abdomen). The segments of the cephalon and pygidium were fused, while those of the thorax were free and articulating. The body was demarcated by two longitudinal grooves into a median and two lateral lobes ("tri-lobite"). The cephalon had one pair of preoral antennae; all other appendages were postoral and more or less similar to one another, with a robust locomotory telopod to which was attached at the base a long filamentous branch (thought to be a protopodal exite). Most seem to have had compound eyes (an apomorphy of Arthropoda), including both appositional and nonappositional eyes.

Although trilobites were exclusively marine, they exploited a variety of habitats and lifestyles. Most were benthic, either crawling about over the bottom or plowing through the top layer of sediment. Most benthic species were a few centimeters long, although some giants reached lengths of 60–70 cm. A few trilobites appear to have been planktonic; they were mostly small forms, less than 1 cm long and equipped with spines that presumably aided in flotation. Most of the benthic trilobites were probably scavengers or direct deposit feeders, although some species may have been predators that lay partially burrowed in soft sediments and grabbed passing prey. Some workers speculate that at least some trilobites may have suspension fed by using the filamentous parts of their appendages. One group of Olenidae may have had symbiotic relationships with sulfur-oxidizing bacteria; these late Cambrian–Lower Ordovician trilobites had vestigial mouthparts and large "gill filaments" (epipods) that might have been sites for bacterial cultivation.

In addition to trilobites, the Cambrian seas saw a great diversity of stem arthropods and stem panarthropods that had undergone arthrodization (sclerotization and jointing of the exoskeleton) but not complete arthropodization, as well as many other groups

of arthropods that cannot be assigned to any of the extant groups and that are thus considered stem chelicerates, stem mandibulates, stem myriapods, or stem crustaceans.

SYNOPSES OF THE LIVING ARTHROPOD SUBPHYLA

SUBPHYLUM CRUSTACEA Crabs, lobsters, shrimps, beach hoppers, pillbugs, etc. About 72,000 described living species. Body usually divided into 3 tagmata: head (cephalon), thorax, and abdomen (the notable exception being the class Remipedia, which has only head + trunk); appendages uniramous or biramous; 5 pairs of cephalic appendages—the preoral first antennae (antennules) and 4 pairs of postoral appendages: second antennae (which migrate to a "preoral position" in adults), mandibles, first maxillae (maxillules), and second maxillae; with compound eyes usually having tetrapartite crystalline cones; gonopores located posteriorly on thorax or anteriorly on abdomen. Crustacea is now known to be a paraphyletic group, because the Hexapoda arose from within it (see Chapter 21).

SUBPHYLUM HEXAPODA Insects and their kin; monophyletic. Close to a million described living species. Body divided into 3 tagmata: head (cephalon), thorax, and abdomen; with 4 pairs of cephalic appendages: antennae, mandibles, maxillae, and labium (fused second maxillae); 3-segmented thorax with uniramous legs and often 2 pairs of wings; with compound eyes having tetrapartite crystalline cones; gas exchange by spiracles and tracheae; with ectodermally derived (proctodeal) Malpighian tubules; gonopores open on abdominal segment 7, 8, or 9 (see Chapter 22).

SUBPHYLUM MYRIAPODA Millipedes, centipedes, etc.; monophyletic. Over 16,000 described living species. Body divided into 2 tagmata: head (cephalon) and long, homonomous, many-segmented trunk; with 3–4 pairs of cephalic appendages (antennae, mandibles, first maxillae, and sometimes second maxillae); first maxillae free or coalesced; second maxillae often absent or partly (or wholly) fused; all appendages uniramous; living species mostly lack compound eyes (but they are present in Scutigeromorpha); with ectodermally derived (proctodeal) Malpighian tubules; gonopores on third or last trunk somite (see Chapter 23).

SUBPHYLUM CHELICERATA Horseshoe crabs, scorpions, spiders, mites, daddy longlegs, sea spiders, etc.; monophyletic. Over 113,000 described species. Body divided into two tagmata, anterior prosoma (cephalothorax) and posterior opisthosoma (abdomen); opisthosoma with up to 12 segments (plus telson); prosoma of 6 somites, each with a pair of uniramous appendages (chelicerae, pedipalps, 4 pairs of legs); gas exchange by gill books, book lungs, tracheae, or cuticular; excretion by coxal glands and/or endodermally derived (midgut) Malpighian tubules; with simple median eyes and lateral compound eyes (see Chapter 24).

The Arthropod Body Plan and Arthropodization

If we are to grasp the "essence of arthropod," we must first understand the effects of one of the major synapomorphies of this phylum—the hard, jointed exoskeleton. Just imagine living your life encased in a rigid exoskeleton, a permanent suit of armor, if you will. What kinds of structural and functional problems would have to be solved in order for such an animal to survive? The approach arthropods evolved to live in their hard casing comprises a suite of adaptations collectively known as arthropodization. Arthropodization has some of its roots in the Onychophora and Tardigrada but came to full fruition in the phylum Arthropoda itself.

Being encased in an exoskeleton resulted in some obvious constraints on growth and locomotion. The fundamental problem of locomotion was solved by the evolution of body and appendage joints and highly regionalized muscles. Flexibility was provided by thin intersegmental areas (joints) in the otherwise rigid exoskeleton, imbued with a unique and highly elastic protein called **resilin**. As the muscles became concentrated into intersegmental bands associated with the individual body segments and appendage joints (intrinsic appendage muscles), the circular muscles were lost almost entirely.

With the loss of peristaltic capabilities resulting from body rigidity, and the loss of circular muscles, the coelom became nearly useless as a hydrostatic skeleton. The ancestral body coelom was lost, and an open circulatory system evolved—the body cavity became a **hemocoel**, or blood chamber, in which the internal organs could be bathed directly in body fluids.[1] But the large bodies of these animals still required some way of moving the blood around through the hemocoel, hence a highly muscularized dorsal vessel was developed as a pumping structure—a heart. The excretory organs became closed internally, thereby preventing the blood from being drained from the body. Surface sense organs (the "arthropod setae") differentiated, becoming numerous and specialized and acquiring various devices for transmitting sensory impulses to the nervous system in spite of the hard exoskeleton. Gas exchange structures evolved in various ways that overcame the barrier of the exoskeleton.

For these animals, now encased in a rigid outer covering, growth was no longer a simple process of gradual increase in body size. Thus the complex

[1] The hemocoel is not a true coelom, either evolutionarily or ontogenetically, but it may be viewed as a persistent blastocoelic remnant. Thus, one might at first reason that the arthropods technically are blastocoelomates. However, the absence of a large body coelom in arthropods is probably a secondary condition resulting from a loss/reduction of the ancestral coelomic body cavity during the evolution of the arthropod body plan, not a primary condition like that seen in the true blastocoelomates, most of which probably never have had a true coelom in their ancestry. A similar secondary loss of the coelom has occurred, in a different way, in the molluscs (see Chapter 13).

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process of **ecdysis**, a specific hormone-mediated form of molting or cuticular shedding, was "perfected." As we have already seen, some form of ecdysis occurs in all eight phyla belonging to the clade Ecdysozoa. In arthropods, it is also through this process of ecdysis (molting) that the exoskeleton is periodically shed to allow for an increase in real body size. If we add to this suite of events the notion of arthropods invading terrestrial and freshwater environments, the evolutionary challenges become compounded by osmotic and ionic stresses, the necessity for aerial gas exchange, and the need for structural support and effective reproductive strategies.

While the origin of the exoskeleton demanded a host of coincidental changes to overcome the constraints it placed on arthropods, it clearly endowed these animals with great selective advantages, as evinced by their enormous success. One of the key advantages is the protection it provides. Arthropods are armored not only against predation and physical injury, but also against physiological stress. In many cases the cuticle is an effective barrier against osmotic and ionic gradients, and as such it is a major means of homeostatic control. It also provides the strength needed for segmental muscle attachment and for predation on other shelled invertebrates.

If we start with a generalized, rather homonomous arthropod prototype with a fairly high number of segments, and with paired appendages on each of those segments, we can set the stage for arthropod diversification. The diversity seen today has resulted largely from the differential specialization of various segments, regions, and appendages. The arthropod body has itself undergone various forms of regional specialization, or **tagmosis**, to produce segment groups specialized for different functions. These specialized body regions (e.g., the head, thorax, and abdomen of insects) are called **tagmata**. Tagmosis is mediated by Hox genes and the other developmental genes they influence. Our emerging understanding of Hox genes tells us that the most fundamental aspects of animal design arise from spatially restricted expression of these "master developmental genes." However, tagmosis varies among the arthropod groups (see the Synopsis of the Living Arthropod Subphyla section). The genetic and evolutionary plasticity of regional specialization, like limb variation, has been of paramount importance in establishing the diversity of the arthropods and their dominant position in the animal world.

One of the best examples of arthropod tagmosis is revealed by the expression pattern of the segment polarity gene *engrailed* (*en*) in the head, or cephalon, of Crustacea, Hexapoda, and Myriapoda, three arthropod subphyla comprising the clade known as Mandibulata. In each of these subphyla, the same six head regions emerge during embryogenesis. The most anterior region is usually called the **acron**, and it is often regarded as presegmental. The acron is also known as the protocerebral, or ocular segment because it contains the protocerebrum and eyes; it lacks appendages (Table 20.2). Next come the first and second antennal segments, the mandibular segment, and the first and second maxillary segments.

While segmentation in the various arthropod lineages likely shares a common developmental origin, the way it is described and interpreted can differ between

TABLE 20.2 Homologies of Arthropod (and Onychophoran) Anterior/Head Appendages[a]

Segment	Onychophora	Pycnogonida	Chelicerata	Myriapoda	Crustacea	Hexapoda
1 Protocerebral segment, or ocular segment	Antennae	–	–	–	–	–
2 Deutocerebral segment	Jaws	Chelifores	Chelicerae	Antennae	First antennae (= antennules)	Antennae
3 Tritocerebral segment)	Slime papillae (Note: Onychophorans may not have a tritocerebrum)	Palps	Pedipalps	–	Second antennae	–
4	Leg pair	Leg pair	Leg pair	Mandibles	Mandibles	Mandibles
5	Leg pair	Leg pair	Leg pair	First maxillae	First maxillae (= maxillules)	Maxillae
6	Leg pair	Leg pair	Leg pair	Second maxillae (or without appendages)	Second maxillae	Labium (= second maxillae)

[a]Gene expression studies have revealed the likelihood that the anterior-most appendages (the "protocerebral appendages") have been lost in all modern arthropods. A labrum (or "upper lip") occurs in all arthropod subphyla and also in Onychophora; its function is thought to be to prevent food particles from escaping ingestion. The evolutionary origin of the labrum has long been a mystery, and most workers have not regarded it as a true appendage of the head. However, recent gene expression studies suggest it might represent the remnant of a pair of ancient fused appendages. In insects and spiders, the labrum has been shown to arise from two primordia that fuse during embryogeny, controlled by the genes *decapentaplegic* (*dpp*) and *wingless* (*wg*), the same gene expressions as seen in the buds of regular appendages in arthropods.

groups and the nature of each fundamental segment is not always obvious. In centipedes, for instance, the composition of the trunk is usually reported in terms of the number of leg bearing segments, excluding one anterior segment that bears a pair of maxillipeds, and a posterior ano-genital region of uncertain segmental composition (possibly 2–3 segments plus the telson). In notostracan crustaceans, uncertainty about segment identity led to a recommendation that the term "segment" be replaced with "ring" for the units of the dorsal segmental series (and "leg pair" for the ventral ones).

In a similar vein, an evolutionary-developmental understanding of the head of panarthropods has been one of the greatest challenges to biologists, and we have only recently begun to understand head homologies across major lineages. One of the biggest challenges is the nature of the anteriormost "segment" in Arthropoda, or what has traditionally been called the acron. As we have noted, this anterior piece has no appendages in extant arthropods but houses the protocerebrum and the eyes—hence it might better be called the protocerebral segment or ocular segment. "Acron" is a term borrowed from annelid development when the two phyla were thought to be very closely related (i.e., the Articulata hypothesis), as the larval episphere in annelids is of pre-segmental origin and gives rise to the adult prostomium. As in annelids, the arthropod acron (and telson/pygidium) have been considered not to be "true" segments—the acron being viewed as presegmental and the telson as postsegmental. However, the demise of the Articulata hypothesis, and the realization that arthropods are ecdysozoans (and annelids are spiralians), undermined the concept of acron (and telson) homology between the two phyla. Further, unlike the arthropod acron/ocular segment, the acron in annelids (usually called the prostomium) commonly bears both eyes and antennae, as well as a variety of palps, tentacles, and sense organs. Within the Panarthropoda (Onychophora, Tardigrada, Chelicerata, Mandibulata), however, the acron/ocular segment appears homologous. In Onychophora, the protocerebrum also innervates a pair of antennae on this first segment, as also seems to be the case of several Cambrian taxa with "great appendages," such as *Anomalocaris*.

As we discuss the various aspects of the arthropod body plan here and in subsequent chapters, do not lose sight of the "whole animal" and the "essence of arthropod" described in this section.

The Body Wall

A cross section through a body segment of an arthropod reveals a good deal about its overall architecture (Figure 20.21). As noted, the body cavity is an open hemocoel, and the organs are bathed directly in the hemocoelic fluid, or blood (although discrete blood vessels do occur, notably in Crustacea and Chelicerata). The body wall is composed of a complex, layered **cuticle** secreted by the underlying epidermis (Figure 20.22). The epidermis, often referred to in arthropods as the **hypodermis**, is typically a simple cuboidal epithelium. In general, each body segment (or **somite**) is "boxed" by skeletal plates called **sclerites**. Each somite typically has a large dorsal and ventral sclerite, the **tergite** and **sternite** respectively.[2] The side regions, or **pleura**, are flexible unsclerotized areas in which are embedded various minute, "floating" sclerites, the origins of which are hotly debated. The legs (and wings) of arthropods articulate in this pleural region. Numerous secondary deviations from this plan exist, such as fusion or loss of adjacent sclerites. Muscle bands are attached at points where the inner surfaces of sclerites project inward as ridges or tubercles, called **apodemes**.

The structure of the multilayered arthropod cuticle is similar to that of other ecdysozoans, although the layers can have different names in different phyla. Figure 20.22

[2]The terms *tergum, sternum,* and *pleuron* are often used interchangeably with *tergite, sternite,* and *pleurite*. However, the term *tergum* refers more precisely to the dorsal, or tergal, region, and sternum to the ventral, or sternal, region. Thus we restrict the use of the terms *tergite* (pl., *tergites*) and *sternite* (pl., *sternites*) to the specific skeletal plates, or sclerites. In some cases, the sternum is formed of multiple fused sternites.

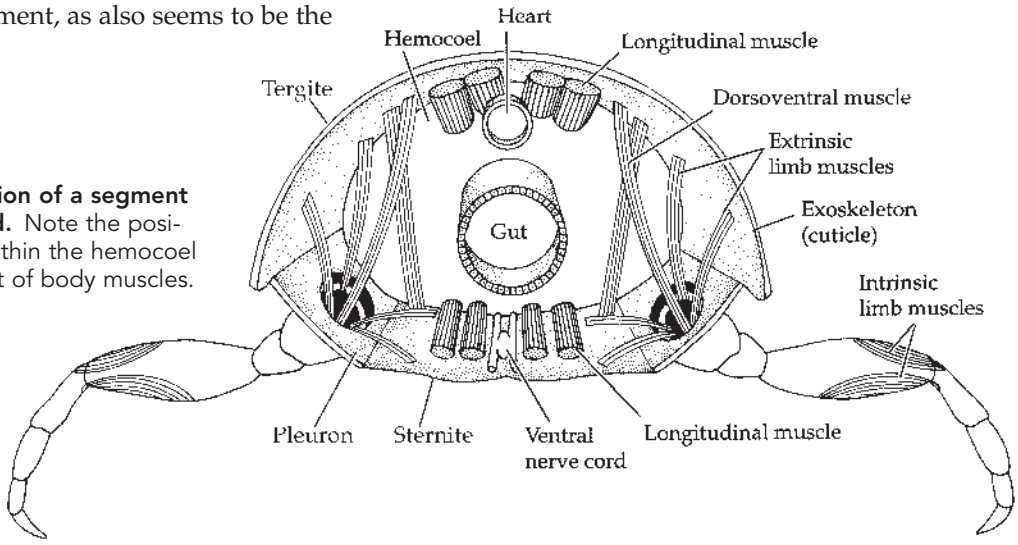

FIGURE 20.21 Cross section of a segment of a generalized arthropod. Note the positions of the major organs within the hemocoel and the typical arrangement of body muscles.

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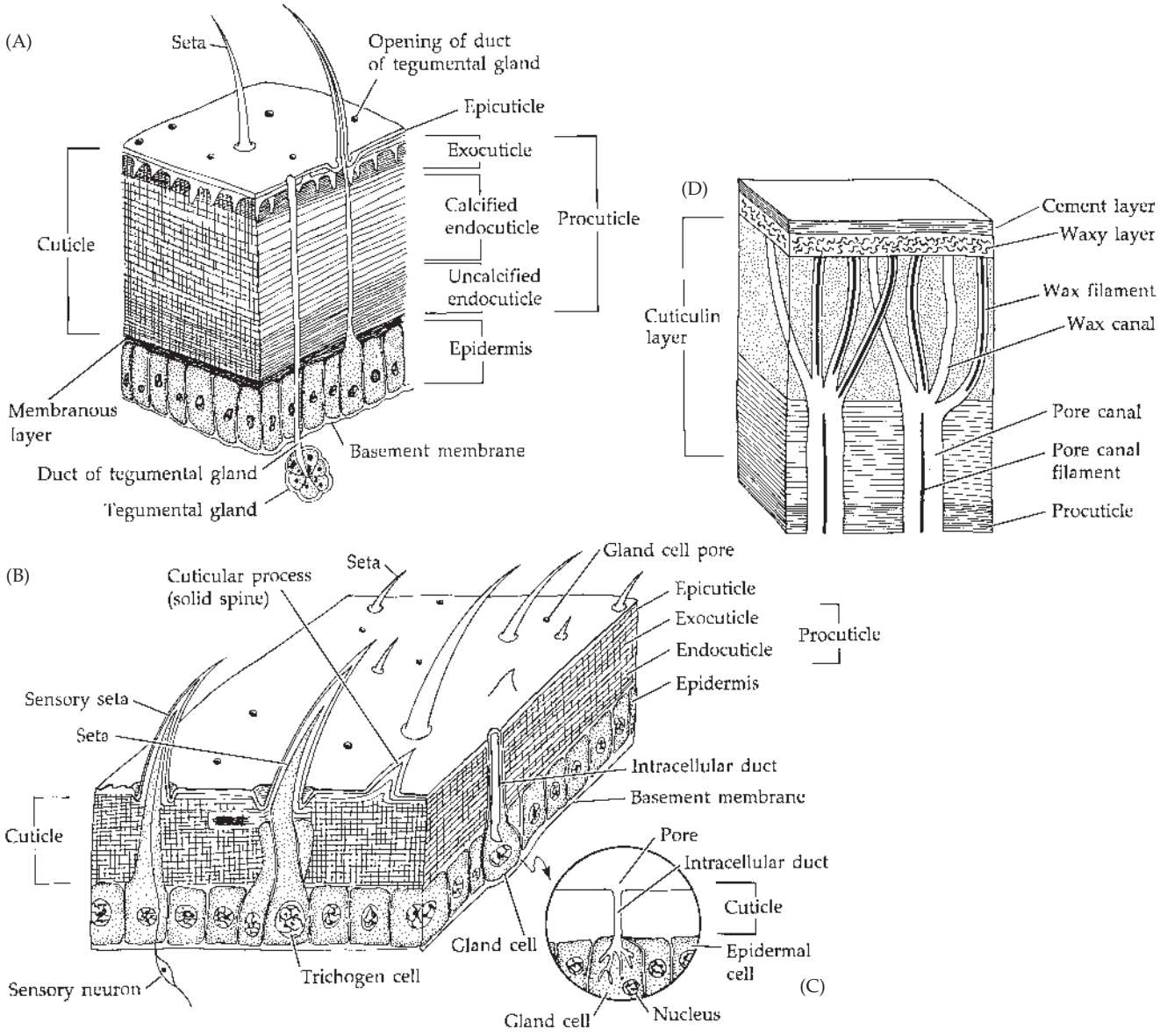

FIGURE 20.22 Arthropod cuticles. (A,B) The cuticle and epidermis of (A) a crustacean and (B) an insect. (C) A simple unicellular arthropod gland. (D) The epicuticle of an insect. (A after R. Dennell. 1960. In T. H. Waterman [Ed.], *The Physiology of Crustacea, Vol. 1*, pp. 449–472. Academic Press, New York.)

illustrates the cuticles of an insect and a marine crustacean. The outermost layer is the **epicuticle**, which is itself multilayered (Figure 20.22D). The external surface of the epicuticle is a protective lipoprotein layer—sometimes called the cement layer. Beneath this is a waxy layer that is especially well developed in terrestrial arachnids and insects. The waxes in this layer, which are long-chain hydrocarbons and the esters of fatty acids and alcohols, provide an effective barrier to water loss and, coupled with the outer lipoprotein layer, protection against bacterial invasion. These outermost two layers of the epicuticle largely isolate the arthropod's internal milieu from the external environment. No doubt, the development of the epicuticle was critical to the invasion of land and fresh water by various arthropod lineages. The innermost layer of the epicuticle is a **cuticulin layer**, which consists primarily of proteins and is particularly well developed in insects. The cuticulin layer usually has two components: a thin but dense outer layer and a thicker, somewhat less dense inner layer. The cuticulin layer is involved in the hardening of the exoskeleton and contains canals through which waxes reach the waxy layer.

Beneath the epicuticle is the relatively thick **procuticle**, which may be subdivided into an outer **exocuticle** and an inner **endocuticle** (Figure 20.22A,B).[3] The procuticle consists primarily of layers of protein and chitin (but no collagen). It is intrinsically tough, but flexible. In fact, certain arthropods possess rather soft and pliable exoskeletons (e.g., many insect larvae, parts of spiders,

[3]Caution: Some authors use the term *endocuticle* to refer to the entire procuticle of crustaceans, and they use the two subdivision terms only when referring to insects.

some small crustaceans and arachnids). However, in most arthropods, the cuticle is hard and inflexible except at the joints, a condition brought about by one or both of two processes: sclerotization and mineralization.

Cuticular hardening by **sclerotization** (a process known as **tanning**) occurs to various degrees in all arthropods. The layered arrangement of untanned proteins yields a flexible structure. To produce a rigid sclerotized structure, the protein molecules are cross-bonded to one another by orthoquinone linkages. Sclerotization generally begins in the cuticulin layer of the epicuticle and progresses to various degrees into the procuticle, where it is associated with a distinct darkening in color. The relationship between cuticular hardening, joints, and molting is discussed in more detail below. **Mineralization** of the skeleton is largely a phenomenon of some crustaceans, millipedes, and horseshoe crabs and is accomplished by the deposition of calcium carbonate in the outer region of the procuticle.

The epidermis is responsible for the secretion of the cuticle, which it does with various unicellular glands (Figure 20.22C), some of which bear ducts to the surface of the cuticle. Because the cuticle is secreted by the epidermal cells, it often bears their impressions in the form of microscopic geometric patterns. The epidermis is underlain by a distinct basement membrane that forms the outer boundary of the body cavity or hemocoel.

Arthropod Appendages

Appendage anatomy In an evolutionary sense, one might be tempted to say "arthropods are all legs." Certainly, much of arthropod evolution has been about the appendages, modified in myriad ways over the 521-million-year fossil history of this group. The unique combination of body segmentation and serially homologous appendages, in combination with the evolutionary potential of developmental genes, has allowed arthropods to develop modes of locomotion, feeding, and body region/appendage specialization that have been unavailable to the other metazoan phyla. The enormous variety of limb designs in arthropods has, unfortunately, also driven zoologists to create a plethora of terms to describe them. Read on, and we will try to guide you through this terminological jungle in the clearest fashion we can.

Primitively, every true body somite, or segment, probably bore a pair of appendages, or limbs, as found in the other panarthropods, in the fossil trilobites, and in some extant arthropod groups like centipedes or remipedes. Arthropod appendages are articulated outgrowths of the body wall, equipped with sets of extrinsic muscles (connecting the limb to the body) and intrinsic muscles (wholly within the limb). The limbs of the other panarthropod phyla (Tardigrada and Onychophora) do not have intrinsic musculature and thus must rely strongly on hydraulics for movement. In the arthropods, muscles move the various limb segments or pieces, which are called **articles** (or podites).[4] The limb articles are organized into two groups, the basal-most group constituting the **protopod** (= sympod) and the distal-most group constituting the **telopod** (Figure 20.23). Whether the protopod is composed of one or more articles, the basal-most article is always called the **coxa** (in living arthropods). The telopod arises from the distal-most protopodite, or protopodal article. Sometimes the exoskeleton of the telopodites becomes annulated, forming a flagellum, as in the antennae of many arthropods, but these annuli should not be confused with true articles.

A great variety of additional structures can arise from articles of the protopod (the protopodites), either laterally (collectively called **exites**) or medially (collectively called **endites**) (Figure 20.23A). Evolutionary creativity among the protopodal exites has been exceptional among arthropods. In crustaceans and trilobites they form a diversity of structures such as gills, gill cleaners, and swimming paddles. Broad or elongate exites that function as gills or gill cleaners are often called **epipods**. Exites may become annulated, like the flagella of some antennae. Protopodal endites, on the other hand, often form grinding surfaces, or "jaws," usually termed **gnathobases**. Figure 20.23 illustrates some arthropod appendage types and the terms applied to their parts.[5]

Appendages with large exites, such as gills, gill cleaners, or swimming paddles (the last often developed in combination with a paddlelike telopod) are

[4] Although some authors refer to the articles of the appendages as "segments," we attempt to restrict the use of the latter term to the true body segments, or somites, reserving the term *articles* for the separate "segments" of the limb.

[5] A basic morphological view of arthropod limb evolution is rooted in 30 years of detailed comparative morphology by Jarmila Kukalová-Peck, who studies both fossil and living arthropod limbs. In the Kukalová-Peck model, the ancestral arthropod appendage comprised a series of 11 articles (4 protopodites, 7 telopodites), each of which could theoretically bear an articulated endite or exite. The number of articles in her arthropod limb ground plan is not so important as her concept of a single series of articles, with endites and exites that specialized to become the diversity of structures seen in modern taxa. Over evolutionary time, so her theory goes, the basal-most protopodites fused with the pleural region of the body to form pleural sclerites in various taxa. On the thoracic segments of hexapods, the exite of the first protopodite (the epicoxa) migrated dorsally and gave rise to insect wings (see Chapter 22). On the other hand, many of the earliest known arthropod fossils (including trilobites) have protopods of a single article, as do many living arthropods, suggesting to some workers that multiarticulate protopods might be derived conditions. Kukalová-Peck's hypothesis, however, holds that such uniarticulate protopods represent cases in which protopodal articles have fused together (e.g., in trilobites) or migrated onto the pleural region of the body somites. The number of articles in the telopods of living arthropods varies greatly, reflecting, in Kukalová-Peck's view, various kinds of loss or fusion of articles. The elegance of Kukalová-Peck's theory is that it simply explains the origin of all arthropod limb structures. Viewing the arthropod limb ground plan as a series of articles from which endites and exites were modified in a variety of ways eliminates 100 years of confusion over the nature of uniramous, biramous, and polyramous limbs (these terms now having little phylogenetic significance).

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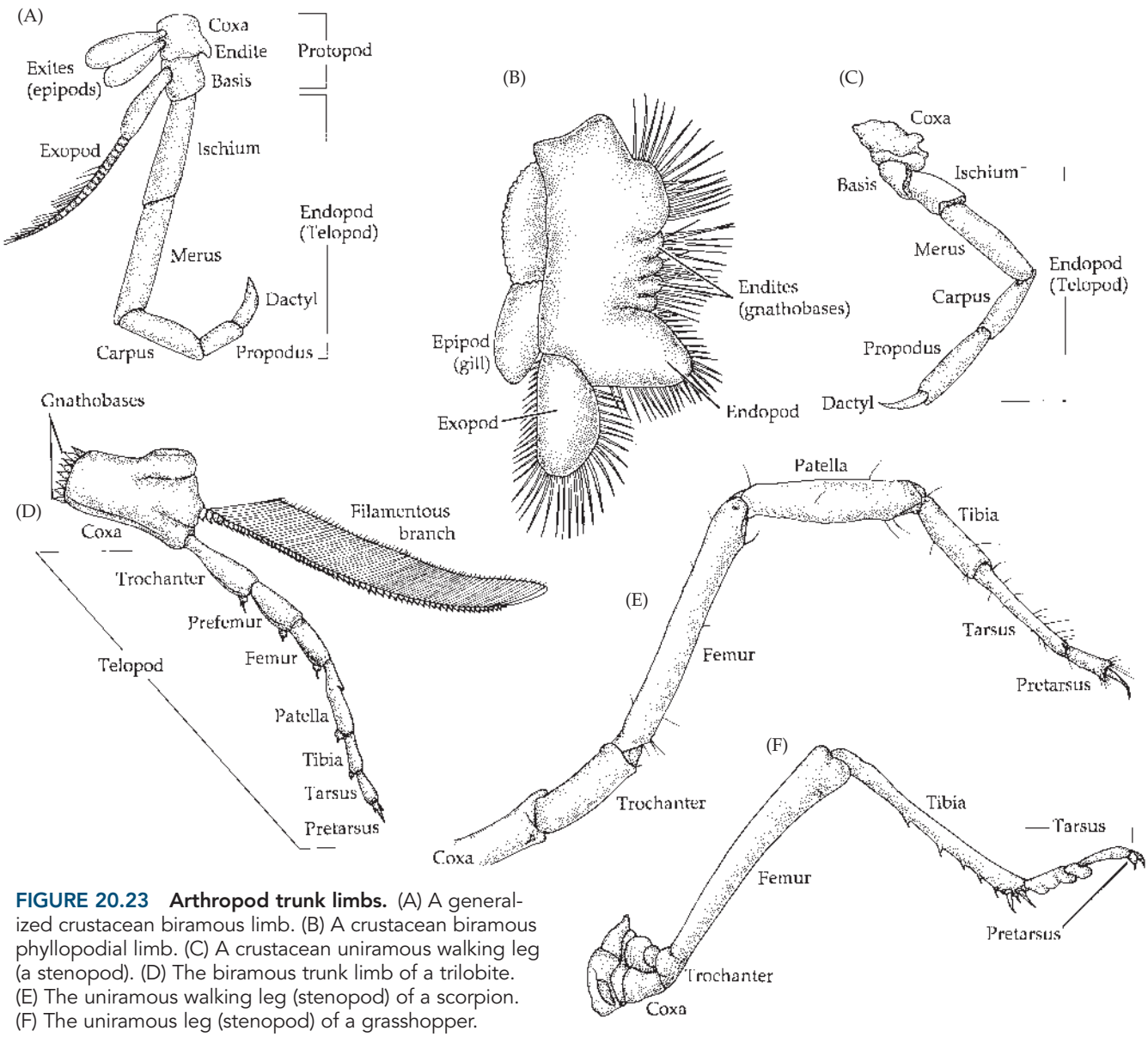

FIGURE 20.23 Arthropod trunk limbs. (A) A generalized crustacean biramous limb. (B) A crustacean biramous phyllopodial limb. (C) A crustacean uniramous walking leg (a stenopod). (D) The biramous trunk limb of a trilobite. (E) The uniramous walking leg (stenopod) of a scorpion. (F) The uniramous leg (stenopod) of a grasshopper.

often called **biramous limbs** (or, sometimes, triramous or polyramous limbs). Biramous limbs occur only in crustaceans and trilobites, although their ancestral occurrence in chelicerates is suggested by the gills and other structures that may be derivatives of early limb exites. In crustaceans, the exite on the last protopodite can be as large as the telopod itself, and in these cases it is termed an **exopod**, the telopod then being called the **endopod** (Figure 20.23A). Biramous limbs are commonly associated with swimming arthropods, and in crustaceans in which they are greatly expanded and flattened (e.g., Cephalocarida, Branchiopoda, Phyllocarida), they may also be called foliacious limbs, or **phyllopodia** (Greek *phyllo*, "leaf-shaped"; *podia*, "feet") (Figure 20.23B).

Appendages without large exites are called **uniramous limbs** (or **stenopods**; Greek *steno*, "narrow"; *podia*, "feet") (Figure 20.23C,E,F). Uniramous limbs are characteristic of the chelicerates, hexapods, myriapods, and some crustaceans, although these appendages were probably secondarily derived from biramous limbs on more than one occasion. Uniramous legs are typically ambulatory (walking legs).

The combination of protopodal and telopodal articles, and their evolutionarily "plastic" endites and exites, has created in arthropods a veritable "Swiss army knife" of appendages. This diversity has no equal in the animal kingdom, and it has played a pivotal role in the evolutionary success of the phylum. As you peruse the following chapters, be sure to notice the phenomenal array of limb morphologies and adaptations among the arthropods.

Appendage Evolution The amazing diversity seen in arthropod limbs has come about through the unique potential of homeobox (Hox) genes and other

developmental genes and the downstream genes they regulate, which are conserved and yet flexible in their expression. We are just beginning to understand how these genes work, and new information in this field is appearing so fast that we hesitate to go into great detail—our understanding of arthropod developmental biology is literally changing from one month to the next! We now know that the fates of arthropod appendages are largely under the ultimate control of Hox genes, which dictate where body appendages form and the general types of appendages that form. Hox genes can either suppress limb development or modify it to create alternative appendage morphologies. These unique genes have played major roles in the evolution of new body plans among arthropods (and other phyla).

A good example of the evolutionary potential of Hox genes is seen in the abdominal limbs of insects. Abdominal limbs (prolegs) occur on the larvae (but not the adults) of various insects in several orders, and they are ubiquitous in the order Lepidoptera (i.e., caterpillars). Abdominal limbs were almost certainly present in the crustacean ancestry of insects. Hence, prolegs may have reappeared in groups such as the Lepidoptera through something as simple as the de-repression of an ancestral limb development program (i.e., they are a Hox gene–mediated atavism). We have learned that proleg formation is initiated during embryogenesis by a change in the regulation and expression of the bithorax gene complex (which includes the Hox genes *Ubx*, *abdA*, and *AbdB*).

Molecular developmental biology has also begun to unravel the origins of arthropod appendages themselves. We now know that appendage development is orchestrated by a complex of developmental genes, in particular the genes *Distal-less* (*Dll*) and *Extradenticle* (*Exd*). Evidence suggests that *Exd* is necessary for the development of the proximal region of arthropod limbs (the protopod), whereas *Dll* is expressed in the distal region of developing appendages (the telopod). Thus the protopod and the telopod of arthropod appendages are somewhat distinct, each under its own genetic control and each, presumably, free to respond to the whims and processes of evolution. So, whether an arthropod mandible is a "telomeric," or "whole-limb," appendage (i.e., built of all, or most, of the full complement of articles) or a "gnathobasic" appendage (i.e., built of only the basal-most, or protopodal, articles) depends on whether or not (or how much) the gene *Dll* is expressed.

Dll is expressed throughout the development of the multiarticulate, telomeric chelicerae and the pedipalps of chelicerates, but it is only transiently expressed in myriapod mandibles and in crustacean mandibles lacking palps. It is expressed throughout embryogeny in the mandibular palp of crustaceans, but not at all in the mandibles of hexapods. This expression pattern suggests that only the chelicerae and pedipalps of chelicerates are fully telomeric appendages, although the palp of the crustacean mandible represents the telopod of that limb. It also suggests that the development of a telopod is an evolutionarily flexible feature that can easily show homoplasy (i.e., parallelism). *Dll* is also expressed in the endites of arthropod limbs (e.g., in the phyllopodous limbs of Branchiopoda). In fact, *Dll* is an ancient gene that occurs in many animal phyla, where it is expressed at the tips of ectodermal body outgrowths in such different structures as the limbs of vertebrates, the parapodia and antennae of polychaete worms, the tube feet of echinoderms, and the siphons of tunicates.

So, we see that despite their considerable diversity, all arthropod limbs have a common ground plan and similar genetic mechanisms in their development. For example, developmental biology has now identified the appendage homologies of the head region for the major arthropod groups. A good example of developmental gene potential is revealed in Table 20.2, where we see the diversity of homologous head appendages across the onychophoran–arthropod spectrum. Imagine the jaws of velvet worms, chelicerae of scorpions, and antennae of insects all being derived from the same ancestral appendage! Evidence now suggests that the uniramous legs of hexapods arose from the biramous (or uniramous) appendages of crustacean ancestors. And elegant new research in gene patterning, using knockout methodology, backs 100 years of comparative anatomy and embryology in support of the idea that insect wings arose from crustacean leg segments that fused with the body wall in the evolutionary past (crustacean proximal leg-segment exites evolved into body wall lobes, then into wings). Although morphologists have struggled to establish homologies among the specific articles, or podites, of arthropod legs, considerable debate still exists on that issue. But we are beginning to acquire the developmental genetic toolkit needed to resolve this and other issues across the arthropod subphyla.

Support and Locomotion

Arthropods rely on the exoskeleton for support and maintenance of body shape. Their muscles are arranged as short bands that extend from one body segment to the next, or across the joints of appendages and other regions of articulation. An understanding of the nature of these articulation points—the areas where the cuticle is notably thin and flexible—is crucial to an understanding of the action of the muscles and hence of locomotion. In contrast to most of the exoskeleton, the articulations (joints) between body and limb segments are bridged by areas of very thin, flexible cuticle in which the procuticle is much reduced and unhardened (Figure 20.24). These thin areas are called **arthrodial or articular membranes**. Generally, each articulation is bridged by one or more pairs of antagonistic muscles.

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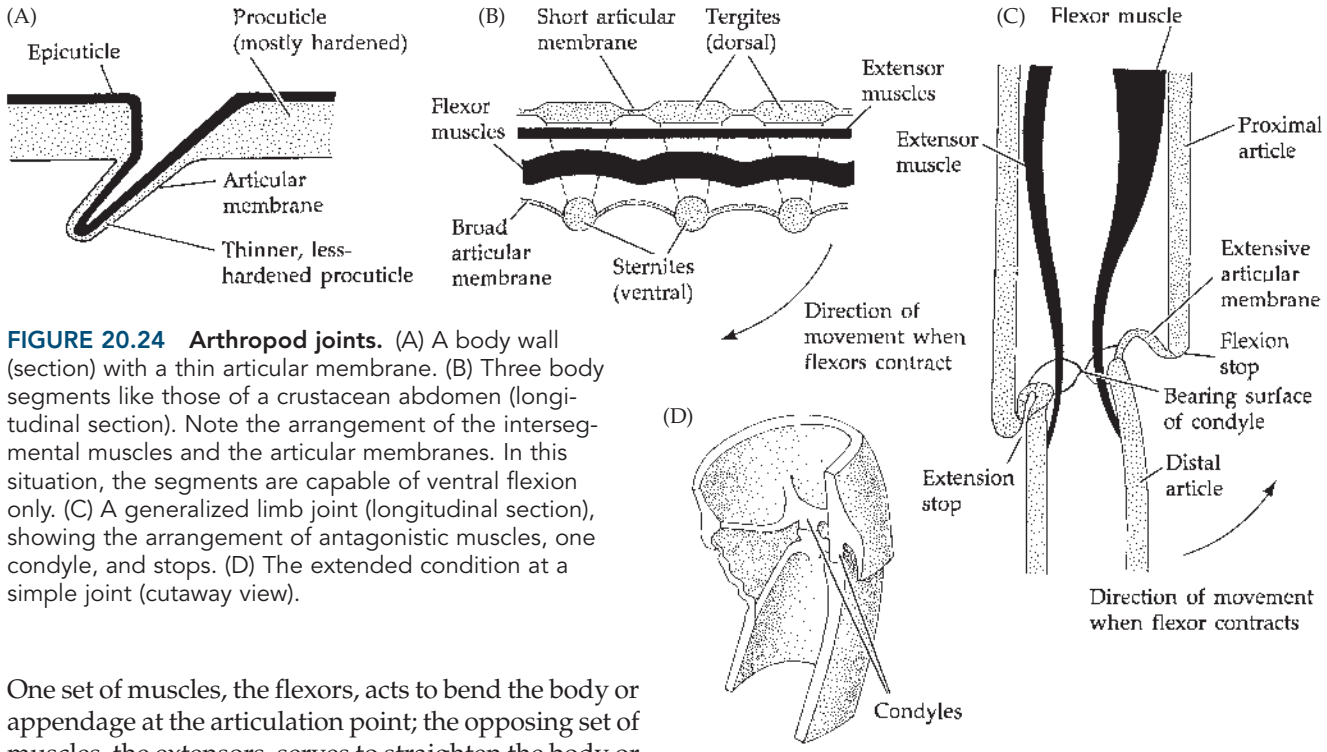

FIGURE 20.24 Arthropod joints. (A) A body wall (section) with a thin articular membrane. (B) Three body segments like those of a crustacean abdomen (longitudinal section). Note the arrangement of the intersegmental muscles and the articular membranes. In this situation, the segments are capable of ventral flexion only. (C) A generalized limb joint (longitudinal section), showing the arrangement of antagonistic muscles, one condyle, and stops. (D) The extended condition at a simple joint (cutaway view).

One set of muscles, the flexors, acts to bend the body or appendage at the articulation point; the opposing set of muscles, the extensors, serves to straighten the body or appendage. The same principles apply in the opposing sets of muscles of our own arms and legs.

Joints that operate as just described generally articulate in only a single plane (much like your own knee or elbow joints). Such movement is limited not only by the placement of the antagonistic muscle sets, but also by the structure of the hard parts of the cuticle that border the articular membrane. In such cases the articular membrane may not form a complete ring of flexible material, but will be interrupted by points of contact between hard cuticle on either side of the joint. These contact points, or bearing surfaces, are called **condyles** and serve as the fulcrum for the lever system formed by the joint. A dicondylic joint allows movement in one plane, but not at angles to that plane. The motion at a joint is also usually limited by hard cuticular processes called locks or stops, which prevent overextension and overflexion (Figure 20.24C,D).

Some joints are constructed to allow movement in more than one plane, much like a ball-and-socket joint. For example, in most arthropods the joints between walking legs and the body (the coxal-pleural joints) lack large condyles, and the articular membranes form complete bands around the joints. In other cases, two adjacent dicondylic limb joints articulate at 90° to one another, forming a gimbal-like arrangement that facilitates movement in two opposing planes.

Arthropods have evolved a plethora of locomotor devices for movement in water, on land, and in the air. Only the vertebrates can boast a similar range of abilities, albeit utilizing a far less diverse set of mechanisms. Like so many other aspects of arthropod biology, their methods of movement reflect the extreme evolutionary plasticity and adaptive qualities associated with the segmented body and appendages.

Movement through water involves various patterns of swimming that include smooth paddling by shrimps, jerky stroking by certain insects and small crustaceans, and startling backward propulsion by tail flexion in lobsters and crayfish. Aerial locomotion has been mastered by the pterygote (winged) insects but is also practiced by certain spiders that drift on threads of silk. Many arthropods burrow or bore into various substrata (e.g., ants, bees, termites, burrowing crustaceans). Some terrestrial arthropods that are normally associated with the ground engage in short-term aerial movements that serve as escape responses. Some, like fleas, simply jump, whereas others jump and glide, giving us possible clues to the evolutionary origin of flight. Some crustaceans jump as well, such as the familiar beach hoppers (amphipods) that bound away over the sand when disturbed. Arthropods that move in contact with the surface of the substratum, under water or on land, by various forms of walking, creeping, crawling, or running are referred to as pedestrian or reptant.

All of the common forms of arthropod locomotion except flight depend on the use of typical appendages and thus are based on the principles of joint articulation just described, coupled with specialized architecture of the appendages. Next we discuss some aspects of two fundamental types of appendage-dependent locomotion in arthropods, swimming and pedestrian locomotion, exploring variations on these methods and others in subsequent chapters.

Many examples of swimming arthropods are found among the crustaceans. Most swimming crustaceans (e.g., anostracans and shrimps) and even those that swim only infrequently (e.g., isopods and amphipods) employ ventral, flaplike setose appendages as paddles (Figure 20.23B). The appendages used for swimming may be restricted to particular body regions (e.g., the abdominal swimmerets of shrimps, stomatopods, and isopods; the metasomal limbs of swimming copepods) or may occur along much of the trunk (e.g., the appendages of anostracans, remipedes, and cephalocarids) (Figure 20.25). These appendages engage in a backward power (propulsive) stroke and a forward recovery stroke. In all cases, the appendages are constructed in such a way that on the recovery stroke, they are flexed and the flaps and marginal setae passively "collapse" to reduce the coefficient of friction (drag). On the power stroke the limbs are held erect, with their largest surface facing the direction of limb movement, thus increasing thrust efficiency (by increasing the coefficient of friction and the distance through which the limb travels). These swimming appendages typically articulate with the body only on a plane parallel to the body axis. Less sophisticated swimming is accomplished in other arthropods by use of various other appendages, including the antennae of many minute crustaceans and larvae and the thoracic stenopods of many aquatic insects.

Pedestrian locomotion in arthropods is highly variable, both among different groups and even in individual animals. With the exception of a few strongly homonomous "vermiform" types (e.g., centipedes and millipedes), most arthropods are incapable of lateral body undulations. Thus, they cannot amplify the stride length of their appendages by body waves (as many polychaetes do, for example). Walking arthropods depend almost entirely on the mobility of specialized groups of appendages. The structure of these ambulatory legs is quite different from that of paddle-like swimming appendages, and their action is much more complex and variable.

Consider the general movement of an ambulatory leg as it passes through its power and recovery strokes (Figure 20.26). At the completion of the power stroke, the appendage is extended posteriorly and its tip is in contact with the substratum. The recovery stroke involves lifting the limb, swinging it forward, and placing it back down on the substratum; by then the limb is extended anterolaterally. The power stroke is accomplished by first flexing and then extending the leg while the tip is held in place against the substratum. Thus the body is first pulled and then pushed forward by each limb.

These complicated movements obviously would not be possible if all of the limb joints and limb-body joints were dicondylic articulations in the same plane, parallel to the body axis. The leg must be able to move up and down as well as forward and backward, and the action at each joint must be coordinated with the actions of all the others. In general, the distal limb joints are dicondylic, with articulation (and movement) planes parallel to the limb axis. They allow the appendage to flex and extend, that is, to move the tip closer to (adduction) or farther from (abduction) the point of limb origin. The actions of these joints typically involve the usual sets of antagonistic flexor and extensor muscles described earlier. In some arachnids and a few crustaceans, however, certain limb joints lack extensor muscles, and the limbs are extended by an increase in blood pressure. Raising and lowering of the limb are also accomplished by extensor and flexor muscles, which thus serve as levators and depressors, respectively; the muscles in the proximal leg joints usually serve these purposes.

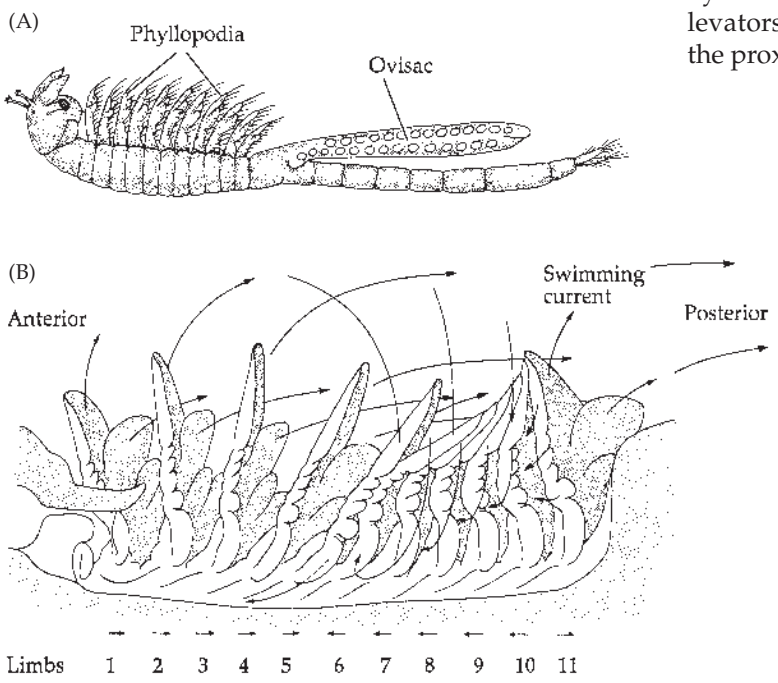

FIGURE 20.25 Swimming motions in a branchiopod crustacean. (A) A fairy shrimp (Anostraca) on its back in its normal swimming posture. (B) The appendages "in motion," producing a posteriorly directed flow of water that propels the animal forward. Arrows near the bases of the appendages indicate feeding currents. The small arrows below the drawing indicate the direction of movement of each numbered appendage at this moment in the anterior progression of the metachronal wave. Water is drawn into the interlimb spaces as adjacent appendages move away from one another, and water is pressed out of the spaces as adjacent limbs move together. The lateral articles of these phyllopodial appendages are hinged in such a way that they extend on the power stroke to present a large surface area and collapse on the recovery stroke, thereby producing less drag.

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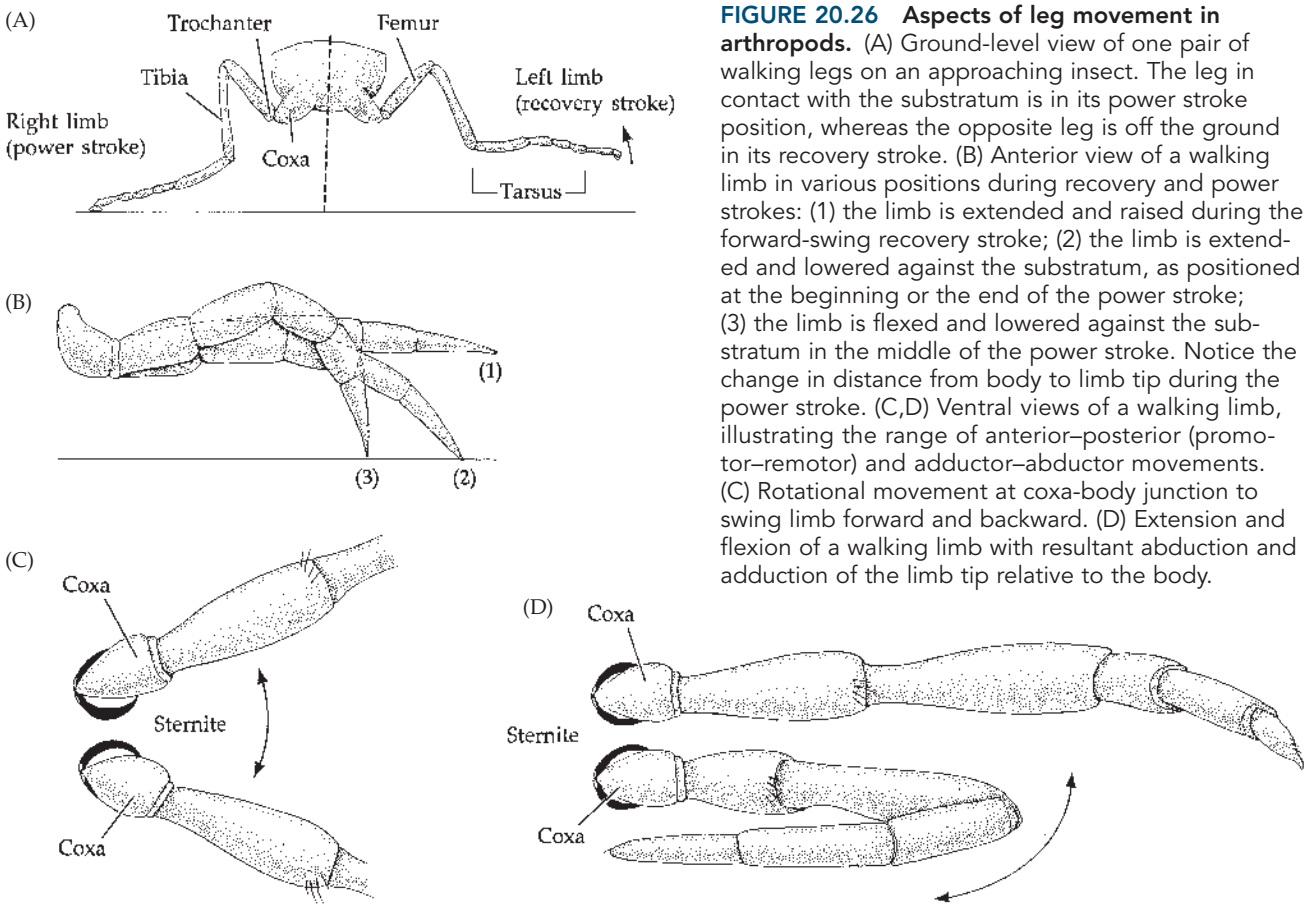

FIGURE 20.26 Aspects of leg movement in arthropods. (A) Ground-level view of one pair of walking legs on an approaching insect. The leg in contact with the substratum is in its power stroke position, whereas the opposite leg is off the ground in its recovery stroke. (B) Anterior view of a walking limb in various positions during recovery and power strokes: (1) the limb is extended and raised during the forward-swing recovery stroke; (2) the limb is extended and lowered against the substratum, as positioned at the beginning or the end of the power stroke; (3) the limb is flexed and lowered against the substratum in the middle of the power stroke. Notice the change in distance from body to limb tip during the power stroke. (C,D) Ventral views of a walking limb, illustrating the range of anterior–posterior (promotor–remotor) and adductor–abductor movements. (C) Rotational movement at coxa-body junction to swing limb forward and backward. (D) Extension and flexion of a walking limb with resultant abduction and adduction of the limb tip relative to the body.

Anterior–posterior limb movements are accomplished in two basic ways. First, the ball-and-socket type of joint at the point of limb-body articulation typically carries out these actions in most crustaceans, insects, and myriapods. Promotor and remotor muscles that are associated with these joints rotate the limb forward and backward, respectively. Second, many arachnids accomplish multidirectional limb movements by using only uniplanar dicondylic joints. In these arthropods, one or more of the proximal joints articulate perpendicular to the limb axis, and thus to the rest of the limb joints, providing forward and backward movement.

Understanding how a single limb moves does not, of course, describe the locomotion of the whole animal. The various patterns of pedestrian locomotion in arthropods, called gaits, are the result of many factors (e.g., leg number, leg movement sequences, stride lengths, speed). The number of patterns is great, but it is limited by certain biological and physical constraints. Speed is limited by rates of muscle contraction and the necessity for coordinating leg movements to avoid tangling. Furthermore, the animal must maintain an appropriate distribution of legs at all times in various phases of power and recovery strokes so that its weight is fully supported.

The gaits of insects have been more extensively studied than those of other arthropods. Studies on insects and myriapods led to an attempt to establish principles under which all pedestrian arthropod locomotion could be unified. The most frequently used descriptions of arthropod walking, crawling, and running are based on the "metachronal model." The basic idea of this model is that the legs on each side of the body move in metachronal (repeated) waves from back to front and that the waves overlap to various degrees, depending on the speed of movement. This model does work for some arthropods, some of the time, but things are not so simple, and attempts to overgeneralize have been misleading. A good deal of the work on crustaceans and arachnids (and even insects) indicates that leg movement sequences, stepping patterns, stride lengths, and other characteristics are extremely variable, even within individuals, and depend on a host of factors other than speed. The actions of the joints are coordinated by information supplied to the central nervous system by proprioceptors in the joints themselves.

Growth

The imposition of a rigid exoskeleton on the arthropods precludes growth by means of a gradual increase in external body size. Rather, an overall increase in body size takes place in staggered increments associated with the periodic loss of the old exoskeleton and

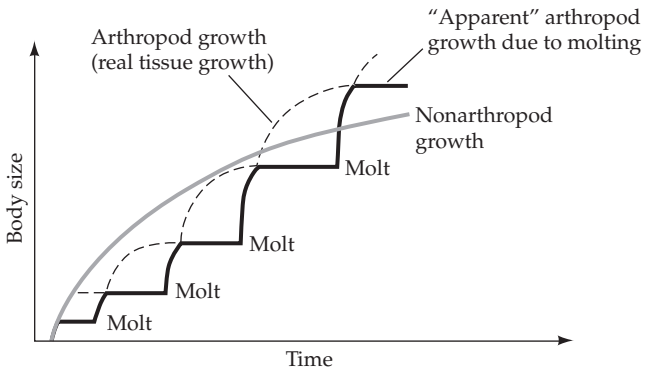

FIGURE 20.27 Arthropod versus nonarthropod growth. The heavy solid line indicates the incremental ("stair-step") growth pattern of an arthropod as measured by changes in external body size associated with molts. The dotted line depicts real tissue growth in the same arthropod. The gray line depicts the typical growth of a nonarthropod.

the deposition of a new, larger one (Figure 20.27). The process of shedding the exoskeleton is called **molting**, and it is a phenomenon characteristic of arthropods and all other ecdysozoans. The molting process varies in detail even among the arthropods. It has been best studied in certain insects and crustaceans, and the description here is based primarily on those two groups. We first outline the basic steps in the arthropod molt cycle and then briefly discuss the hormonal control of those events. In all arthropods (and probably all ecdysozoans) molting is regulated by a hormone called **ecdysone**; thus, the entire molting process in these groups is also known as **ecdysis**.

The stages between molts are called **intermolts** (or **instars**, in insects). It is during these intermolt stages that real tissue growth occurs, although with no increase in external size. When such tissue growth reaches the point at which the body "fills" its exoskeletal case, the animal usually enters a physiological state known as **premolt or proecdysis**. During this stage there is active preparation for the molt, including accelerated growth of any regenerating parts. Certain epidermal glands secrete enzymes that begin digesting the old endocuticle, thus separating the exoskeleton from the epidermis. In many crustaceans, some of the calcium is removed from the cuticle during this period and stored within the body for later redeposition. As the old cuticle is loosened and thinned, the epidermis begins secreting a soft new cuticle. Figure 20.28 depicts some of these events.

Once the old cuticle has been substantially loosened and a new cuticle formed, actual molting occurs. The old cuticle splits in such a way that the animal can wriggle free and pull itself out. The lines along which the cuticle splits vary among the arthropods but are consistent within particular groups. It is important to remember that all cuticular linings are lost during ecdysis, including the linings of the foregut and hindgut, the eye surfaces, and the cuticle that lines every pit, groove, spine, and seta on the body surface. When you see a cast-off intact exoskeleton, or **exuvium**, of an arthropod, you are bound to be impressed with its wonderfully perfect detail. It is at first difficult to imagine how the animal could extricate itself from each and every tiny part of the old cuticle (Figure 20.28C,D). The ability to do so depends, of course, on the great flexibility of the body within its new and unhardened exoskeleton.

As soon as the arthropod emerges from its old cuticle, and while the new cuticle is still soft and pliable, its body swells rapidly by taking up air or water. Once the new cuticle is thus enlarged, the animal enters a postmolt period (**postecdysis**), during which the cuticle is hardened by sclerotization and/or the redeposition of calcium salts. The excess water (or air) is then actively pumped from the body, and real tissue growth occurs during the subsequent **intermolt** period. During the sclerotization process, the cuticle becomes drier, stiffer, and resistant to chemical and physical degradation through the molecular cross-linking process in the protein-chitin matrix described earlier.

We have stressed the adaptive significance of the arthropod exoskeleton in terms of its protective and supportive qualities. However, during the **postmolt period**, before the new exoskeleton is hardened, the animal is quite vulnerable to injury, predation, and osmotic stress. Many arthropods become reclusive at this time, hiding in protective nooks and crannies and not even feeding when in this "soft-shell" condition. The time required for hardening of the new exoskeleton varies greatly among arthropods, generally being longer in larger animals. The well-known and delectable "soft-shell crabs" of the eastern United States are simply blue crabs (*Callinectes sapidus*) caught during their postmolt period.

Many genes and a complex hormonal system regulate the molt cycle (Figure 20.29). Several models have been proposed to explain the hormonal pathways involved in molting in insects and crustaceans, but the picture is still somewhat incomplete, despite having whole genomes available for so many arthropods. The hormonal activities of the crustacean ecdysial cycle have been most extensively studied in decapods. In some (e.g., lobsters and crayfish), molting occurs periodically throughout the animal's life, but in many others (e.g., copepods and some crabs), molting, and therefore growth, ceases at some point, and a maximum size is attained. Animals that have engaged in their final molt are said to have entered a state of **anecdysis**, or permanent intermolt—they are in their final instar. Among insects, molting is largely associated with metamorphosis from one developmental stage to the next (e.g., pupa to adult), and except for the most primitive hexapods, adults do not molt (i.e., they are in anecdysis).

In both crustaceans and hexapods (and probably all arthropods), the initiation of molting, beginning with the events of proecdysis, is brought about by the

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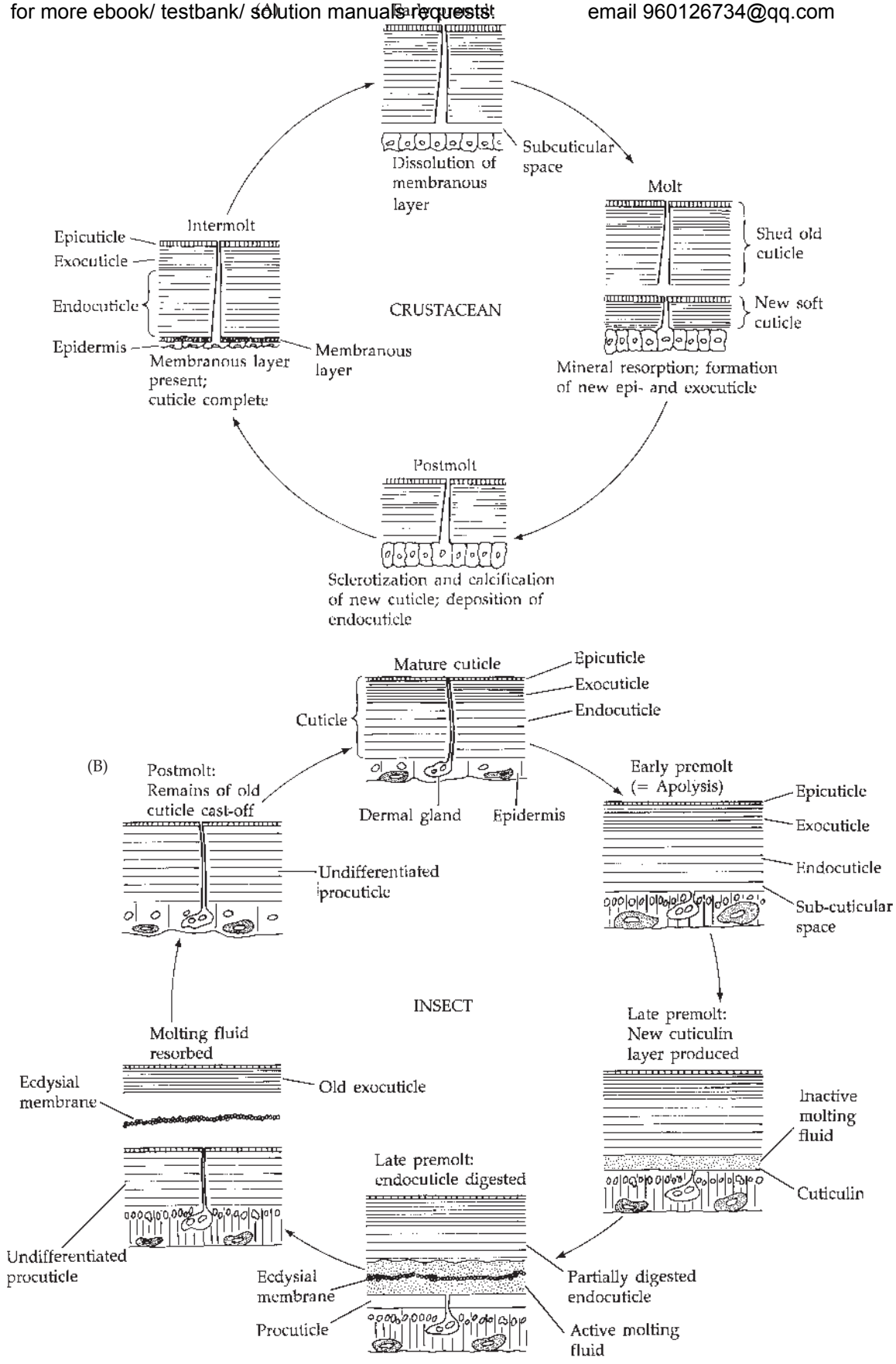

FIGURE 20.28 Arthropod molting. Schematic representations of some events in the molting of (A) a crustacean and (B) an insect. The separation of the old cuticle from the body is generally accomplished by dissolution of the membranous layer in large crustaceans and by digestion of the inner boundary of the cuticle in insects.

(*Continued*)

(C)

Courtesy of R. Brusca

(D)

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FIGURE 20.28 (*continued*) Arthropod molting. (C) A swimming crab in the final stage of extracting itself from its old, molted exoskeleton; only the chelipeds remain to be pulled out of the exuvium. (D) The cast-off exoskeleton of a tarantula. (A after R. Roer and R. Dillaman. 1984. *Am Zool* 24: 893–909; B after V. B. Wigglesworth. 1954. *The Physiology of Insect Metamorphosis*. Cambridge University Press, Cambridge.)

action of a molting hormone called ecdysone. Apparently, however, the pathways controlling the secretion of ecdysone are different in insects and crustaceans, as diagrammed in Figure 20.29. In crustaceans ecdysone is secreted by an endocrine gland called the Y-organ located at the base of the antennae or near the mouthparts. The action of the Y-organ is controlled by a complex neurosecretory apparatus located near the eyes or in the eyestalks. During the intermolt period, a **molt-inhibiting hormone (MIH)** is produced by neurosecretory cells of the X-organ, located in a region of the eyestalk nerve (or ganglion) called the medulla terminalis (Figure 20.29A). MIH is carried by axonal transport to a storage area called the sinus gland, which appears to control MIH release into the blood. As long as sufficient levels of MIH are present in the blood, the production of ecdysone by the Y-organ is inhibited.

The active premolt and subsequent molt phases are initiated by sensory input to the central nervous system. The stimulus is external for some crustaceans (e.g., day length or photoperiod for certain crayfishes) and internal for others (e.g., growth of soft tissues in certain crabs). External stimuli are transmitted via the central nervous system to the medulla terminalis and X-organ (Figure 20.29B). Appropriate stimuli inhibit the secretion of MIH, ultimately resulting in the production of ecdysone and the initiation of a new molt cycle.

The sequence of events in insects is somewhat different from that in crustaceans in that a molt inhibitor is apparently not involved. When an appropriate stimulus is introduced to the central nervous system, certain neurosecretory cells in the cerebral ganglia are activated. These cells, which are located in the pars intercerebralis, secrete **ecdysiotropin**. This hormone is carried by axonal transport to the corpora cardiaca, paired neural masses associated with the cerebral ganglia. Here, thoracotropic hormone is produced and carried to the prothoracic glands, stimulating them to produce and release ecdysone (Figure 20.29C).

The Digestive System

It will come as no surprise that the great diversity among arthropods is reflected in their expression of nearly every feeding method imaginable. As a group, the only real constraint on arthropods in this regard is the absence of external (as well as internal), functional cilia. Evolutionarily, many arthropods have overcome even this limitation and suspension feed by other means. So varied are arthropod feeding strategies that we postpone discussion of them to the sections and chapters on particular taxa, and here we simply generalize about the basic structure and function of arthropod digestive systems.

The digestive tract of arthropods is complete (a through gut) and generally straight, extending from a ventral mouth on the head to a posterior anus. Various appendages (the mouthparts and other associated appendages) may be associated with processing food and moving it to the mouth. Regional specialization of the gut occurs in most taxa. In almost all cases there is a well-developed, cuticle-lined, stomodeal foregut and proctodeal hindgut (both derived from embryonic ectoderm), connected by an endodermally derived midgut (Figure 20.30). In general, the foregut serves for ingestion, transport, storage, and mechanical digestion of food; the midgut for enzyme production, chemical digestion, and absorption; and the hindgut for water absorption and the preparation of fecal material. The midgut typically bears one or more evaginations in the

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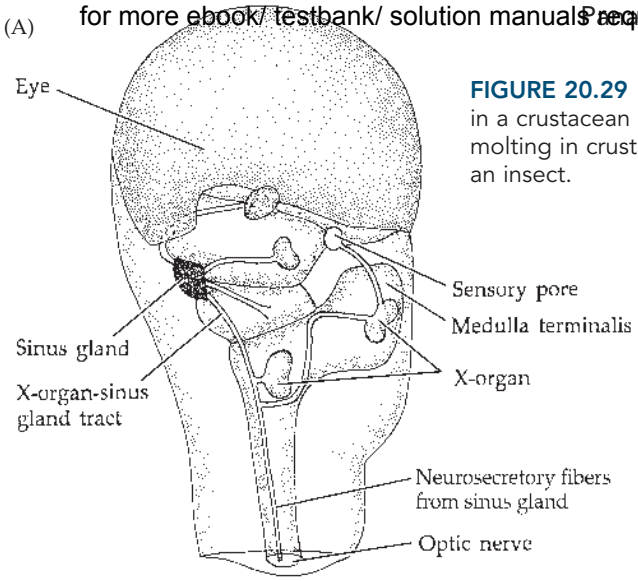
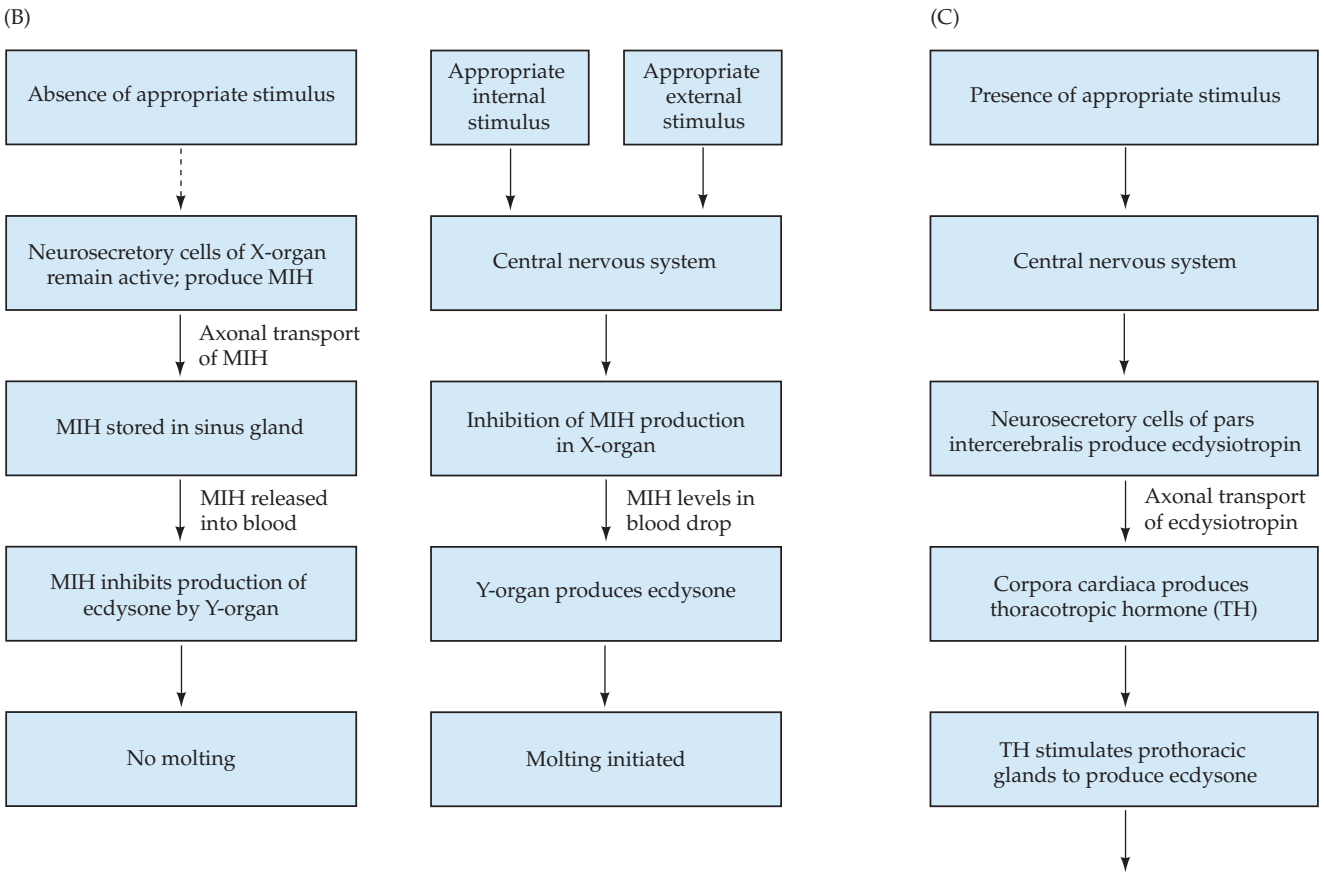


FIGURE 20.29 Molting in arthropods. (A) The neurosecretory apparatus in a crustacean eyestalk. (B) Flow diagram of events inhibiting and initiating molting in crustaceans. (C) Flow diagram of events initiating molting in an insect.



form of **digestive ceca** (often referred to as the "digestive gland," "liver," or "hepatopancreas"). The number of ceca and the arrangement of the other gut regions vary among the different taxa. In almost all arthropods, the inner layer of midgut epithelium is typically coated with a **peritrophic matrix**—a very thin but complex chitinous sheet that is continuously formed by delamination from the epithelium such that the inner surface of

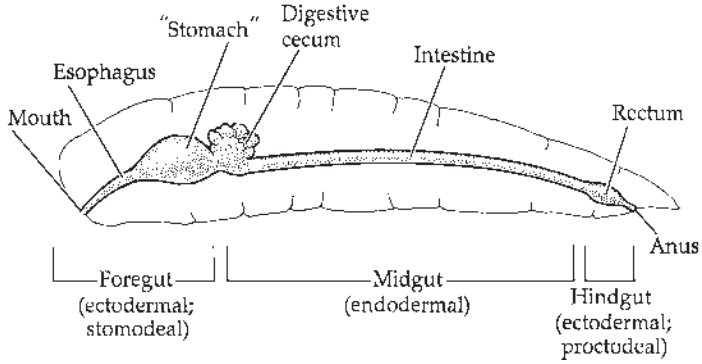


FIGURE 20.30 The major gut regions of arthropods. The myriad variations on this theme are discussed in subsequent chapters on particular taxa.

the midgut is constantly being "cleaned." As this layer lifts off the epithelium, it surrounds ingested materials as a **peritrophic membrane**, including microbes and food particles, wrapping and compartmentalizing them as "pellets." This membrane protects the gut epithelium from damage by food particles and pathogens; it can also play a role in the accumulation and metabolism of certain elements (e.g., calcium, copper) as well as the inactivation of potentially toxic metals. Microscopic pores in the membrane allow passage of enzymes and digested nutrients. Arthropod feces are thus typically "packaged" in the remains of the peritrophic membrane.

The various terrestrial arthropods have convergently evolved many similar features as adaptations to life on land. Many of these convergent structures are associated with (although not necessarily derived from) the gut. For example, excretory structures called **Malpighian tubules** that develop from the midgut or hindgut of insects, arachnids, myriapods, and tardigrades appear to be convergences (i.e., nonhomologous structures). The excretory structures of onychophorans also used to be called Malpighian tubules, but they have recently been shown to be complex metanephridia with secondarily derived, closed end sacs. Many unrelated terrestrial taxa have special **repugnatorial glands**, which may or may not be associated with the gut and which produce noxious substances used to deter predators.

Many different groups of terrestrial arthropods also have evolved the ability to produce silks or silklike substances for use outside their bodies. These silklike fibers are produced by nonhomologous structures among different arthropods. Although they vary greatly in chemical composition, all share a common molecular feature that gives them strength and elasticity; they are composed of regular assemblies of long-chain macromolecules (most being fibrous proteins), and many also incorporate collagens. Modified salivary glands are common silk-producing organs, but silks are also secreted by the digestive tract, Malpighian tubules, accessory reproductive glands, and assorted dermal glands. Silk production occurs in chelicerates (false scorpions, spiders, and mites), many insect orders (such as adult webspinners, or Embioptera, and the larvae of commercial silkworm moths *Bombyx* and *Anaphe*), some myriapods, and some crustaceans (e.g., amphipods). Arthropod silks are used in the production of cocoons, egg cases, webs, larval "houses," flotation rafts, prey entrapment threads, draglines, spermatophore receptacles, intraspecific recognition devices, and other sundry items. The truly spectacular array of silk uses by spiders is discussed in Chapter 24. Silk production and use provide one of the more impressive examples of evolutionary convergence seen in the arthropods.

A number of arthropod groups are capable of digesting plant material and produce their own cellulase, although in most cases digestion is enhanced by symbiotic microbes (bacteria and fungi) in the gut. Some herbivorous crabs (e.g., many Gecarcinidae) and isopods (e.g., Valvifera, Sphaeromatidae, Limnoriidea) appear to use only endogenously produced cellulases to break down plant tissues. In other herbivorous isopod species (Oniscidea, the terrestrial isopods) there is a mix of endogenous cellulases and microbial symbiont-produced cellulases, and this is also the case for termites and herbivorous beetles. Over a dozen endogenous lignocellulose-degrading enzymes have been identified in the common land isopod *Armadillidium vulgare*, attesting to the complexity of the process. In these cases, there is a complementary and synergistic action of the lignocellulose-degrading enzyme repertoire from the host and its microbial symbionts. In marine species, hemocyanins in the gut appear to modify lignin and thus facilitate digestion.

Circulation and Gas Exchange

A major aspect of the arthropod body plan is reflected in the nature of the circulatory system. The largely open hemocoelic system is in part a result of the imposition of the rigid exoskeleton and the loss of an internally segmented and fluid-filled coelom. We have seen that isolated coelomic spaces (such as the segments of annelids) require a closed circulatory system to service them, but this requirement is not present in arthropods. Furthermore, without a muscular, flexible body wall to augment blood movement, a pumping mechanism becomes necessary, resulting in the elaboration of a muscular heart. The result is a system wherein the blood is driven from the heart chamber through short vessels and into the hemocoel, where it bathes the internal organs. The blood returns to the heart via a noncoelomic pericardial sinus and perforations in the heart wall called ostia (Figure 20.31). The blood flows back to the heart along a decreasing pressure gradient resulting from lowered pressure within the pericardial sinus as the heart contracts. The complexity of the circulatory system varies greatly among arthropods, the differences being dependent in large part on body size and shape. These differences include variations in the size and shape of the heart (Figure 20.31B–D), the number of ostia, the length and number of vessels, the arrangement of hemocoelic sinuses, and the circulatory structures associated with gas exchange.

Arthropod blood, or **hemolymph**, serves to transport nutrients, wastes, and usually gases. It includes a variety of types of amebocytes and, in some groups, clotting agents. The blood of many kinds of small arthropods is colorless, simply carrying gases in solution. Most of the larger forms, however, contain

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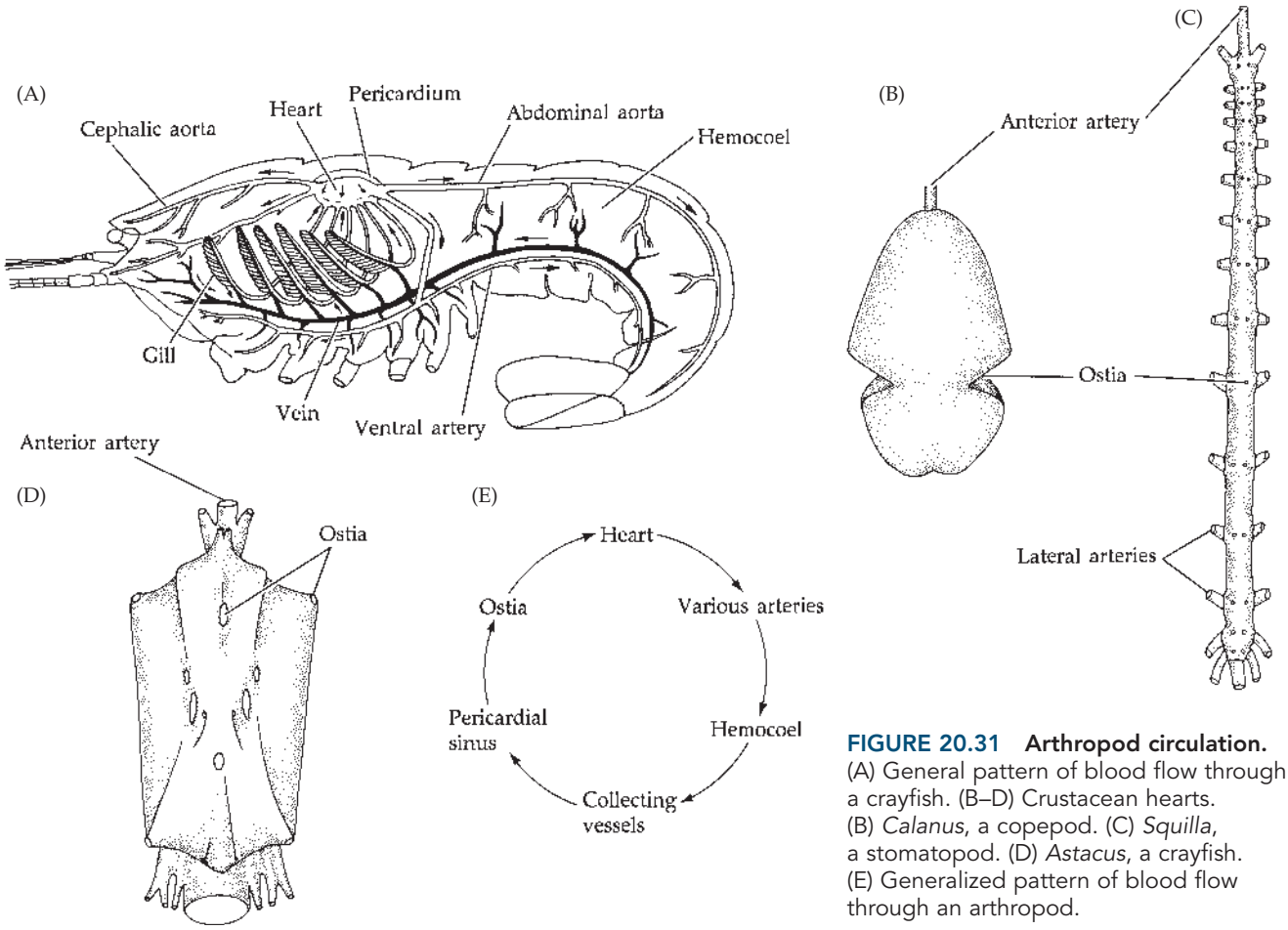


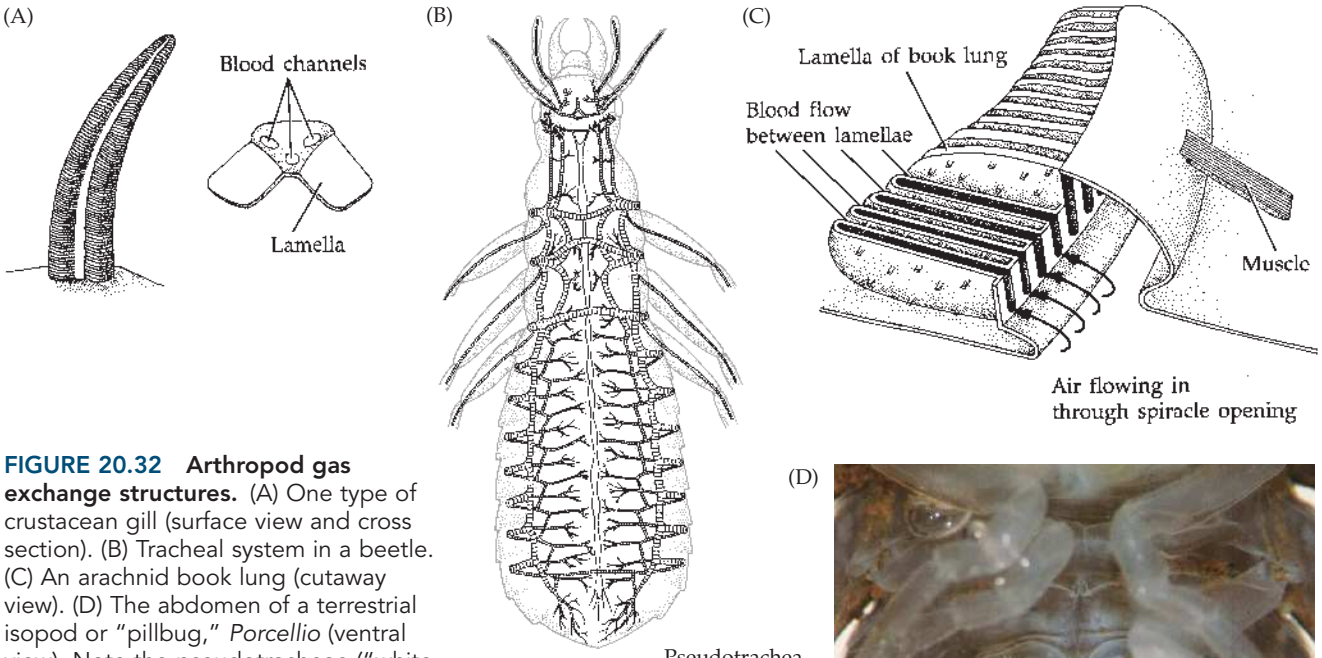
FIGURE 20.31 Arthropod circulation. (A) General pattern of blood flow through a crayfish. (B–D) Crustacean hearts. (B) *Calanus*, a copepod. (C) *Squilla*, a stomatopod. (D) *Astacus*, a crayfish. (E) Generalized pattern of blood flow through an arthropod.

hemocyanin, and a few contain hemoglobin. Both pigments are always dissolved in the hemolymph rather than contained within cells. In most groups of arthropods, the circulatory route takes at least some of the blood past the gas exchange surfaces (e.g., gills) before returning to the heart.

One of the major evolutionary problems arising from the acquisition of a relatively impermeable exoskeleton involves gas exchange, particularly for terrestrial arthropods. On land, any increase in cuticular permeability to facilitate gas exchange also increases the threat of water loss. Remember that gas exchange surfaces not only must be permeable but also must be kept moist (see Chapter 3). Evolutionarily, the challenge for the arthropods becomes one of disrupting the integrity of the exoskeleton in such a way as to allow gas exchange without seriously jeopardizing the survival of the animal by abandoning the principal benefits of the exoskeleton.

The design of arthropod gas exchange structures has taken one form in aquatic groups and quite another in terrestrial taxa (Figure 20.32). The former is best exemplified by the crustaceans and the latter by the insects and terrestrial chelicerates. Some very tiny crustaceans (e.g., copepods) with a low surface-area-to-volume ratio exchange gases cutaneously across the general body surface or at thin cuticular areas such as articulating membranes. However, most of the larger aquatic crustaceans have evolved various types of gills in the form of thin-walled, hemolymph-filled cuticular evaginations. Gills are commonly branched or folded, providing large surface areas (Figure 20.32A). The gills of some crustaceans (e.g., euphausiacians) are exposed, unprotected, to the surrounding medium, whereas in others (e.g., crabs and lobsters) the gills are carried beneath protective extensions of the exoskeleton.

Terrestrial arthropods—the insects, myriapods, and arachnids, but also some terrestrial crustaceans—have evolved gas exchange structures in the form of invaginations of the cuticle, rather than the evaginations seen in aquatic crustaceans. Obviously, external gills would be unacceptable in dry conditions, but placed internally, these gas exchange structures remain moist and act as humidity chambers, allowing oxygen to enter solution for uptake. Many arachnids possess invaginations called **book lungs**, which are sacciform pockets with thin, highly folded walls called lamellae (Figure 20.32C). Hexapods, myriapods, and many arachnids possess inwardly directed branching tubules called **tracheae**, which open externally through pores called **spiracles** (Figure 20.32B). In insect tracheal systems



Courtesy of J. DeMartini

FIGURE 20.32 Arthropod gas exchange structures. (A) One type of crustacean gill (surface view and cross section). (B) Tracheal system in a beetle. (C) An arachnid book lung (cutaway view). (D) The abdomen of a terrestrial isopod or "pillbug," *Porcellio* (ventral view). Note the pseudotracheae ("white bodies") on the abdominal appendages, or pleopods.

the inner ends of the tubules lie in the hemocoel or are embedded in organ tissues, allowing direct gas exchange between the air and the blood and internal organs. The tracheae of arachnids are probably not directly homologous with those of insects. Some terrestrial crustaceans (isopods) have **pseudotracheae** on the abdominal appendages; these structures are short, branching tubes that bring air close to the blood-filled spaces in these appendages (Figure 20.32D).

Excretion and Osmoregulation

With the evolution of a hemocoelic circulatory system in arthropods, nephridia with open nephrostomes became functionally untenable. It simply would not do to drain the blood directly from an open hemocoel to the outside. Arthropods have evolved a variety of highly efficient excretory structures that share a common adaptive feature in that they are internally closed. In addition to this major difference between the nephridia of arthropods and those of other coelomate protostomes, there has been a reduction in the overall number of excretory units.

In most adult crustaceans a single pair of nephridia (nephromixia) persists, usually associated with a particular segment of the head (i.e., as antennal glands or maxillary glands) (Figure 20.33A). In arachnids there may be as many as four pairs of nephridia (and in onychophorans, many more) opening at the bases of the walking legs (i.e., coxal glands).

A second type of excretory structure occurs in four terrestrial panarthropod taxa: arachnids, myriapods, insects, and tardigrades. These structures, known as **Malpighian tubules**, arise as blind tubules extending into the hemocoel from the gut wall (Figure 20.33C). However, anatomical and developmental evidence suggest that these Malpighian tubules may have evolved independently in each of these groups, representing yet another exemplary case of convergent evolution among the Arthropoda.

The excretory physiology of arthropods is a complex and extensively studied topic, and we present only a very general summary here. The various nephridial types of coelomic origin are functionally much more complex and efficient than open metanephridia. The uptake of materials from the hemocoel by the inner ends of these nephridia apparently involves passive movement in response to filtration pressure, as well as active transport. The fluid entering the nephridium is generally similar in composition to the hemolymph itself, but as it passes along the plumbing system of the nephridium, a good deal of selective reabsorption occurs, particularly of salts and nutrients such as glucose. Thus, the urine exiting the nephridial pores is markedly different from the hemolymph and represents a concentration of nitrogenous waste products (Figure 20.33B).

Malpighian tubules accomplish the same process, but they must rely on assistance from the gut.

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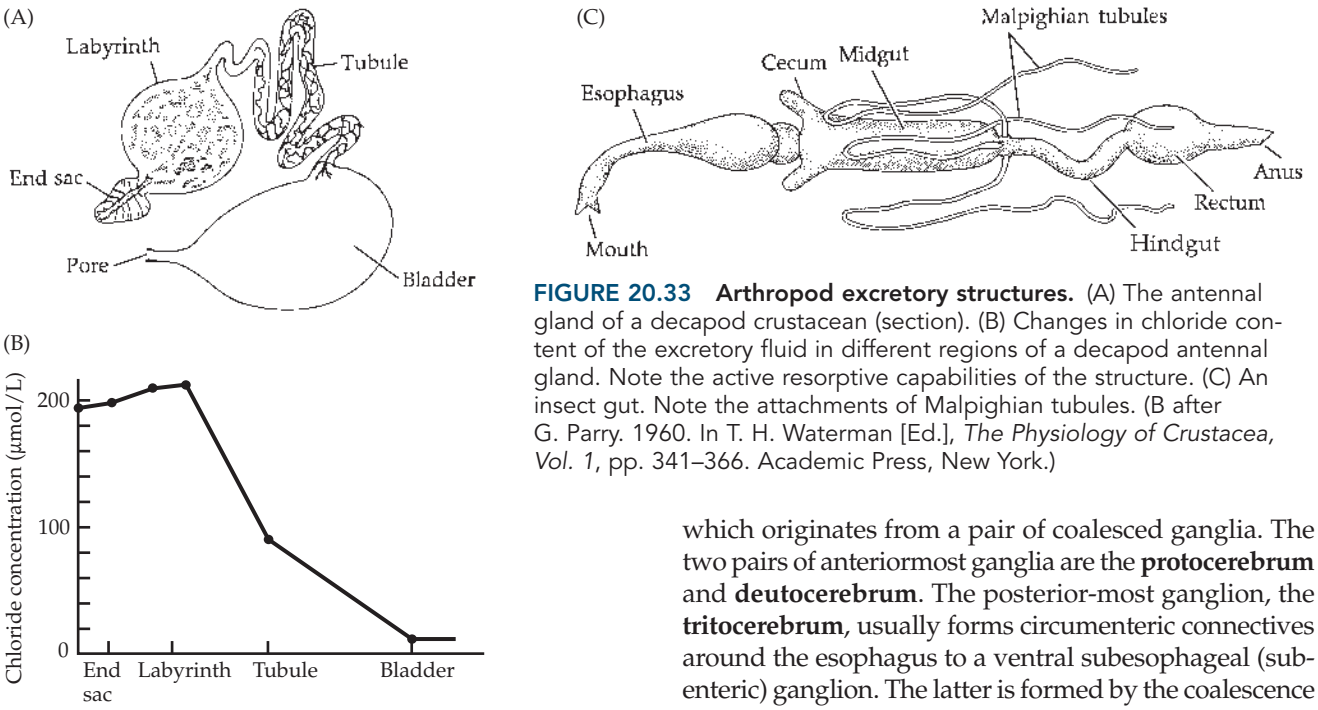

FIGURE 20.33 Arthropod excretory structures. (A) The antennal gland of a decapod crustacean (section). (B) Changes in chloride content of the excretory fluid in different regions of a decapod antennal gland. Note the active resorptive capabilities of the structure. (C) An insect gut. Note the attachments of Malpighian tubules. (B after G. Parry. 1960. In T. H. Waterman [Ed.], *The Physiology of Crustacea, Vol. 1*, pp. 341–366. Academic Press, New York.)

Malpighian tubule uptake from the hemocoel is relatively nonselective, and the resulting "primary urine" (containing nutrients, water, salts, and so on) is emptied directly into the gut. Very little reabsorption of non-waste material occurs along the length of the tubule itself. The hindgut is mostly responsible for concentrating the urine by reabsorbing the non-waste fractions. The ability of the gut to reabsorb water plays a critical role in osmoregulation in terrestrial and freshwater arthropods. Like most aquatic invertebrates, marine crustaceans excrete most (about 70%–90%) of their nitrogenous waste as ammonia; the remainder is excreted in the forms of urea, uric acid, amino acids, and some other compounds. Terrestrial arachnids, myriapods, and insects excrete predominantly uric acid (via the hindgut and anus). In Chapter 3 we reviewed some of the relationships between excretory products and osmoregulation in terms of adaptation to terrestrial habitats. The ability to produce large quantities of uric acid, and thus conserve water, has doubtless contributed significantly to the success of arachnids and insects on land. The crustaceans, on the other hand, have not been able to make a major shift from ammonotelism to uricotelism. Only the terrestrial crustaceans (i.e., isopods—woodlice and pillbugs) show a slight increase in uric acid excretion over that of their marine counterparts.

Nervous System and Sense Organs

The general plan of the arthropod nervous system is similar to that seen in many other protostomes, and many obvious homologies exist (Figure 20.34A). The arthropod brain (**cerebral ganglia**) comprises three regions, each of which originates from a pair of coalesced ganglia. The two pairs of anteriormost ganglia are the **protocerebrum** and **deutocerebrum**. The posterior-most ganglion, the **tritocerebrum**, usually forms circumenteric connectives around the esophagus to a ventral subesophageal (subenteric) ganglion. The latter is formed by the coalescence of several other head ganglia, usually those associated with the mandibles and maxillae in mandibulates. A double or single, ganglionated ventral nerve cord extends through some or all of the body segments. Each of these regions gives rise to a major pair of nerves to particular head appendages (Figure 20.34B,C). The regions have been used as the key landmarks to establish homology of the head appendages across arthropods—the famous "arthropod head problem." In extant arthropods, the protocerebrum innervates the eyes, whereas the deutocerebrum innervates the antennae (only the first antennae in Crustacea), the chelifores of pycnogonids, and the cheliceres of chelicerates. Recall that in onychophorans the protocerebrum innervates both the eyes and the antennae, and the deutocerebrum innervates the jaws.[6]

The segmental ganglia of the ventral nerve cord show various degrees of linear fusion with one another in different groups of arthropods. Hence, just as tagmosis is reflected in the joining of body segments externally, it is also apparent in the union of groups of ganglia along the ventral nerve cord. This pattern has been found in the oldest arthropod fossils. Modifications of the central nervous system are examined more closely in the following chapters on the arthropod subphyla.

Although the presence of an exoskeleton has had little evolutionary effect on the structure of the cerebral ganglia and nerve cord, it has had a major effect on the nature of sensory receptors. Unmodified, the exoskeleton would impose an effective barrier

[6] The concentration of nervous tissue in the arthropod head has been called a brain, cerebrum, cerebral ganglion, and cerebral ganglionic mass. Some of these terms may seem vertebrate derived, or might suggest the presence of a single head ganglion. In fact, the cerebral ganglia comprise a cluster of associated ganglia (concentrations of nervous tissue composed primarily of neuronal cell bodies)—hence the term *cerebral ganglia* is probably the most accurate.

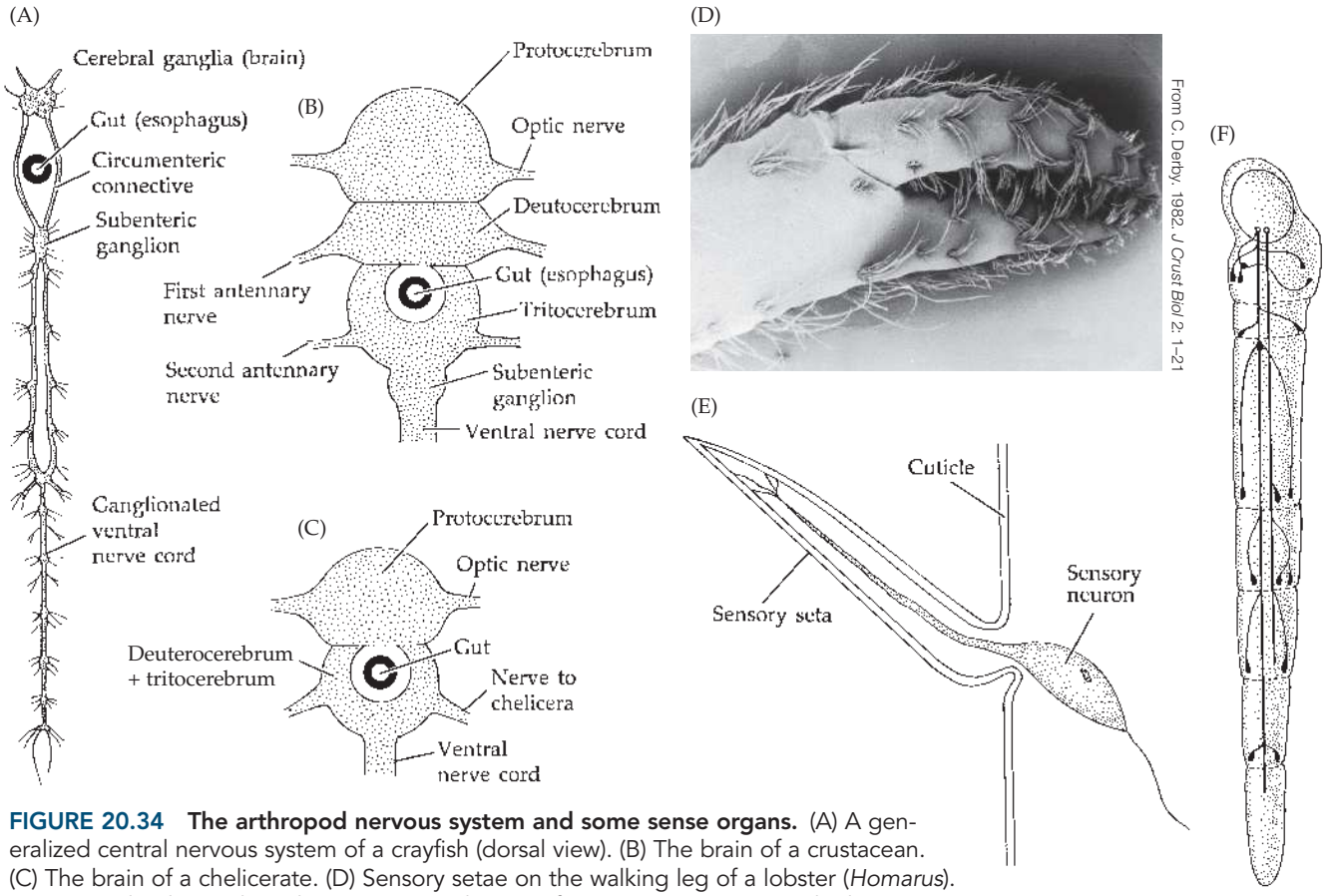

FIGURE 20.34 The arthropod nervous system and some sense organs. (A) A generalized central nervous system of a crayfish (dorsal view). (B) The brain of a crustacean. (C) The brain of a chelicerate. (D) Sensory setae on the walking leg of a lobster (*Homarus*). (E) A typical arthropod tactile seta. (F) Distribution of proprioceptors in a spider leg.

between the environment and the epidermal sensory nerve endings. Hence, most of the external mechanoreceptors and chemoreceptors are actually cuticular processes (setae, hairs, bristles), pores, or slits, collectively called sensilla.

Most arthropod tactile receptors (mechanoreceptors) are cuticular projections in the form of movable bristles or setae, the inner ends of which are associated with sensory neurons (Figure 20.34D,E). When the cuticular projections are touched, that movement is translated into a deformation of the nerve ending, thereby initiating a nerve impulse. Sensitivity to environmental vibrations is similar to tactile reception. Sensilla in the form of fine "hairs" or setae are mechanically moved by external vibrations and impart that movement to underlying sensory neurons. Some terrestrial arthropods bear thin, membranous cuticular windows overlying chambers lined with sensory nerves. When struck by airborne vibrations (e.g., sound), these windows vibrate in turn and impart the stimulus to the chamber and thence to the nerves below.

We have seen in soft-bodied invertebrates that chemoreception is usually associated with ciliated epithelial structures (e.g., nuchal organs, ciliated pits), across which dissolved chemicals diffuse to nerve endings. In arthropods, in the presence of a relatively impermeable cuticle and in the absence of free cilia, such arrangements are obviously not possible. Thus, many arthropods possess special thin or hollow setae, often associated with the head appendages, with permeable cuticular coverings or minute pores that bring the environment into contact with chemoreceptor neurons.

Proprioception is of particular importance to animals with jointed appendages, such as arthropods and vertebrates. The way in which these stretch receptors span the joints enables them to convey information to the central nervous system about the relative positions of appendage articles or body segments (Figure 20.34F). Through this system, an arthropod (or vertebrate) knows where its appendages are, even without seeing them. Arthropod versions of these "strain gauges" are called **campaniform sensilla** in hexapods, **slit sensilla** in arachnids, and **force-sensitive organs** in most crustaceans. Despite subtle differences in their anatomy, all are linked to the central nervous system in similar ways, and all record exoskeletal strain by means of neuronal stretching or deformation.

Arthropods possess three basic kinds of photoreceptors, including simple ocelli, complex lensed ocelli, and faceted or compound eyes. Ocelli were described in Chapter 3; although they vary in anatomical detail, their basic structure and operation is consistent in all invertebrates. Compound eyes, though found in all arthropod subphyla, have been lost or modified in various groups throughout the phylum. Because of their unique structure and function, compound eyes are described here in some detail. Importantly, the origin of compound eyes dates back at least to the lower

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Cambrian, and a number of fossils from the early arthropod stem lineage had compound eyes.

As their name indicates, **compound eyes** comprise from a few to many distinct photoreceptive units, called **ommatidia**. Each ommatidium is supplied with its own nerve tracts leading to the major optic nerve, and each has its own field of vision through square or hexagonal cuticular facets on the eye surface. The visual fields of neighboring ommatidia overlap to some extent, such that a shift in the position of an object within the visual field generates impulses from several ommatidia; hence compound eyes are especially suitable for detecting movement. However, visual acuity is affected by the degree of overlap among the fields of vision of neighboring ommatidia—the greater the overlap, the poorer the visual acuity. In general, compound eyes with many small facets probably produce higher-resolution images than eyes with fewer, larger facets. Note that the function of an ommatidium is to concentrate light from a reasonably narrow direction into a receptor area, and an individual ommatidium cannot "focus" in the sense of image formation. Image formation is the result of multiple signals from multiple ommatidia.

Among living arthropods, two major types of compound eyes are known. In some mandibulates (crustaceans, hexapods, some myriapods) the ommatidia have a dioptric apparatus comprising a cuticular lens and a cellular crystalline cone usually made up of four cone cells. In the chelicerate horseshoe crabs, the cuticular lens has a conelike extension that serves to collect light and guide it to the **retinula** (= retinular element) cells.

The following discussion describes the structure and function of compound eyes, using the crustacean-hexapod (pancrustacean) model (Figure 20.35). Each ommatidium is covered by a modified portion of the cuticle called the **cornea** (= corneal lens); the special epidermal cells that produce the corneal elements are called **corneagen cells**. The corneagen cells may later withdraw to the sides of the ommatidium to form (usually two) **primary pigment cells** (= iris cells). When viewed externally, the facets on the surface of each cornea produce the characteristic mosaic pattern so frequently photographed by microscopists. The core of each ommatidium comprises a group of **crystalline cone cells** and the crystalline cone that they produce, sometimes a crystalline cone stalk, and a basal retinula. There are typically four (rarely three or five) crystalline cone cells; an ommatidium with a four-part crystalline cone is highly diagnostic of crustacean-hexapod eyes and is

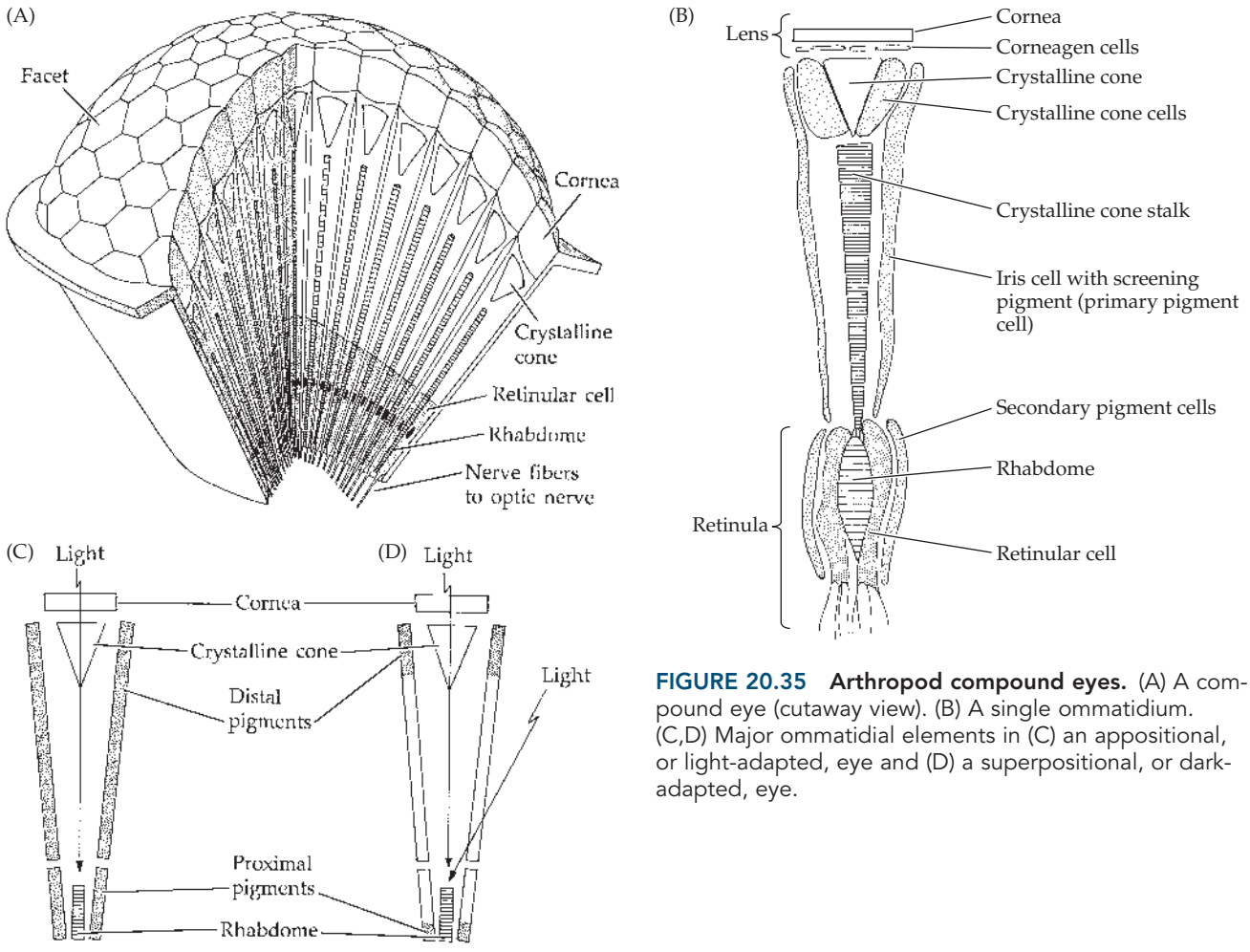

FIGURE 20.35 Arthropod compound eyes. (A) A compound eye (cutaway view). (B) A single ommatidium. (C,D) Major ommatidial elements in (C) an appositional, or light-adapted, eye and (D) a superpositional, or dark-adapted, eye.

termed a **tetrapartite ommatidium**.[7] The crystalline cone is a hard, clear structure bordered laterally by the primary pigment cells. The retinula is a complex structure formed from several retinular cells, which are the actual photosensitive units that give rise to the sensory nerve tracts. These retinular cells, usually numbering 8 but ranging from 5 to 13 in various derived conditions, are arranged in a cylinder along the long axis of the ommatidium. The retinular cells are surrounded by secondary pigment cells, which isolate each ommatidium from its neighbors. The core of the cylinder is the **rhabdome**, which is made up of rhodopsin-containing microtubular folds (microvilli) of the cell membranes of the retinular cells. Each retinular cell's contribution to the rhabdome is called a **rhabdomere**. The microvilli of the rhabdomeres extend toward the central axis of the ommatidium at right angles to the long axis of the retinular cell.

The initiation of an impulse depends upon light striking the rhabdome portion of the retinular element. Light that enters through the facet of a particular ommatidium is directed to its rhabdome by the lens-like qualities of the cornea and the crystalline cone. The lens has a fixed focal length, so accommodation to objects at different distances is not possible. Light is shared among all the rhabdomeres of a given rhabdome, although not necessarily equally.[8]

In contrast to those of insects and crustaceans, the lateral eyes of most myriapods are probably not true compound eyes, but clusters of simple ocelli. However, there is evidence that the eyes of scutigeromorph centipedes (and of some fossil myriapods) may be true compound eyes. The only chelicerates with typical compound eyes, the xiphosurans, have ommatidia that differ in most details from the insect-crustacean design. There is some evidence that the lateral eye groups of terrestrial chelicerates may be derived from reduced and fused compound eye ommatidia. The pigment cells are arranged in a cuplike manner, and the bottom of the "cup" is occupied by a sheet of cells secreting a protuberance of the cuticle, which is a functional but not a morphological equivalent of a crystalline cone. In fact, crystalline cones are generally regarded as an apomorphy unique to the Mandibulata (they do not occur in chelicerates). A special "eccentric cell"—a large specialized photoreceptor—found in chelicerate ommatidia has no equivalent in the insect or crustacean retina.

Compound eyes evolved early in arthropod history and were present in trilobites and many stem-group arthropods, including anomalocaridids. Compound eyes remarkably similar to modern ones have been described from 521-million-year-old trilobite fossils, although those had calcite lenses beneath the cuticle. The versatility of compound eyes is to a large degree a result of the distal and proximal screening pigments located in cells that wholly or partially surround the core of the ommatidium (Figure 20.35B–D). Distal screening pigments are located in the primary pigment cells (iris cells), and proximal pigments are often located in the retinular cells and secondary pigment cells. In many cases, these screening pigments are capable of migrating in response to varying light conditions and thus changing their positions somewhat along the length of the ommatidium. In bright light, the screening pigments may disperse so that nearly all of the light that strikes a particular rhabdomere must have entered through the facet of its ommatidium. In other words, the screening pigment prevents light that strikes the facets at an angle from passing through one ommatidium and into another. Many crustacean eyes are fixed in this condition. Such **appositional eyes** (= light-adapted eyes) are thought to maximize resolution, in that the image from the visual field of each ommatidium is maintained as a discrete unit. It is thought that even trilobite compound eyes were of the appositional type, and the overall similarity of trilobite eyes to those of the Mandibulata is evidence that Trilobita may hold a position along the stem lineage of mandibulates. Conversely, under conditions of dim light, screening pigments may concentrate, usually distally, thereby allowing light to pass through more than one ommatidium before striking rhabdomeres. The result is that the image formed by each ommatidium is superimposed on the images formed by neighboring ommatidia. This design has the advantage of producing enhanced irradiances on the retinula, but at the cost of reduced resolution. Many crustacean eyes are fixed in this condition also. Such **superpositional eyes** (= dark-adapted eyes) function as efficient light-gathering structures while sacrificing some visual acuity and image formation capabilities.

Some arthropod groups possess compound eyes that are always either appositional or superpositional; thus they lack the ability to switch back and forth with varying light conditions. For example, most "maxillopodans" and branchiopods apparently all possess appositional eyes. However, within the two principal malacostracan clades, Eucarida and Peracarida, both types of eyes occur (e.g., isopods and amphipods have appositional eyes, but mysidans have superpositional eyes). Furthermore, crustacean larvae that possess compound eyes almost always have the appositional type, which metamorphose into superpositional eyes in those groups that possess them in adulthood.

Among the arthropods, compound eyes elevated on stalks occur mostly in certain crustaceans (and perhaps a few Paleozoic trilobites and anomalocaridids). Stalked eyes also occur in at least one genus of insects, *Scopiastes* (Hemiptera), the stalk-eyed bugs. And a species of *Drosophila* in Hawaii also has stalked eyes. Biologists

[7] The crystalline cone cells are often called Semper cells (especially by entomologists).

[8] The compound eyes of multiple groups of crustaceans, formerly grouped as the maxillopodans, differ considerably from those of other crustaceans; see Chapter 21.

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have long argued over the derivation of such stalked eyes, and the matter is still far from settled—are they the primitive condition in arthropods or in crustaceans, or have they been derived multiple times from unstalked, sessile-eyed ancestors (the latter seems far more likely). The eyestalk is much more than a device to support and move the eye. Eyestalk movements are produced by up to a dozen or more muscles with complex motor innervation. In most malacostracans the eyestalks contain several optic ganglia separated by chiasmata, as well as important endocrine organs, usually including the sinus gland and X-organ. Thus, neither loss of eyestalks nor convergent recreation of these structures would have been a simple evolutionary feat. The loss of functional eyes is a common evolutionary pathway among the Crustacea (and other arthropods), especially in species that inhabit subterranean, deep-sea, or interstitial habitats. But among those clades with stalked eyes, the eyestalk remains even when the eye itself degenerates—testimony to the importance of this complex bit of anatomy.

Reproduction and Development

The great diversity of adult form and habit among arthropods is also reflected in their reproductive and developmental strategies. The extreme evolutionary and ontogenetic plasticity of arthropods has led to a great deal of convergence and parallelism as different groups have developed similar structures under similar selective conditions or pressures.

Nearly all arthropods are gonochoristic, and most engage in some sort of formal mating. Fertilization is usually, although not always, internal and is often followed by brooding or some other form of parental care, at least during early development. Development is frequently mixed, with brooding and encapsulation followed by larval stages, although direct development occurs in many groups.

Arthropod eggs are centrolecithal (Figure 20.36), but the amount of yolk varies greatly and results in different patterns of early cleavage. Cleavage is holoblastic in the relatively weakly yolked eggs of xiphosurans, some scorpions, and various crustaceans (e.g., copepods and barnacles) and is meroblastic in the strongly yolked eggs of most insects and many other crustaceans. A number of arthropods exhibit a unique form of meroblastic cleavage that begins with nuclear divisions within the yolky mass. These intralecithal nuclear divisions are followed by a migration of the daughter nuclei to the periphery of the cell and subsequent partitioning of the nuclei by cell membranes. These processes typically result in a periblastula that consists of a single layer of cells around an inner yolky mass. Holoblastic cleavage is usually more or less radial in appearance.

One of the most striking features of arthropods is their segmentation and the complex way in which it is embryologically derived. This developmental process is very similar to that seen in annelids (and in onychophorans), and until the advent of molecular phylogenetic techniques, it was taken as evidence of a close annelid-arthropod shared ancestry. The process is called **teloblastic segmental growth** (or simply teloblasty) (Greek *telos*, "end"; *blasto*, "bud"). It is characterized by a progressive, anterior-to-posterior addition of segments from a distinct posterior growth zone situated near the anus (i.e., in front of the terminal, or anal, segment—often called the **telson** or **pygidium**). So programmed is the development of the segments that the growth zone is often composed of a fixed number of uniquely identifiable stem cells (**teloblasts**) whose progeny undergo a predictable and stereotyped sequence of segmentally iterated cell divisions. Teloblasty is further characterized by the formation of secondary body cavities (coelomic cavities) at the growth zone as segments are elaborated. In arthropods, the adult body cavity is derived from the fusion of the blood vascular system with these transitory

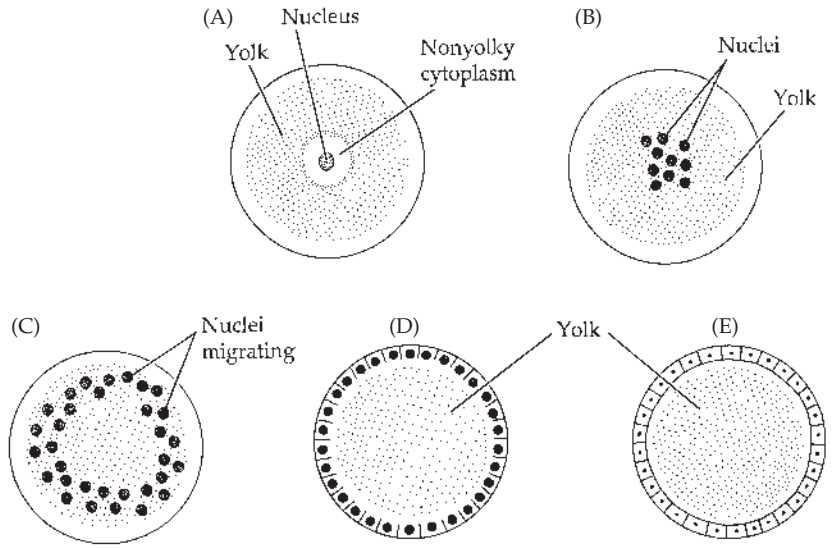

FIGURE 20.36 Superficial cleavage of a centrolecithal egg and the formation of a periblastula in arthropods. (A) Centrolecithal egg. (B) Intralecithal nuclear divisions following fertilization. (C) Migration of nuclei to the periphery of the cell. (D,E) The periblastula is produced by a partitioning of nuclei as cell membranes form.

embryonic coelomic cavities. Although the coelomic cavities are secondarily lost during arthropod embryogenesis, they form by way of schizocoely, originating from a pair of caudally situated mesodermal cell bands. These bands have long been thought to originate from a 4d (mesentoblast) cell, as in annelids, but in fact there is little evidence for this. Adding further nuance to all this is the fact that in some arthropods the appearance of new segments is not completed by the end of embryogenesis, but continues after hatching, in some cases up to the last postembryonic molt. This protracted addition of body segments is called **anamorphosis (**the opposite, hatching with the complete number of segments, is called epimorphosis). In addition, the widespread, α-proteobacterium symbiont *Wolbachia* infects species in all living subphyla of arthropods, and estimates suggest about two-thirds of all arthropod species can be infected with *Wolbachia*. The bacterium is normally transmitted vertically, from mother to offspring, and it manipulates the host's reproduction through a broad variety of mechanisms.

Not only do the segments form in a similar fashion in annelids and arthropods, but the two groups also appear to use a similar genetic mechanism (especially the products of the *engrailed* gene) to define segmental boundaries and polarity. The *engrailed* (*en*) gene belongs to a class of genes known as segment polarity genes. It plays a key role in determining and maintaining the posterior cell fates of segmental structures in all arthropods (and in annelids and onychophorans). Because this gene occurs in iterated transverse stripes in the posterior portion of each developing segment in the germ band of all annelids and arthropods, it can be used to clarify ambiguities in segment position and number. Embryonic *Hedgehog* signaling pathways also play similar roles in annelids and arthropods, in both cases playing a crucial role in the axial patterning of developing segments.

In arthropods, the transitory embryonic coelomic cavities are lined with simple epithelium, but this gradually disappears as the embryo develops, and the large adult body cavity comes to be lined by an extracellular matrix. Hence, the body cavity of adult arthropods is derived by the fusion of a primary body cavity (the blood vascular system) and a secondary body cavity (the coelom) and is therefore termed a hemocoel (or mixocoel). Segmentally arranged pairs of transitory coelomic cavities, and their embryonic fusion, have been reported in the early developmental stages of virtually every onychophoran and arthropod that has been studied.

The Evolution of Arthropods

The Origin of Arthropods

In 1997, a groundbreaking analysis of animal phylogeny based on 18S rRNA sequence data led Maria Aguinaldo and her colleagues to propose a new hypothesis of arthropod relationships—that they belong to a clade of animals that we now know also includes nematodes, nematomorphans, kinorhynchs, priapulans, and loriciferans (as well as tardigrades and onychophorans), but *not* annelids. The newly recognized clade was called **Ecdysozoa**. The idea of this clade of molting animals was perhaps first suggested by R. S. K. Barnes and his colleagues in their 1988 text on invertebrates. Today, scores of molecular phylogenetic studies support this view of animal relationships, and it is broadly accepted that the protostomes comprise two main clades: Ecdysozoa and Spiralia. One of the most revolutionary outcomes is compelling evidence that Annelida and Panarthropoda are not sister groups (a long-held hypothesis based on morphological and developmental studies). This modern view of animal relationships stimulated new morphological and developmental investigations, and significant differences between the annelids and arthropods have emerged, the most obvious being fundamental differences in the adult body cavity and cleavage patterns during embryogenesis. However, the relationships among the three main clades within Ecdysozoa are still uncertain, and we depict the clade Panarthropoda as an unresolved trichotomy with the other two ecdysozoan clades—Nematoida and Scalidophora—on our phylogenetic tree of Metazoa (Chapter 28).

Evolution within the Arthropoda

Molecular clock estimates place the origin of Arthropoda at around 600 million years ago, give or take. They were among the earliest animals to leave a good fossil record, and even the Ediacaran fauna of the Neoproterozoic Era included animals regarded by many as stem arthropods, some of which had stalked eyes as in modern Crustacea. Today, with nearly 1.2 million described species, arthropods are arguably the most successful animal phylum on Earth. They encompass an unparalleled range of structural disparity and taxonomic diversity, have a rich fossil record, and have become favored study animals of evolutionary developmental biology. Some arthropod "model systems" (e.g., *Drosophila melanogaster*) have been studied intensively for many decades and are among the best-known animals genetically and developmentally. For all these reasons, we know a lot about arthropods.

Speculating on arthropod evolution has been a favorite pastime of zoologists for centuries. Every imaginable pattern of relationship has been proposed among the crustaceans, hexapods, chelicerates, and myriapods at one time or another. However, since the 1980s a virtual explosion of new information on this phylum has appeared, much of it concerning phylogeny, paleontology, gene expression, and developmental biology. If we examine the evolution of arthropods in light of these discoveries, especially recent genomic analyses, the phylogeny of the Arthropoda shown in Figure 20.39 is apparent. Extant arthropods comprise two clades, Chelicerata and Mandibulata, the latter including the myriapods and pancrustaceans. Mandibulates are named for their

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homologous biting appendages, whereas in chelicerates the homologous pair of appendages are walking legs. The split between these two large arthropod clades probably dates to the Ediacaran. The Mandibulata, in turn, comprise the sister groups Myriapoda and Pancrustacea, the latter composed of the Crustacea and Hexapoda. The Hexapoda arose from within crustaceans, making Crustacea a paraphyletic group (hence the more inclusive, monophyletic group name "Pancrustacea"). The sister group of Hexapoda appears to be the remipede crustaceans. The Remipedia, with homonomous segmentation in the trunk, were once thought to have arisen near the base of the crustacean tree, but recent phylogenetic work suggests they arose higher in the pancrustacean tree. The hexapod-remipede clade is named Labiocarida (both groups having a functional labium), and branchiopods are a likely sister group to labiocarids.

Some of the most important ancient arthropod fossils are those in which even the soft parts of the animal were preserved—the so-called ancient *Lagerstätten*, such as the faunas of the late Cambrian Orsten deposits of Sweden, the middle Cambrian Burgess Shale of Canada (and elsewhere), and the early Cambrian Chengjiang deposits of China. Recent discoveries from these well-preserved deposits have shown that the fossil record of Crustacea and Pycnogonida date to at least the early Cambrian and possibly to the late Precambrian. In 2015, Ma and colleagues described the brains of an early Cambrian (517 Ma) shrimplike crustacean, *Fuxianhuia protensa*, that were basically identical to those of modern crustaceans. And in 2017, the oldest known arthropod with supposed mandibles was described and named (*Tokummia katalepsis*) from 508-million-year-old fossils in British Columbia (Canada). If this arthropod was truly a mandibulate (a fact that has been debated in the recent literature), these extraordinary faunas are now informing us that crustaceans possibly predate the appearance of trilobites in the fossil record.

The Chengjiang fauna includes around 100 species of animals, many without hard skeletons, including the first known members of many modern groups. However, it is the arthropods that dominate this fauna, including trilobites and bradoriid crustaceans (and also lobopodians with possible affinities to tardigrades and onychophorans). The largest of the Chengjiang animals are the anomalocaridids, stem arthropods that were common during the mid-Cambrian and are also known from a single described species (*Schinderhannes bartelsi*) from the Early Devonian Hunsrück Slate of Germany. Some anomalocaridids reached 2 m in length; most were predators, but some were probably suspension feeders. The Chengjiang fauna is very similar to that of the slightly older Burgess Shale, and it demonstrates that the arthropods were already far advanced by this early date. In fact, arthropods may have been the dominant animals in terms of species diversity since the Cambrian, and they constitute over one-third of all species described from lower Cambrian strata.

The spectacular research by Klaus Müller and Dieter Waloszek since the 1980s on microscopic arthropods from the Cambrian Orsten deposits of Sweden (Cambrian Epoch 3) has brought to light a rich fauna of crustaceans, many of which are onychophoran-like lobopodians, possibly stem tardigrades and pentastomids, or closely resemble modern cephalocarids, mystacocarids, and branchiopods. Orsten-type preservation is a secondary phosphatization of the upper cuticle, apparently occurring soon after death of the animal, as no further destruction takes place. Such preservation can produce exquisite three-dimensional fossils with all the details of eyes, limbs, setae, cuticular pores, and other structures less than a micrometer in size. It generally occurs with a postmortem embedding of the animals in limestone (that later formed into nodules). Since the fossils themselves are phosphatized, they can be etched from their surrounding limestone rock with weak acids. Orsten-type fossils are now known from several continents from the early Cambrian (around 520 Ma) to the mid-Cretaceous (100 Ma). The recovery of these three-dimensionally preserved animals and the developmental series that have been found (with successive larval, juvenile, and adult stages) have provided us with information on the detailed anatomy of the body segments and appendages of many ancient stem arthropods and crustaceans. The Orsten fauna shows that Cambrian Crustacea had all the attributes of modern crustaceans, such as compound eyes, a head shield, naupliar larvae (with locomotory first antennae), and biramous appendages on the second and third head somites (i.e., the second antennae and mandibles).

A modern view of arthropod phylogeny thus places a panorama of crustacean-like early Cambrian lineages at its base—a diverse array of early arthropods that had typical crustacean, or crustaceamorphan, bodies, eyes, development, and naupliar larvae, though perhaps with a smaller number of fused head somites than seen in modern Crustacea. Early in the Cambrian, the trilobites may have emerged from this crustaceamorph stem line, radiating rapidly to become the most abundant arthropods of Paleozoic seas, but then abruptly disappearing in the Permian-Triassic extinction. Next to appear were probably the chelicerates, in the form of giant marine water scorpions nearly 3 m long (eurypterids) and their kin, which had appeared at least by the Ordovician; by the Silurian, eurypterids had probably become keystone predators in the marine realm. Also by the Silurian, the chelicerates had invaded land and begun to leave a fossil record of terrestrial arachnids. By the Late Ordovician or early Silurian the first myriapods had evolved, perhaps marine creatures, and about 15 million years later terrestrial millipedes appear in the fossil record. The last major arthropod group to appear was the hexapods, making their appearance in the Devonian, or perhaps the Silurian, and radiating rapidly to dominate the terrestrial world, ultimately qualifying the Cenozoic to be called "the age of insects."

The relationship of trilobites to living arthropods is still being debated (Figures 20.37 and 20.38). The two main opposing views see them as close to either the Chelicerata or the Mandibulata. Our view, in contrast, positions them as one of many extinct lineages stemming from a crustaceamorph stem-line ancestry (Figure 20.39).

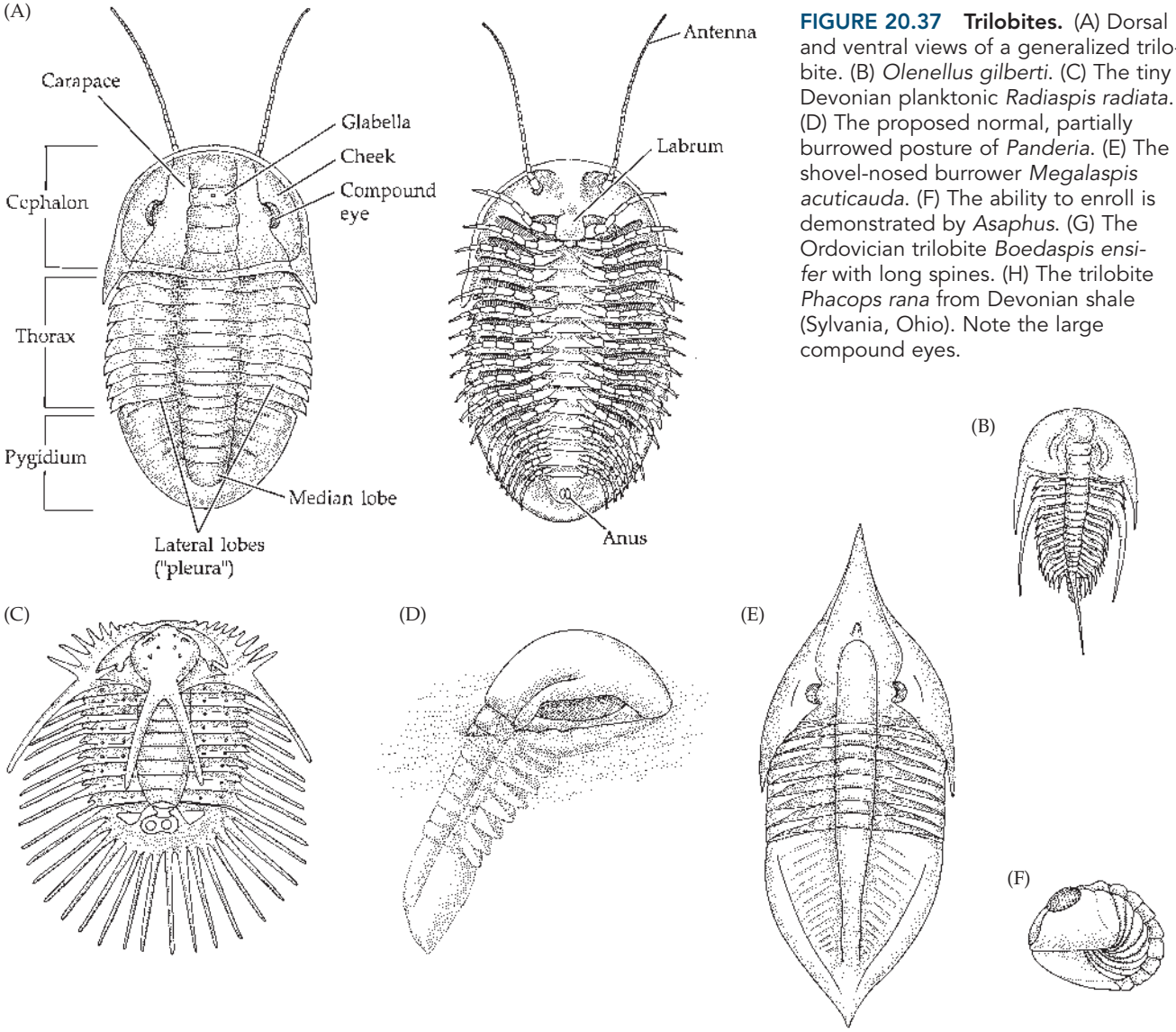

FIGURE 20.37 Trilobites. (A) Dorsal and ventral views of a generalized trilobite. (B) *Olenellus gilberti*. (C) The tiny Devonian planktonic *Radiaspis radiata*. (D) The proposed normal, partially burrowed posture of *Panderia*. (E) The shovel-nosed burrower *Megalaspis acuticauda*. (F) The ability to enroll is demonstrated by *Asaphus*. (G) The Ordovician trilobite *Boedaspis ensifer* with long spines. (H) The trilobite *Phacops rana* from Devonian shale (Sylvania, Ohio). Note the large compound eyes.

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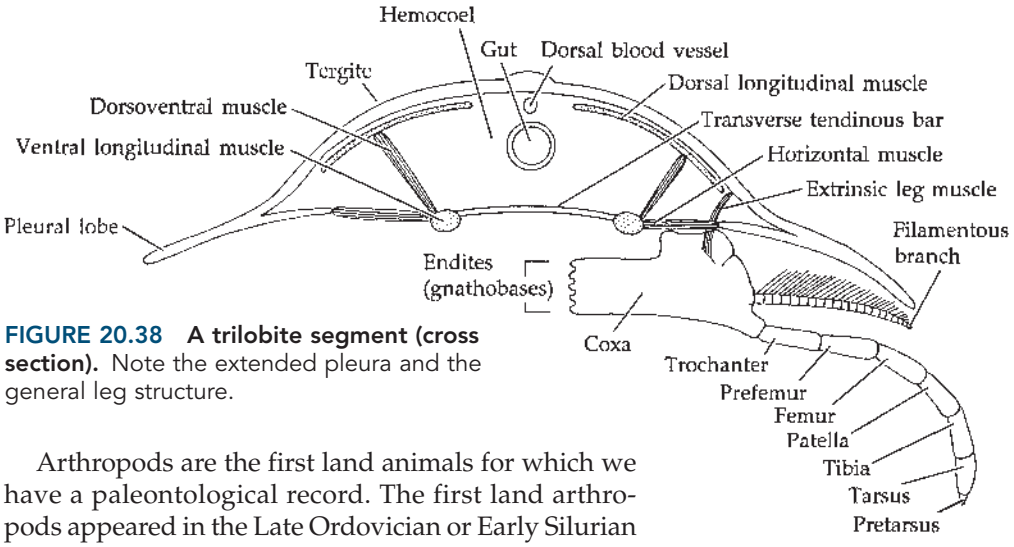

FIGURE 20.38 A trilobite segment (cross section). Note the extended pleura and the general leg structure.

Arthropods are the first land animals for which we have a paleontological record. The first land arthropods appeared in the Late Ordovician or Early Silurian (arachnids, millipedes, centipedes), and these fossils represent the first terrestrial invertebrates for which we have direct evidence. Indeed, animal life on land might not have been possible before the Late Ordovician, when terrestrial plants first made their appearance. The first insects in the fossil record are 390-million-year-old Devonian springtails (Collembola) and bristletails (Archaeognatha). By the mid-Paleozoic all four living arthropod subphyla were in existence and had already undergone substantial radiation. By the Middle Devonian, centipedes, millipedes, mites, amblypygids, opilionids, scorpions, pseudoscorpions, and hexapods were all well established. Hence, terrestrial arthropods seem to have undergone major radiations in the Silurian. The presence of a wide variety of predatory terrestrial arthropods during the early Paleozoic suggests that complex terrestrial ecosystems were in place at least as early as the late Silurian. However, interestingly, molecular dating studies suggest the origin of terrestrial arthropods much earlier, as early as 510 million years ago, in the mid-Cambrian.

Work by the great comparative biologist Robert Snodgrass in the 1930s established a benchmark in arthropod biodiversity research. The Snodgrass classification embraced three important hypotheses: (1) arthropods constitute a monophyletic taxon; (2) myriapods and hexapods are sister groups, together forming a taxon called Atelocerata (= Tracheata, or Uniramia of some authors); and (3) Crustacea and Atelocerata are sister groups, together forming a taxon called the Mandibulata. Snodgrass united the Atelocerata on the basis of several attributes: a tracheal respiratory system, uniramous legs, Malpighian tubules for excretion, and loss of the second antennae (as the name Atelocerata implies). The Mandibulata were united on the basis of the mandibles (which are almost certainly homologous in these taxa) and a similar head and head appendage structure.

It was not until the late 1980s that Snodgrass's long-standing view of arthropod relationships began to be questioned. While the Mandibulata is still supported as a monophyletic group, it now appears almost certain that Hexapoda arose from somewhere within Crustacea, a clade called Pancrustacea, and this then is the sister group to the Myriapoda. It turns out that Snodgrass, and others, were misled by the similarities between myriapods and hexapods, which are now assumed to be convergences (or parallelisms) resulting from adaptations to terrestrial habitats. Recent phylogenomic analyses suggest the sister group of Hexapoda is Remipedia, although remipedes are all restricted to the marine environment today and there is as yet no paleontological evidence that they invaded land in the past. While we treat "Crustacea" as a subphylum in this book, remember

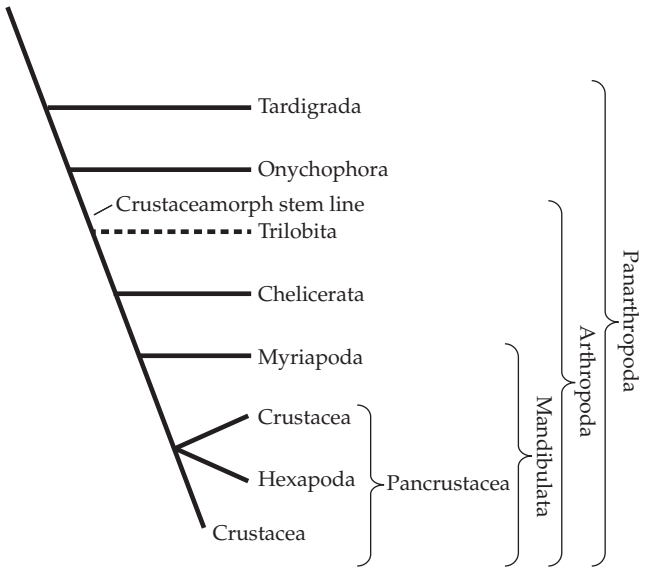

FIGURE 20.39 A phylogeny of the Panarthropoda. Based on a synthesis of paleontological and phylogenetic studies, the arthropods are seen to be rooted in a crustacean-like ancestral line, from which the living subphyla emerged. The subphylum Crustacea is paraphyletic (unless the Hexapoda are included). The position of the Trilobita is uncertain. See text for details.

that the discovery that insects are "flying crustaceans" makes the subphylum Crustacea a paraphyletic group (as long as the Hexapoda are excluded).[9]

Research in the field of developmental biology and gene expression has shown that the Arthropoda are rich with homoplastic characters, and it is now clear that much of the difficulty in reconciling earlier phylogenies based on morphological characters was due to the high levels of parallel evolution seen within the Arthropoda. For example, many characters shared between hexapods and myriapods, which in the past had been assumed to be synapomorphies, are now interpreted as parallelisms (or convergences), including such things as the tracheal gas exchange system, uniramous legs, Malpighian tubules, organs of Tömösvary, loss of the second antennae, and loss of mandibular palps.

The rigid, compartmentalized bodies of arthropods have allowed for body region specialization unavailable to most other metazoan phyla. The fates of segmental units and their appendages are under the ultimate orchestration of Hox and other developmental genes. These genes select the critical developmental pathways followed by groups of cells during morphogenesis. Hox genes determine such basic body architecture as the dorsoventral and anterior–posterior body axes and where body appendages form. Hox genes can either suppress limb development or modify it to create different appendage morphologies. These unique genes have played major roles in the evolution of new body plans among arthropods (and the Metazoa in general). The degree to which such developmental genes have been conserved is remarkable, and most of them probably date back at least to the Cambrian. For example, homologues of the developmental gene *Pax-6* seem to dictate where eyes will develop in all animal phyla. *Pax-6* is so similar in protostomes (e.g., insects) and deuterostomes (e.g., mammals) that their genes can be experimentally interchanged and still function more or less correctly.

It has been known since the late nineteenth century that the compound eyes of hexapods and crustaceans possess many complex homologous features and that they differ markedly from the eyes of myriapods and chelicerates. Recall that in hexapods and crustaceans, each ommatidium consists of a cuticular corneal lens that is, at least partly, secreted by two cells—termed primary pigment cells in Hexapoda and corneagen cells in Crustacea. The crystalline cone, produced by four Semper cells, is fundamentally tetrapartite. A retinula is present, typically composed of eight retinular cells. This common anatomical plan is unique to the Hexapoda + Crustacea and constitutes strong evidence of a close relationship between the two groups. Dohle (2001) even proposed a name on this basis for the clade, the "Tetraconata," although the name "Pancrustacea" has had more popularity.[10]

Recent research on the anatomy and development of the arthropod central nervous system has identified many other neurological features that appear to be unique to the Hexapoda + Crustacea. In fact, Strausfeld (1998) developed a phylogeny of the Arthropoda based solely on the abundant anatomical features of the cerebral ganglia. In particular, numerous anatomical similarities exist in the elements of the optic lobes and "midbrain." Developmental similarities suggest a fundamental distinction between embryonic development in the hexapod + crustacean central nervous system and in that of myriapods and chelicerates. In hexapods and crustaceans, development of the CNS begins with the delamination of enlarged cells, called neuroblasts, from the ectoderm (neuroectoderm) of each segment. The neuroblasts aggregate to form the segmental ganglia. The formation of neuroblasts is highly stereotyped and predictable in both Crustacea and Hexapoda. These large neuroblasts are of a special type, regarded as stem cells, and they divide unequally to generate a specific number of neurons. So far, 29–31 neuroblasts have been identified in each segment of hexapods and 25–30 in crustacean segments, many of which appear to be homologous between the two subphyla. Nothing resembling these stem cell neuroblasts has been seen in myriapods. In both hexapods and crustaceans, longitudinal connectives of the CNS originate in the segmental neurons, whereas in myriapods they derive from neurons in the cerebral ganglia that send their axons posteriorly to set up long parallel connectives. Thus, myriapod segmental ganglia receive contributions from more widely distributed neurons.

Their great size range, especially at the smaller end of the scale, allows arthropods to adapt to a great variety of ecological niches. The Cambrian Orsten deposits inform us that a whole fauna of interstitial/meiofaunal arthropods already existed as early as the mid-Cambrian, and this habitat has continued to be rich in adaptive radiation

[9] Although the idea of a Crustacea-Hexapoda sister-group relationship may seem new to many, the idea was actually proposed at the turn of the twentieth century, when William T. Calman presented detailed arguments from comparative anatomy that argued for an alliance between the Crustacea and the Hexapoda.

[10] Although tetrapartite ommatidia appear to be restricted to the Hexapoda and Crustacea, they may not be a synapomorphy for this clade. We don't yet know when the tetrapartite condition first appeared within the Crustacea or the Arthropoda, but it probably was well before the insects emerged (perhaps in the early Cambrian crustacean stem line). Crustacean fossils from Cambrian Lagerstätten deposits have eyes that strongly resemble modern crustacean eyes, at least superficially. In any case, tetrapartite ommatidia are probably a symplesiomorphy retained in both Hexapoda and crown Crustacea (their transformation in myriapods perhaps being a synapomorphy defining that clade). The compound eyes of xiphosurans are very different from those of other Arthropoda, suggesting they might have evolved apart from the tetrapartite condition seen in Crustacea and Hexapoda (or that they are somehow derived from the crustacean tetrapartite condition).

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and specialized species ever since. Similar small-body-size niches are filled by arthropods in a great many environments today. We find high diversities of minute arthropods in habitats such as marine sediments, coral reefs, among the fronds of algae, on mosses and other primitive plants, and on the bodies of every kind of animal imaginable. Small insects and mites have exploited virtually every terrestrial microhabitat available. And some of the arthropods (the insects) were presumably the first flying animals, and the ability to fly also led them into niches that other invertebrates simply could not penetrate.

Chapter Summary

Now you are familiar with the wide world of Panarthropoda—the phyla Arthropoda, Tardigrada, and Onychophora. The clade Panarthropoda is characterized by metamerism, reduced coeloms and a hemocoel, ecdysis (molting), muscles isolated in bands (although only weakly so in the tardigrades and onychophorans), and paired ventrolateral segmental appendages with terminal "claws." All Panarthropoda have a ganglionic supraesophageal brain, but the numbers of pairs of ganglia differ among the three phyla: tardigrades have one pair, onychophorans have two pairs (protocerebrum and deutocerebrum), and arthropods have three pairs (protocerebrum, deutocerebrum, tritocerebrum).

Only the phylum Arthropoda has complete "arthropodization," with the body fully segmented (externally and internally) and with segmental sclerites, and the appendages segmented and divided into articles/podomeres separated by arthrodial membranes and with intrinsic musculature. Complete arthropodization also includes tagmosis, in which body segments are regionalized as head + trunk, or head + thorax + abdomen; head (and sometimes thorax) may be covered by a shield or carapace; strong cephalization, with compound eyes; and extreme specialization of appendages.

With an estimated 1,196,816 named living species (995,816 of which are hexapods), the phylum Arthropoda is far and away the largest animal phylum (Mollusca comes in a distant second, with about 73,000 species). Arthropods include four living subphyla: Myriapoda, Chelicerata, Crustacea, and Hexapoda. However, because hexapods (insects and their close relatives) arose from among the crustaceans, Crustacea is a paraphyletic group; the two subclasses together comprise the clade Pancrustacea. Arthropods occur in virtually every environment on Earth, exploiting every imaginable lifestyle. Modern forms range in size from microscopic mites and crustaceans less than 1 mm long, to Japanese spider crabs (*Macrocheira kaempferi*) with leg spans that reach nearly 4 m. Arthropoda is an old group, with Ediacaran fossils likely representing stem arthropods.

Tardigrades are found in aquatic and semiaquatic habitats such as the water film on plants, or in soil and forest litter. Others live in freshwater or marine benthic habitats, often interstitially or among shore algae. Some species live in hot springs. Some marine species are commensals or ectoparasites on other invertebrates. Tardigrades can occur in high densities, up to 300,000 per square meter in soil and more than 2 million per square meter in moss. All are small, usually on the order of 0.1–0.5 mm in length, although some l.3 mm giants have been reported. They are famous for their powers of anabiosis (dormancy) and cryptobiosis (extreme dormancy, in which all external signs of metabolism are absent), as well as the production of a cryptobiotic tun stage. Embryos of one species, *Milnesium tardigradum*, were kept for three months in an outer space hatch and had 100% survival rate after rehydration. Tardigrades have short bodies and four pairs of telescoping lobopodal legs. Free-living species feed on plant or animal cell fluids, bacteria, or algae or decaying plant matter or as predators on small invertebrates. They lack discrete blood vessels, gas exchange structures, or nephridia.

Onychophorans are all terrestrial and are the only animal phylum without aquatic species. They are an old group that has changed very little over the past 310 million years. They have 13–43 pairs of legs and range in length from 5 to 150 mm. Although resembling arthropods in many ways, onychophorans have unjointed, fleshy head appendages and rather unique jaws and lobopodal legs. They are primarily carnivores on small invertebrates, and they have special slime glands that open at the ends of the two oral papillae to discharge powerful jets of fast-drying glue that entangles prey or possible predators. The circulatory system is well developed, and a pair of nephridia lies in each leg-bearing body segment (except the genital segment).

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Photo by Simon Richards, courtesy of J. Yager

CHAPTER 21

Phylum Arthropoda

Subphylum Crustacea: Crabs, Shrimps, and Their Kin

Crustaceans are one of the most popular invertebrate groups, even among nonbiologists, for they include some of the world's most delectable gourmet fare, such as lobsters, crabs, shrimps,[1] and goose barnacles. There are about 72,000 described living species of Crustacea, and probably five times that number waiting to be discovered and named. They exhibit an incredible diversity of form, habit, and size (Figure 21.1). The smallest known crustaceans are less than 100 μm in length and live on the antennules of copepods. The largest are Japanese spider crabs (*Macrocheira kaempferi*) with leg spans of 4 m, and giant Tasmanian crabs (*Pseudocarcinus gigas*) with carapace widths of nearly a half-meter. The heaviest crustaceans are probably American lobsters (*Homarus americanus*) that, before the present era of overfishing, attained weights in excess of 20 kg. The world's largest land arthropod by weight (and possibly the largest land invertebrate) is the coconut crab (*Birgus latro*), weighing in at up to 4 kg, and the largest freshwater invertebrate is the Tasmanian giant freshwater crayfish (*Astacopsis gouldi*) or *lutaralipina* in Tasmanian Aboriginal language. Crustaceans are found at all depths in every marine, brackish, and freshwater environment, including in pools at 6,000 m elevation (fairy shrimp and cladocerans in northern Chile). A few have become successful on land, the most notable being sowbugs and pillbugs (the terrestrial isopods) and species in several groups of Brachyura (crabs). Beginning

[1] When most people hear the word "shrimp," they think of edible shrimps, two crustacean groups nested within the order Decapoda (in the suborders Dendrobranchiata and Pleocyemata). However, the term "shrimp" is applied to a number of long-tailed crustaceans, many not closely related at all to decapods. So, in this general sense, there are fairy shrimps, tadpole shrimps, mantis shrimps, etc. In much of the English-speaking world, the word "prawn" is used for the edible shrimps, thus eliminating some of the confusion.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

(A)

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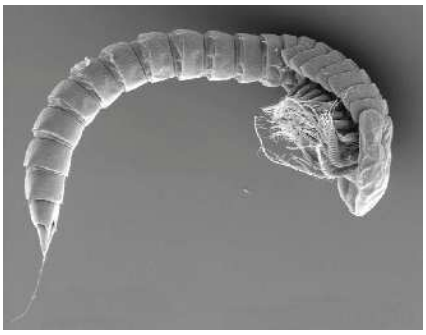
(B)



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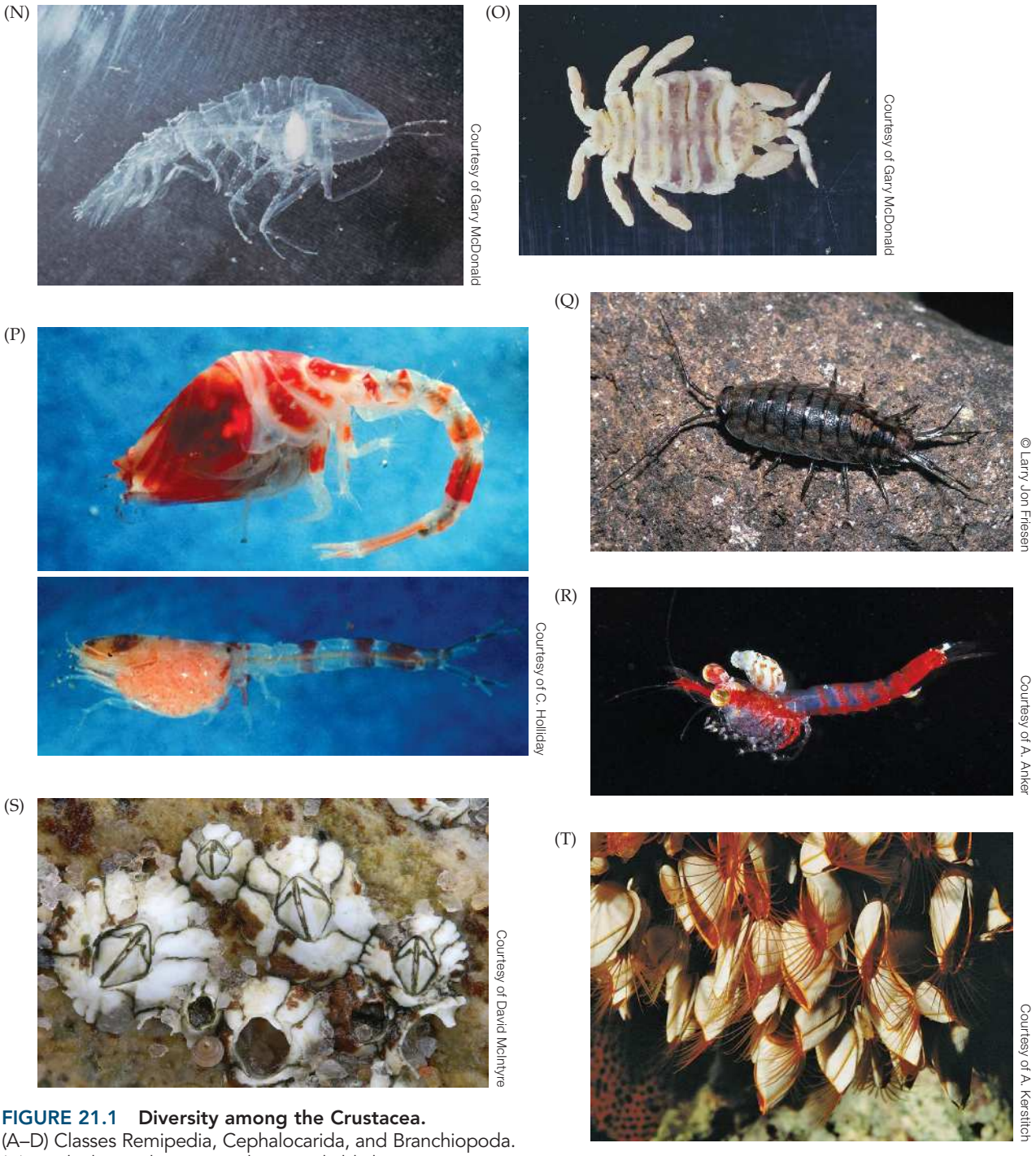

FIGURE 21.1 Diversity among the Crustacea.
(A–D) Classes Remipedia, Cephalocarida, and Branchiopoda. (A) *Morlockia ondinae*; note the remarkably homonomous segmentation of this swimming crustacean (Remipedia). (B) *Lightiella monniotae*, from New Caledonia (Cephalocarida). (C) A tadpole shrimp (Notostraca) from an ephemeral pool. (D) A clam shrimp (Diplostraca), carrying eggs. (E–Q) Class Malacostraca. (E) A fiddler crab, *Uca princeps* (Brachyura). (F) A giant Caribbean hermit crab, *Petrochirus diogenes* (Anomura). (G) A hermit crab (*Paragiopagurus fasciatus*) removed from its snail shell (Anomura). (H) A coconut crab, *Birgus latro* (Anomura), climbing a tree. (I) *Emerita analoga*, a Pacific mole crab (Anomura). (J) A pelagic lobsterette, *Pleuroncodes planipes* (Anomura). (K) A cleaner shrimp, *Lysmata californica* (Caridea). (L) *Alienaxiopsis clypeata*, a coral reef lobster-shrimp from Bali, Indonesia (Axiidae). (M) A Hawaiian regal lobster, *Enoplometopus* (Achelata). (N,O) Two unusual amphipods (Amphipoda). (N) *Cystisoma*, a huge (some exceed 10 cm), transparent, pelagic hyperiid amphipod. (O) *Cyamus scammoni*, a parasitic caprelloidean amphipod that lives on the skin of gray whales. (P) A male and female cumacean; note the eggs in the marsupium of the female (Cumacea). (Q) *Ligia* (Isopoda), the rock louse; *Ligia* are inhabitants of the high spray zone on rocky shores worldwide. (R) A mysid *Siriella* sp. (Mysida) with a parasitic epicaridean isopod (Dajidae) attached to its carapace (Western Australia). (S,T) Class Thecostraca. (S) Acorn barnacles, *Semibalanus balanoides* (Thoracica). (T) *Lepas anatifera* (Thoracica), a pelagic barnacle hanging from a floating timber.

(*Continued on next page*)

(U)

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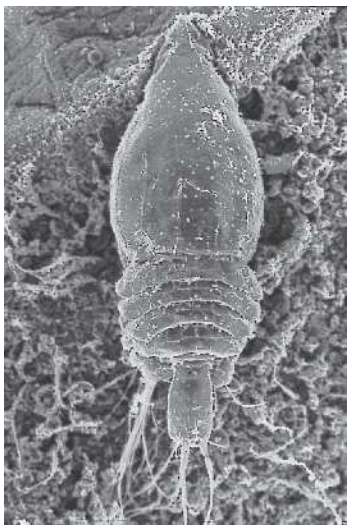
(V)



From G. A. Boxshall and R. J. Lincoln 1987. *Philos Trans R Soc B* 315: 267–303

FIGURE 21.1 (*continued*) Diversity among the Crustacea. (U) Class Copepoda; the calanoid copepod *Gaussia*, a common planktonic genus. (V) Class Tantulocarida, *Deoterthron*, parasitic on other crustaceans.

early in the twenty-first century, negative effects of ocean acidification on crustaceans began to be recognized, especially on the larval stages and subadults (see Selected References section).

Crustaceans are commonly the dominant organisms in aquatic subterranean ecosystems, and new species of these stygobionts continue to be discovered as new caves are explored. They also dominate ephemeral pool habitats, where many undescribed species are known to occur.[2] And crustaceans are the most widespread, diverse, and abundant animals inhabiting the world's oceans. The biomass of one species of Euphausiacea, the Antarctic krill (*Euphausia superba*), has been estimated at 500 million tons at any given time, probably surpassing the biomass of any other group of marine animals (and rivaling that of the world's ants, summing up all their species!). In fact, krill are the dominant fished species in the Southern Ocean in terms of catch weight. The range of morphological disparity among Crustacea far exceeds that of even the insects. Many species of crustaceans are threatened by environmental degradation; over 3,000 are listed on the IUCN Red List, and about two dozen are protected by the U.S. Environmental Protection Agency. Crustaceans are also among the most common invasive invertebrates, and well over 100 invasive species have established themselves in marine and estuarine waters of North America alone.

Because of their taxonomic diversity and numerical abundance, it is often said that crustaceans are the "insects of the sea." We prefer to think of insects as "crustaceans of the land." And indeed, there is now very strong phylogenetic evidence that insects arose from a branch within the Crustacea and this larger clade is known as **Pancrustacea** (or **Tetraconata**).

[2]One study of ephemeral pools in Northern California discovered 30 probable undescribed/unnamed crustacean species (King et al. 1996).

Despite the enormous morphological disparity seen among crustaceans (Figures 21.1–21.20), they display a suite of fundamental unifying features (Box 21A). In an effort to introduce both the diversity and the unity of this enormous group of arthropods, we first present a classification and synopses of the major taxa. We

BOX 21A Characteristics of the Subphylum Crustacea

1. Body composed of a six-segmented head, or cephalon, and a long postcephalic trunk; trunk divided into two more or less distinct tagmata (e.g., thorax and abdomen) in all but the remipedes and ostracods (Figure 21.2)
2. Cephalon composed of (anterior to posterior) ocular or protocerebral segment (lacking appendages), antennular segment (deutocerebral), antennal segment (tritocerebral), mandibular somite, maxillulary somite, and maxillary somite; one or more anterior thoracomeres fused with the head in some members of some classes (e.g., Remipedia and Malacostraca), their appendages forming maxillipeds
3. Cephalic shield or carapace present (highly reduced in anostracans, amphipods, and isopods)
4. Appendages multiarticulate, uniramous or biramous
5. Mandibles usually multiarticulate limbs that function as biting, piercing, or chewing/grinding jaws
6. Gas exchange by aqueous diffusion across specialized branchial surfaces, either gill-like structures or specialized regions of the body surface
7. Excretion by structures derived from nephridia (e.g., antennal glands, maxillary glands)
8. Both simple ocelli and compound eyes in most taxa (not Remipedia), at least at some stage of the life cycle; compound eyes often elevated on stalks
9. Gut with digestive ceca
10. With nauplius larva (unknown from any other arthropod subphylum); development mixed or direct

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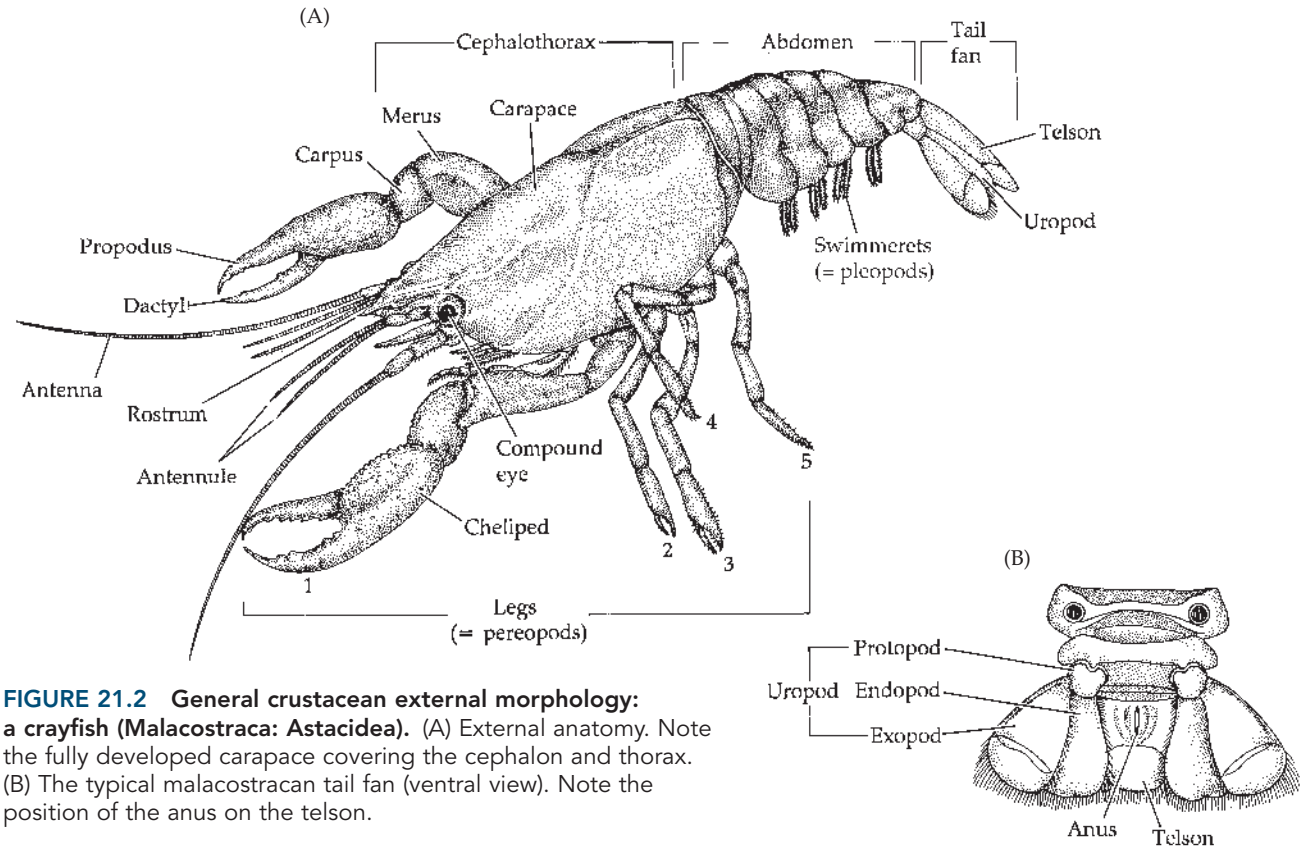

FIGURE 21.2 General crustacean external morphology: a crayfish (Malacostraca: Astacidea). (A) External anatomy. Note the fully developed carapace covering the cephalon and thorax. (B) The typical malacostracan tail fan (ventral view). Note the position of the anus on the telson.

then discuss the biology of the group as a whole, drawing examples from its various members. As you read this chapter, we ask that you keep in mind the general account of arthropods presented in Chapter 20.

Classification of the Crustacea

Crustaceans have been known to humans since ancient times and have provided us with sources of both food and legend. It is somewhat comforting to carcinologists (those who study crustaceans) to note that Cancer, one of the two invertebrates represented in the zodiac, is a crab (the other, of course, is Scorpio—another arthropod). Our modern view of Crustacea as a taxon can be traced to Lamarck's scheme in the early nineteenth century. He recognized most crustaceans as such but placed the barnacles and a few others in separate groups. For many years barnacles were classified with molluscs because of their thick, calcareous outer shell. Crustacean classification as we know it today was more or less established during the second half of the nineteenth century, although internal revisions continue. Martin and Davis (2001) presented an overview of crustacean classification, and readers are referred to that publication for a window into the labyrinthine history of this subphylum. Multigene phylogenetics strongly supports the division of Crustacea into two major lineages, Oligostraca and Altocrustacea, which we herein recognize as superclasses. Multigene phylogenetics also supports the division of Altocrustacea into two major clades, which have been named Multicrustacea and Allotriocarida, the latter including Hexapoda (insects and allies). See Crustacean Phylogeny at the end of this chapter for further details.

CLASSIFICATION OF CRUSTACEA

SUPERCLASS OLIGOSTRACA

CLASS OSTRACODA Ostracods

SUBCLASS MYODOCOPA

ORDER MYODOCOPIDA (e.g., *Cypridina*, *Euphilomedes*, *Eusarsiella*, *Gigantocypris*, *Photeros*, *Polycope*, *Skogsbergia*, *Vargula*)

ORDER HALOCYPRIDA (e.g., *Conchoecia*)

SUBCLASS PODOCOPA

ORDER PODOCOPIDA (e.g., *Baffinicythere*, *Cypris*, *Candona*, *Darwinula*, *Limnocythre* , *Loxoconcha*, *Sclerocypris*)

ORDER PLATYCOPIDA (e.g., *Cytherella*)

ORDER PALAEOCOPIDA Almost entirely extinct; living genera are *Manawa* and *Puncia*.

CLASS MYSTACOCARIDA Mystacocarids, with a single family (Derocheilocarididae) and 13 species (e.g., *Ctenocheilocaris, Derocheilocaris*)

CLASS BRANCHIURA Fish lice, or argulids. A single family (Argulidae) (e.g., *Argulus, Chonopeltis, Dipteropeltis, Dolops*)

CLASS PENTASTOMIDA Tongueworms. Two orders, numerous families (e.g., *Cephalobaena, Linguatula, Pentastoma, Waddycephalus*). In some recent classifications combined with the Branchiura in the clade Ichthyostraca.

SUPERCLASS ALTOCRUSTACEA

clade MULTICRUSTACEA

CLASS MALACOSTRACA

SUBCLASS PHYLLOCARIDA

ORDER LEPTOSTRACA Leptostracans or nebaliaceans (e.g., *Dahlella*, *Levinebalia*, *Nebalia*, *Nebaliella*, *Nebaliopsis*, *Paranebalia*)

SUBCLASS HOPLOCARIDA

ORDER STOMATOPODA Mantis shrimps (e.g., *Echinosquilla*, *Gonodactylus*, *Hemisquilla*, *Squilla*)

SUBCLASS EUMALACOSTRACA

SUPERORDER SYNCARIDA Syncarids

ORDER BATHYNELLACEA (e.g., *Bathynella*)

ORDER ANASPIDACEA (e.g., *Allanaspides*, *Anaspides*, *Paranaspides*, *Psammaspides*)

SUPERORDER EUCARIDA

ORDER EUPHAUSIACEA Euphausiaceans, or krill (e.g., *Bentheuphausia*, *Euphausia*, *Meganyctiphanes*, *Nyctiphanes*)

ORDER DECAPODA Crabs, shrimps, lobsters, etc.

SUBORDER DENDROBRANCHIATA Penaeid and sergestid shrimps (e.g., *Lucifer*, *Penaeus*, *Sergestes*, *Sicyonia*)

SUBORDER PLEOCYEMATA All other decapods (shrimp, lobster, crabs, etc.; classified in 10 infraorders: Caridea, Stenopodidea, Brachyura, Anomura, Astacidea, Achelata, Axiidea, Gebiidea, Glypheidea, Polychelida)

SUPERORDER PERACARIDA Ten orders, all of which brood their embryos in a pouch

ORDER MYSIDA Mysidans or opossum shrimps (e.g., *Acanthomysis, Hemimysis, Mysis, Neomysis*)

ORDER STYGIOMYSIDA Stygiomysidans (e.g., *Lepidomysis, Stygiomysis*)

ORDER LOPHOGASTRIDA Lophogastridans (e.g., *Gnathophausia, Lophogaster*)

ORDER CUMACEA Cumaceans (e.g., *Campylaspis, Cumopsis, Diastylis, Diastylopsis*)

ORDER TANAIDACEA Tanaidaceans (e.g., *Apseudes, Heterotanais, Paratanais, Tanais*)

ORDER MICTACEA Mictaceans (e.g., *Mictocaris*, etc.). Some researchers separate out the family Hirsutiidae as a distinct order (Bochusacea, containing *Hirsutia*, *Montucaris*, and *Thetispelecaris*).

ORDER SPELAEOGRIPHACEA Spelaeogriphaceans. Four described living species (*Potiicoara brazilienses, Spelaeogriphus lepidops,* and two species of *Mangkurtu*), and two known fossil species (the Carboniferous *Acadiocaris novascotica* and the Upper Jurassic *Liaoningogriphus quadripartitus*)

ORDER THERMOSBAENACEA Thermosbaenaceans (e.g., *Halosbaena, Limnosbaena, Monodella, Theosbaena, Thermosbaena, Tulumella*)

ORDER ISOPODA Isopods (sea slaters, rock lice, pillbugs, sowbugs, roly-polies)

SUBORDER ASELLOTA (e.g., *Asellus*, *Eurycope*, *Jaera*, *Janira*, *Microcerberus*, *Munna*)

SUBORDER CALABOZOIDEA (*Calabozoa*)

SUBORDER CYMOTHOIDA

SUPERFAMILY ANTHUROIDEA (e.g., *Anthura*, *Colanthura*, *Cyathura*, *Mesanthura*)

SUPERFAMILY CYMOTHOOIDEA (including the families Aegidae, Anuropidae, Barybrotidae, Cirolanidae, Corallanidae, Cymothoidae, Gnathiidae, Protognathiidae, and Tridentellidae)

INFRAORDER EPICARIDEA (e.g., *Bopyrus*, *Dajus*, *Hemiarthrus*, *Ione*, *Pseudione*)

SUBORDER LIMNORIDEA (e.g., *Limnoria*, *Keuphylia*, *Hadromastax*)

SUBORDER MICROCERBERIDEA (e.g, *Atlantasellus*, *Microcerberus*)

SUBORDER ONISCIDEA (e.g., *Armadillidium*, *Ligia*, *Oniscus*, *Porcellio*, *Trichoniscus*, *Tylos*, *Venezillo*)

SUBORDER PHORATOPIDEA (*Phoratopus*)

SUBORDER PHREATOICIDEA (e.g., *Mesamphisopus*, *Phreatoicopis*, *Phreatoicus*)

SUBORDER SPHAEROMATIDEA

SUPERFAMILY SEROLIDEA (*Serolis*)

SUPERFAMILY SPHAEROMATOIDEA (*Ancinus, Paracerceis, Sphaeroma*)

SUBORDER TAINISOPIDEA (*Pygolabis*, *Tainisopus*)

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SUBORDER VALVIFERA (e.g., *Arcturus*, *Idotea*, *Saduria*)

ORDER AMPHIPODA Amphipods (beach hoppers, sand fleas, scuds, skeleton shrimps, whale lice, etc.)

SUBORDER AMPHILOCHIDEA (e.g., *Alicella*, *Ampelisca*, *Byblis*, *Haustorius*, *Ipanema*, *Kroyera*, *Leucothoe*, *Liljeborgia*, *Lysianassa*, *Phoxocephalus*, *Stenothoides*)

SUBORDER COLOMASTIGIDEA (e.g., *Colomastix*)

SUBORDER HYPERIIDEA (e.g., *Cystisoma*, *Hyperia*, *Phronima*, *Primno*, *Themisto*, *Vibilia*)

SUBORDER HYPERIOPSIDEA (e.g., *Hyperiopsis*, *Podosirus*)

SUBORDER PSEUDINGOLFIELLIDEA (e.g., *Pseudingolfiella*)

SUBORDER SENTICAUDATA (e.g., *Ampithoe*, *Caprella*, *Crangonyx*, *Cyamus*, *Elasmopus*, *Gammarus*, *Grandidierella*, *Hadzia*, *Hyale*, *Hyalella*, *Maera*, *Melita*, *Niphargus*, *Pontogeneia*, *Pseudamphithoides*, *Talitrus*)

ORDER INGOLFIELLIDA Ingolfiellidans (e.g. *Ingolfiella*)

CLASS COPEPODA

SUBCLASS PROGYMNOPLEA

ORDER PLATYCOPIOIDA Platycopioids (e.g., *Antrisocopia, Platycopia*)

SUBCLASS NEOCOPEPODA

SUPERORDER GYMNOPLEA

ORDER CALANOIDA Calanoids (e.g., *Bathycalanus*, *Calanus*, *Diaptomus*, *Eucalanus*, *Euchaeta*)

SUPERORDER PODOPLEA

ORDER CYCLOPOIDA Cyclopoids (e.g., *Cyclopina*, *Cyclops*, *Lernaea*, *Notodelphys*)

ORDER GELYELLOIDA Gelyelloids (e.g., *Gelyella*)

ORDER HARPACTICOIDA Harpacticoids (e.g., *Harpacticus*, *Hase*, *Longipedia*, *Peltidium*, *Porcellidium*, *Psammus*, *Sunaristes*, *Tisbe*)

ORDER MISOPHRIOIDA Misophriods (e.g., *Boxshallia*, *Misophria*)

ORDER MONSTRILLOIDA Monstrilloids (e.g., *Monstrilla*, *Stilloma*)

ORDER MORMONILLOIDA Mormonilloids. Monogeneric: *Mormonilla*

ORDER POECILOSTOMATOIDA Poecilostomatoids (e.g., *Chondracanthus*, *Erebonaster*, *Ergasilus*, *Pseudanthessius*)

ORDER SIPHONOSTOMATOIDA Siphonostomatoids (e.g., *Clavella*, *Nemesis*, *Penella*, *Pontoeciella*, *Trebius*)

CLASS THECOSTRACA Barnacles and their kin (about 367 genera and 2120 species)

SUBCLASS FACETOTECTA Monogeneric (*Hansenocaris*): the mysterious "y-larvae," a group of marine nauplii and cyprids for which adults are unknown

SUBCLASS ASCOTHORACIDA Two orders (Laurida, Dendrogastrida) of parasitic thecostracans (e.g., *Ascothorax, Dendrogaster, Laura, Synagoga, Zoanthoecus*)

SUBCLASS CIRRIPEDIA Cirripedes, the barnacles, and their kin

SUPERORDER THORACICA True (stalked and acorn) barnacles, e.g., *Balanus, Chthamalus, Conchoderma*, *Coronula, Lepas*, *Pollicipes, Scalpellum*, *Tetraclita, Verruca*.

SUPERORDER ACROTHORACICA Burrowing barnacles. Two orders, Cryptophialida and Lythoglyptida (e.g., *Cryptophialus, Trypetesa*)

SUPERORDER RHIZOCEPHALA Thirteen families of highly modified parasitic barnacles (e.g., *Heterosaccus, Lernaeodiscus, Mycetomorpha, Peltogaster, Sacculina, Sylon*)

CLASS TANTULOCARIDA Deep water, marine parasites (e.g., *Basipodella, Deoterthron, Microdajus*)

clade ALLOTRIOCARIDA

CLASS CEPHALOCARIDA Cephalocarids (e.g., *Chiltoniella*, *Hampsonellus*, *Hutchinsoniella*, *Lightiella, Sandersiella*)

CLASS BRANCHIOPODA Branchiopods

SUBCLASS ANOSTRACA Fairy shrimps and brine shrimps (e.g., *Artemia*, *Branchinecta*, *Branchipus*, *Linderiella*, *Streptocephalus*)

SUBCLASS PHYLLOPODA

ORDER NOTOSTRACA Tadpole shrimps (*Lepidurus*, *Triops*)

ORDER DIPLOSTRACA The "bivalved" branchiopods

SUBORDER LAEVICAUDATA Flat-tailed clam shrimps (e.g., *Lynceus*)

SUBORDER ONYCHOCAUDATA Clam shrimps, cladocerans (water fleas), and cyclestherians

INFRAORDER SPINICAUDATA Clam shrimps (e.g., *Cyzicus*, *Imnadia*, *Leptestheria*, *Limnadia*, *Metalimnadia*)

INFRAORDER CLADOCEROMORPHA Water fleas and cyclestheriids

PARVORDER CYCLESTHERIDA Monotypic: *Cyclestheria hislopi*

PARVORDER CLADOCERA Water fleas (e.g., *Anchistropus*, *Daphnia*, *Diaphonosoma*, *Leptodora*, *Moina*, *Polyphemus*)

CLASS REMIPEDIA Remipedes. One living order, Nectiopoda (e.g., *Cryptocorynectes*, *Godzillius*, *Lasionectes*, *Pleomothra*, *Speleonectes*, *Xibalbanus*). Sometimes combined with the Hexapoda as the clade Labiocarida.

Synopses of Crustacean Taxa

The following descriptions of major crustacean taxa will give you an idea of the range of diversity within the group and the variety of ways in which these successful animals have exploited the basic crustacean body plan.

Subphylum Crustacea

Body generally composed of a 6-segmented cephalon or head (the ocular segment, plus 5 limb-bearing segments)[3] and multisegmented postcephalic trunk; trunk divided into thorax and abdomen (except in remipedes and ostracods). First segment of cephalon (ocular segment) bears the eyes and protocerebrum; subsequent segments bear first antennae (antennules), second antennae, mandibles, maxillules, and maxillae (see Table 20.2); one or more anterior thoracomeres may fuse with the head (e.g., in Remipedia and Malacostraca), their appendages forming maxillipeds (secondarily modified for feeding); cephalic shield or carapace present (secondarily lost in some groups); with antennal glands or maxillary glands (excretory nephridia); both simple ocelli and compound eyes in most groups, at least at some stage of the life cycle; compound eyes stalked in many groups. With nauplius larval stage (suppressed or bypassed in some groups), and often a series of additional larval stages.[4]

Superclass Oligostraca

Class Ostracoda

Body segmentation reduced, trunk not clearly divided into thorax and abdomen; trunk with 0 to 3 pairs of limbs; abdomen greatly reduced; caudal rami (furca) present; gonopores on lobe anterior to caudal rami; carapace bivalved, hinged dorsally and closed by a central adductor muscle, enclosing body and head; carapace highly variable in shape and ornamentation, smooth or with various pits, ridges, spines, etc.; most with 1 simple median naupliar eye and sometimes weakly stalked compound eyes (e.g., in Myodocopida); adults with maxillary and (in some) antennal glands; males with distinct copulatory limbs (Figure 21.3).

Ostracods include about 13,000 described living species (and nearly 65,000 fossil species) of small bivalved crustaceans, ranging in length from 0.1 to 2.0 mm, although some giants (e.g., *Gigantocypris*) reach 32 mm. They superficially resemble clam shrimps in having the entire body enclosed within the valves of the carapace. However, ostracod valves lack the concentric growth rings of clam shrimps, and there are major differences in the appendages. The carapace is usually penetrated by pores, some bearing setae, and is shed with each molt. A good deal of confusion exists about the nature of ostracod limbs, and homologies with other crustacean taxa (and even within the Ostracoda) are unclear—this confusion is reflected in the variety of names applied by different authors. We have adopted terms here that allow the easiest comparison with other taxa.

Ostracods possess the fewest limbs of any crustacean class. The four or five head appendages are followed by zero to three trunk appendages. Superficially, the (second) maxillae appear to be absent; however, the highly modified fifth limbs are in fact these appendages. The trunk seldom shows external evidence of segmentation, although all 11 postcephalic somites are discernable in

[3]For a very long time the arthropod ocular segment, which has no appendages but houses the protocerebrum and the eyes, was called the "acron," a term borrowed from annelid development when the two phyla were thought to be very closely related (i.e., the Articulata hypothesis). However, the demise of the Articulata hypothesis, and the realization that arthropods are ecdysozoans (and annelids are spiralians) undermined the concept of acron homology between the two phyla. Further, unlike the arthropod ocular segment, the "acron" in annelids (usually called the prostomium) commonly bears both eyes and antennae, as well as a variety of palps, tentacles, and sense organs. Thus, the term "ocular segment" (or "opthalmic segment") best describes the first, eye-bearing segment of Crustacea and other arthropods.

[4]Segments of the thorax are called thoracomeres (regardless of whether or not any of these segments are fused to the head), whereas appendages of the thorax are called thoracopods. The term "pereon" refers to that portion of the thorax not fused to the head (when such fusion occurs), and the terms "pereonites" (= pereomeres) and "pereopods" are used for the segments and appendages, respectively, of the pereon. Hence, on a crustacean with the first thoracic segment (thoracomere 1) fused to the head, thoracomere 2 is typically called pereonite 1, the first pair of pereopods represents the second pair of thoracopods, and so on. Be assured that we are trying to simplify, not confuse, this issue. Also, we caution you that the homology of the thorax and abdomen among the major crustacean lineages is probably more reverie than reality; the segmental homologies of the thorax and abdomen have not yet been unraveled among the crustacean classes. For summaries of naupliar development across the group and larval features in all crustaceans, see Martin et al. (2014). In most crustacean species the number of body segments is fixed, but in at least two groups (notostracans and remipedes) the segment number can vary within a given species.

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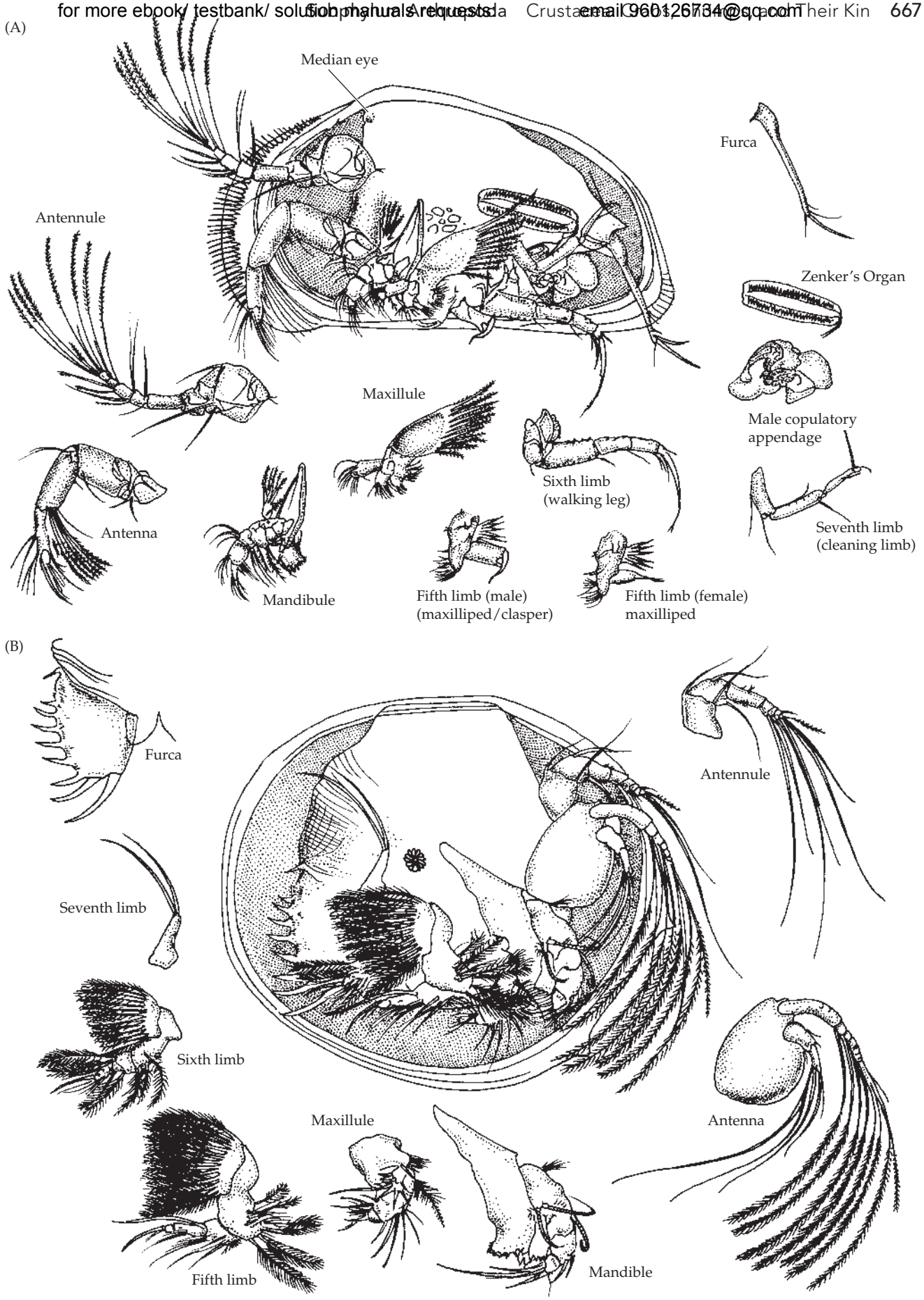

FIGURE 21.3 Anatomy and diversity in the class Ostracoda. (A) Anatomy of *Sclerocypris* (Podocopa). (B) Anatomy of *Thaumatoconcha* (Myodocopa).

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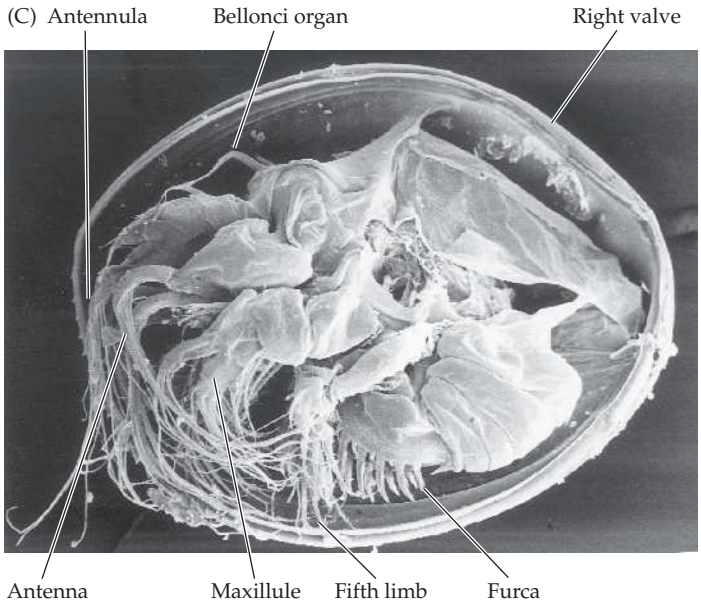
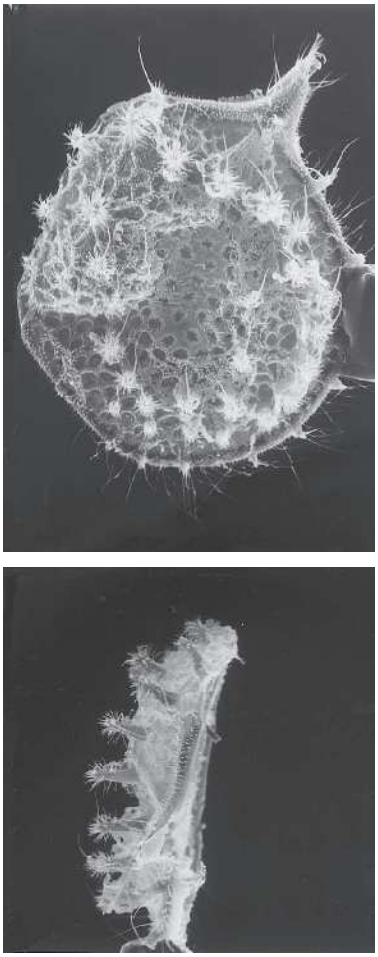


Courtesy of A. Cohen

FIGURE 21.3 (*continued*) Anatomy and diversity in the class Ostracoda. (C) Internal view of *Metapolycope* (Myodocopa), left valve removed. (D) The highly ornate *Eusarsiella* (Myodocopa); side view and edge view, showing the ornate shell. (E) Examples of genera from the major living ostracod groups (arrows point anteriorly). A: *Vargula* (Myodocopa, Myodocopida). B: *Polycope* (Myodocopa, Halocyprida). C: *Cytherelloidea* (Podocopa, Platycopida). D: *Saipanetta* (Podocopa, Podocopida). E: *Neonesidea* (Podocopa, Podocopida). F: *Propontocypris* (Podocopa, Podocopida). G: *Macrocypris* (Podocopa, Podocopida). H: *Ilyocypris* (Podocopa, Podocopida). I: *Centrocypris* (Podocopa, Podocopida). J: *Candona* (Podocopa, Podocopida) K: *Cyprinotus* (Podocopa, Podocopida). L: *Darwinula* (Podocopa, Podocopida). M: *Baffinicythere* (Podocopa, Podocopida). N: *Loxoconcha* (Podocopa, Podocopida). O: *Pterygocythereis* (Podocopa, Podocopida). P: *Cyprideis* (Podocopa, Podocopida). Q: *Semicytherura* (Podocopa, Podocopida). R: *Hemicytherura* (Podocopa, Podocopida). S: *Sahnicythere* (Podocopa, Podocopida). T: *Terrestricythere* (Podocopa, Podocopida).

(D)



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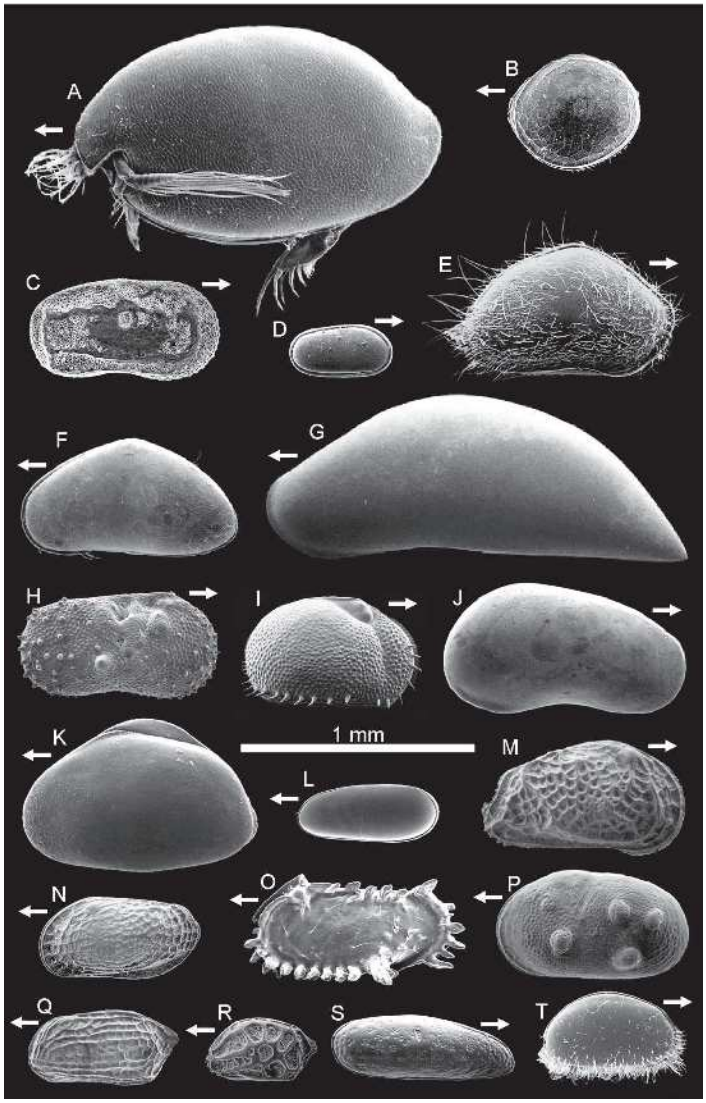

From J. Rodriguez-Lazaro and F. Ruiz-Muñoz. 2012. In D. J. Horne et al. (Eds.), *Developments in Quaternary Sciences Volume 17*, pp. 1–14. Elsevier, Amsterdam; D. J. Horne et al. 2002. In J. A. Holmes and A. R. Chivas (Eds.), *The Ostracoda: Applications in Quaternary Research*. https://doi.org/10.1029/131GM02. © American Geophysical Union

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some taxa. The third pair of trunk limbs bears the gonopores and constitutes the so-called copulatory organ.

Ostracods are one of the most successful groups of crustaceans. They also have the best fossil record of any arthropod group, dating from at least the Ordovician, and an estimated 65,000 fossil species have been described (a bit over 20,000 fossil trilobites have been described). Most are benthic crawlers or burrowers, but many have adopted a suspension-feeding planktonic lifestyle, and a few are terrestrial in moist habitats. One species is known to be parasitic on fish gills—*Sheina orri* (Myodocopida, Cypridinidae). Ostracods are abundant worldwide in all aquatic environments and are known to depths of 7,000 m in the sea. Some are commensal on echinoderms or other crustaceans. A few podocopans have invaded supralittoral sandy regions (members of the family Terrestricytheridae), and members of several families inhabit terrestrial mosses and humus. Two principal taxa (ranked as subclasses here) are recognized within the Ostracoda: Myodocopa and Podocopa.

Myodocopans are all marine. Most are benthic, but the group also includes all of the marine planktonic ostracods. The largest of all ostracods, the planktonic *Gigantocypris*, is a member of this group. Myodocopans include scavengers, detritus feeders, suspension feeders, and some predators. There are two orders: Myodocopida and Halocyprida.

Podocopans include predominantly benthic forms; although some are capable of temporary swimming, none are fully planktonic. Their feeding methods include suspension feeding, herbivory, detritus feeding, and parasitism. The Podocopa are divided into three orders: the exclusively marine Platycopida, the ubiquitous Podocopida, and the Palaeocopida. The Palaeocopida were diverse and widespread in the Paleozoic but are represented today only by the extremely rare Punciidae (known from a few living specimens and from dead valves dredged in the South Pacific).

One of the most remarkable examples of bioluminescence in the animal kingdom occurs among ostracods in the family Cypridinidae. Worldwide, over half of the known 300 species in this family are luminescent, probably all to deter predators, but one clade (that occurs only in the Caribbean) also uses their luminescence for complex courtship displays much the same way fireflies do, only by ejecting pulses of light into the sea in near darkness. The luminescent reaction involves cypridinid luciferin and luciferase that, together with mucus, are ejected separately through specialized nozzles from separate secretory cells in the upper lip, and they mix in the seawater. As a result, light is extracellular, being produced external to the body of the ostracod. Virgin females respond to species-specific male displays by swimming to intercept a signaling male in the water column, but without luminescing themselves. These mating arenas are equivalent to underwater leks. Mated females immediately move to the seafloor and begin brooding embryos. And in a remarkable twist of nature, a number of bioluminescent fishes have been shown to obtain their luciferase from their ostracod prey—a process called kleptoprotein bioluminescence. Fertilization in these luminescent ostracods is internal, with sperm being transferred by a spermatophore. The male eighth limb functions as a copulatory organ, which is enlarged and modified for grasping. In females the eighth limb is reduced and includes a pair of knobs, probably grasped by the males. The spermatophore appears to act as a mating plug to block other male copulations. All offspring in one brood are thus fertilized by the same male, and females can store sperm and produce multiple broods from one insemination.

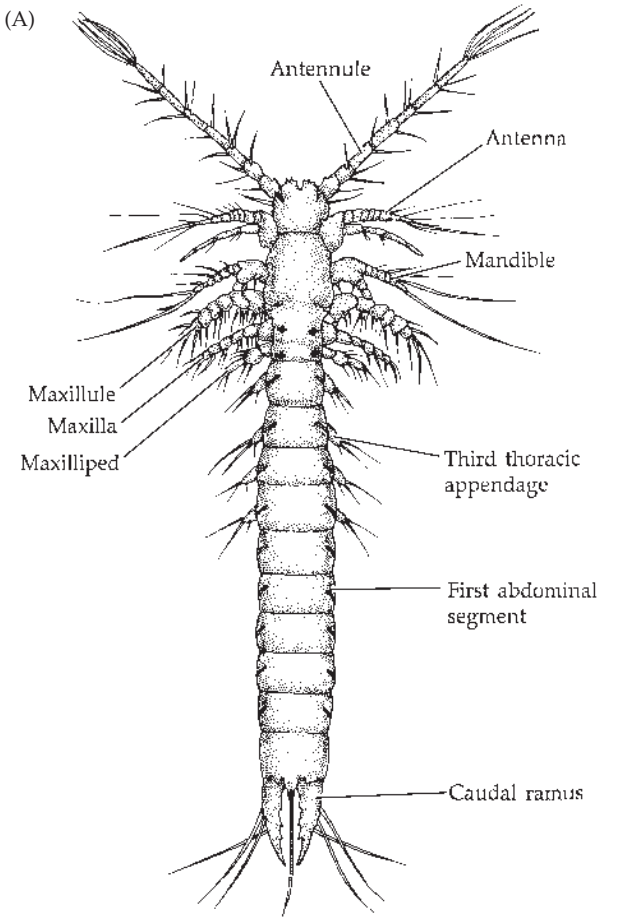
Class Mystacocarida

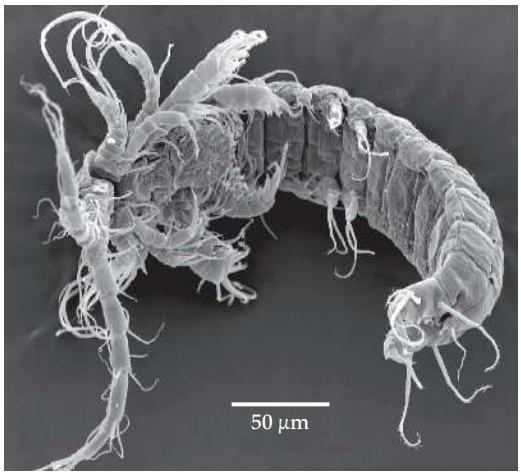
Body divided into cephalon and 10-segmented trunk; telson with clawlike caudal rami; cephalon characteristically cleft; antennae and mandibles biramous; antennules, maxillules, and maxillae uniramous; first trunk segment bears maxillipeds but is not fused with cephalon; no carapace; gonopores on fourth trunk segment; trunk segments 2–5 with short, single-segment appendages (Figure 21.4A).

There are only 13 described species of mystacocarids, 8 in the genus *Derocheilocaris* and 5 in *Ctenocheilocaris*. Most are less than 0.5 mm long, although *D. ingens* reaches 1 mm. The head is marked by a transverse "cephalic constriction" between the origins of the first and second antennae, perhaps a remnant of primitive head segmentation. In addition, the lack of fusion of the cephalon and maxillipedal trunk segment, the simplicity of the mouth appendages, and other features have led some workers to propose that the mystacocarids are among the most primitive living crustaceans. These attributes may, however, be related to a neotenic origin and specialization for interstitial habitats. Mystacocarids are marine, interstitial crustaceans that live in littoral and sublittoral sands throughout the world's temperate and subtropical seas. Their rather vermiform body and small size are clearly adaptations to life among sand grains. Mystacocarids are thought to feed by scraping organic material from the surfaces of sand grains with their setose mouthparts.

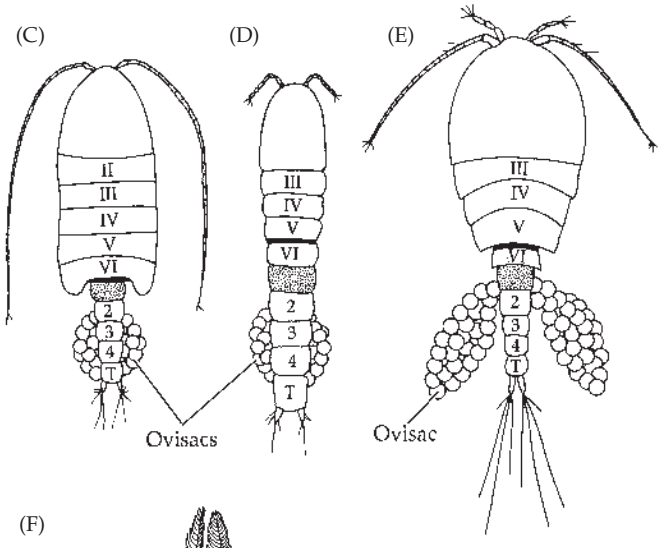
Class Branchiura

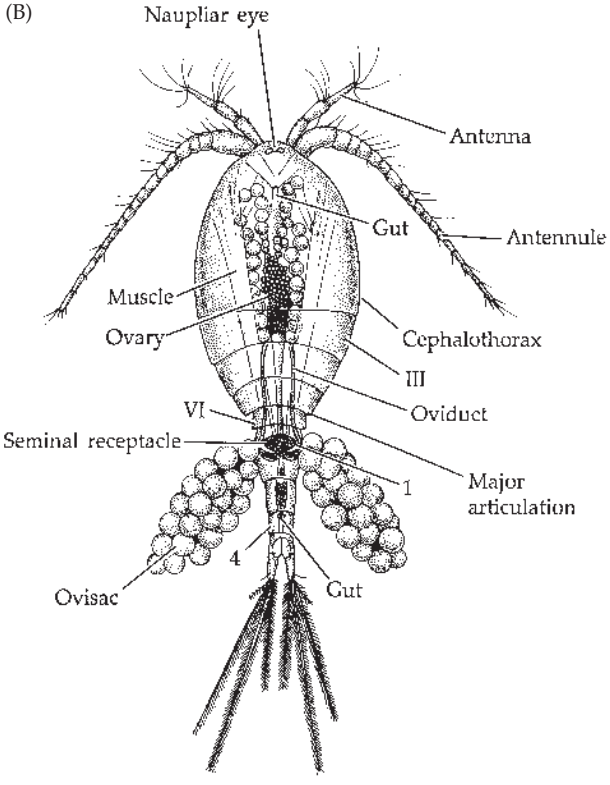
Body compact and oval, head and most of trunk covered by broad carapace; antennules and antennae reduced, the latter sometimes absent; mouthparts modified for parasitism; no maxillipeds; thorax reduced to 4 segments, with paired biramous appendages; abdomen unsegmented, bilobed, limbless, but with minute caudal rami; female gonopores at bases of fourth thoracic legs, male with single gonopore on midventral surface of last thoracic somite; paired, sessile compound eyes and 1 to 3 median simple eyes (Figure 21.4M).

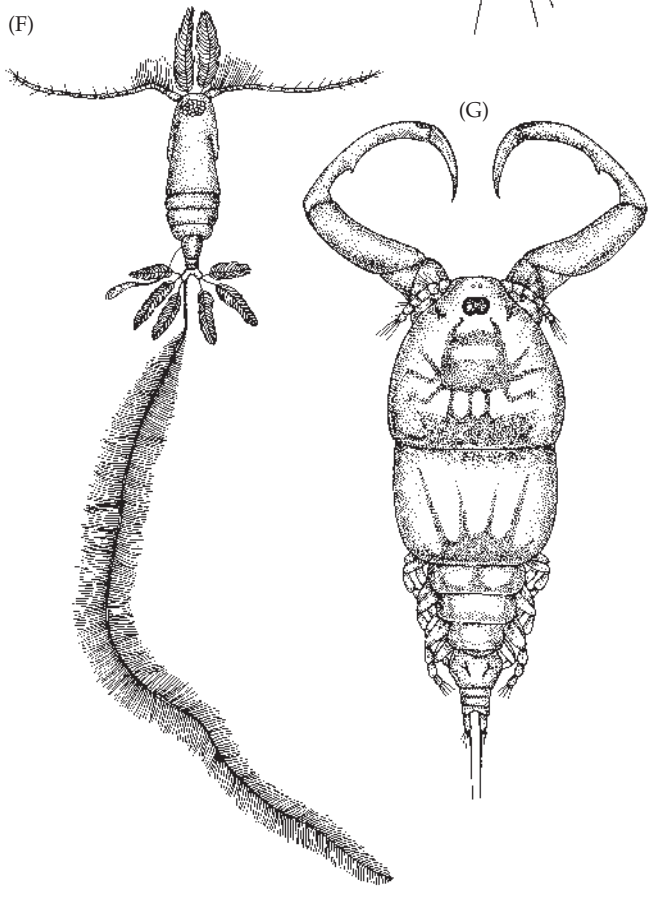




Courtesy of J. Olesen







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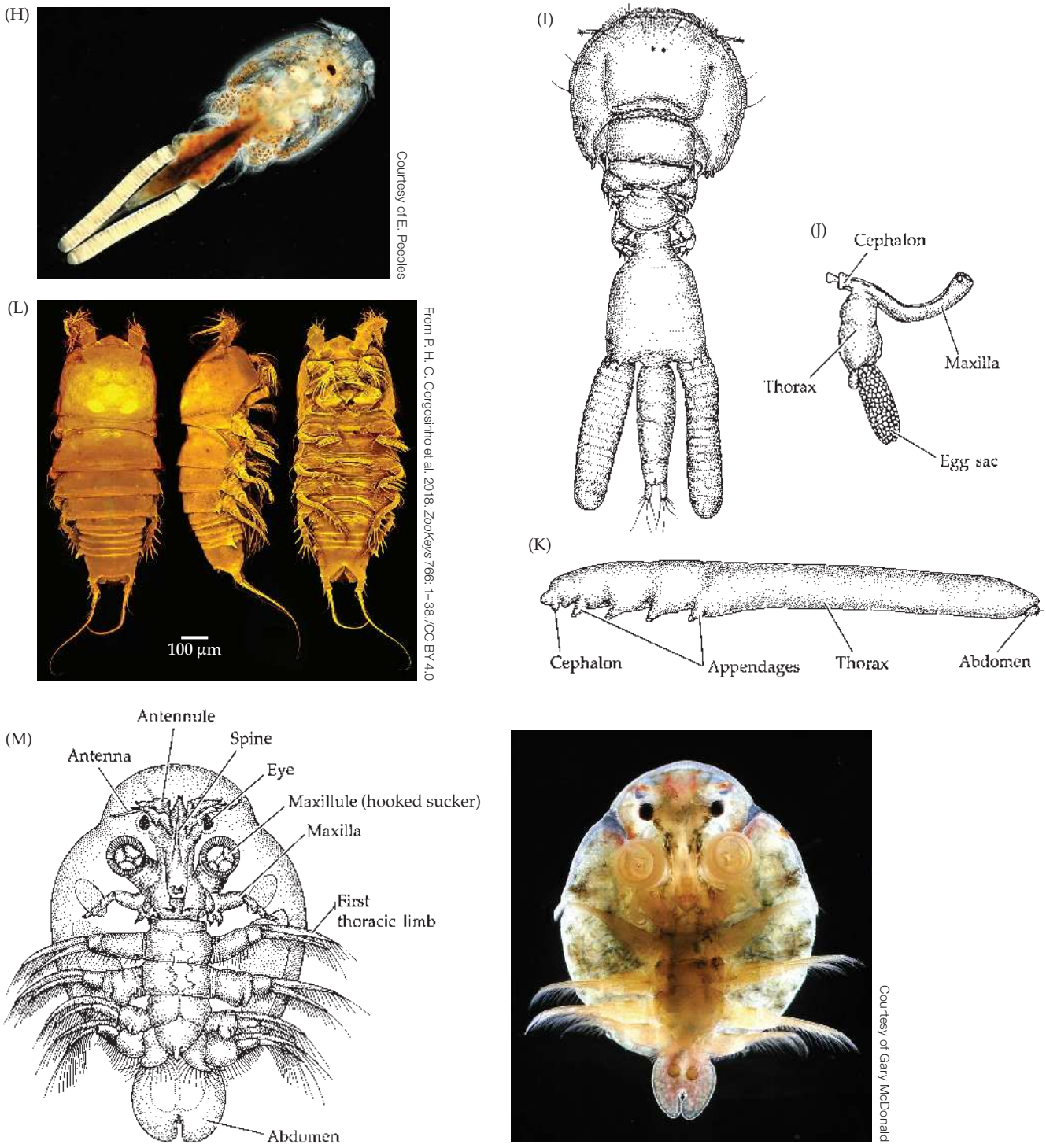

FIGURE 21.4 Anatomy of the classes Mystacocarida, Copepoda, and Branchiura. (A) General anatomy and SEM of the mystacocarid *Derocheilocaris*. (B) General anatomy of a cyclopoid copepod. (C–E) General body forms of (C) a calanoid, (D) a harpacticoid, and (E) a cyclopoid copepod. Note the points of body articulation (dark band) and the position of the genital segment (shaded segment). Roman numerals are thoracic segments; Arabic numerals are abdominal segments; T = telson. (F) An elaborately setose calanoid copepod adapted for flotation. (G) A poecilostomatid copepod, *Ergasilus pitalicus*, ectoparasitic on cichlid fishes. (H) A female siphonostomatid copepod (*Caligus* sp.) with egg sacs. (I) A female siphonostomatid copepod (*Trebius heterodonti*, a parasite of horn sharks in California) with egg sacs. (J) A siphonostomatid copepod, *Clavella adunca*, showing extreme body reduction; this species attaches to the gills of fishes by its elongate maxillae. (K) *Notodelphys*, a wormlike cyclopoid copepod adapted for endoparasitism in tunicates. (L) The harpacticoid copepod *Hase talpamorphicus* (confocal laser scans). (M) Branchiura: *Argulus foliaceus* (drawing and photograph), a branchiuran that parasitizes fishes. Note the powerful hooked suckers (modified maxillules) on the ventral surface. (G after V. E. Thatcher. 1984. *J Crust Biol* 4: 495–501.)

The Branchiura comprise about 230 species of ectoparasites on marine and freshwater fishes. The antennules generally bear hooks or spines for attachment to their host fish. The mandibles are reduced in size and complexity, bear cutting edges, and are housed within a styliform "proboscis" apparatus. The maxillules are clawed in *Dolops*, but they are modified as stalked suckers in the other genera (*Argulus, Chonopeltis, Dipteropeltis*). The uniramous maxillae usually bear attachment hooks. The thoracopods are biramous and used for swimming when the animal is not attached to a host. Branchiurans feed by piercing the skin of their hosts and sucking blood or tissue fluids. Once they locate a host, they crawl toward the fish's head and anchor in a spot where water flow turbulence is low (e.g., behind a fin or gill operculum). Members of the genus *Argulus* occur worldwide, and can pose a serious problem to aquaculture, but members of the other genera have restricted distributions. *Chonopeltis* is found only in Africa, *Dipteropeltis* in South America, and *Dolops* in South America, Africa, and Tasmania.

Class Pentastomida

Obligatory parasites of various amphibians, reptiles, birds, and mammals. Adults inhabit respiratory tract (lungs, nasal passages, etc.) of their host. Body highly modified, wormlike, 2–13 cm in length. Adult appendages reduced to 2 pairs of head appendages, lobelike and with chitinous claws used to cling to host. Body cuticle nonchitinous and highly porous. Body muscles somewhat sheetlike, but clearly segmental and cross-striated. Mouth lacks jaws; often on end of snoutlike projection; connected to a muscular pumping pharynx used to suck blood from host. The combination of the snout and the 2 pairs of legs gives the appearance of there being 5 mouths, hence the name (Greek *penta*, "five"; *stomida*, "mouths"). In many species the appendages are reduced to no more than the terminal claws. No specific gas exchange, circulatory, or excretory organs. Gonochoristic; females larger than males. About 130 described species, including 2 cosmopolitan species that can occasionally infest humans (Figure 21.4K, 21.5).

For years it was believed that pentastomids were allied with the fossil lobopodians, onychophorans, and tardigrades as some kind of segmented, vermiform, proto-arthropod creature. However, molecular phylogenetics informs us that pentastomids are highly modified crustaceans, perhaps derived from the Branchiura. Corroboration has come from studies of sperm and larval morphology, nervous system anatomy, and cuticular fine structure.

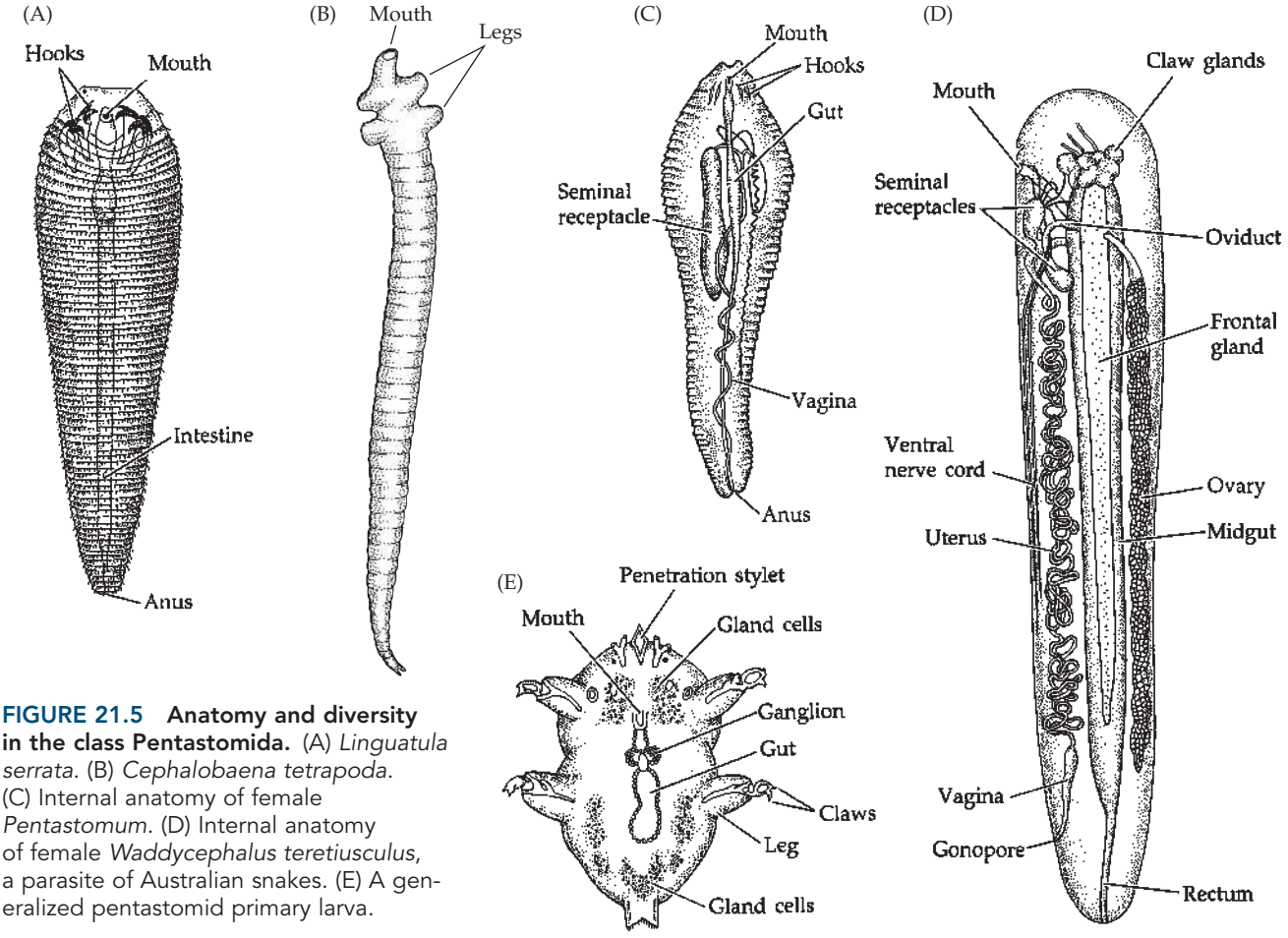

FIGURE 21.5 Anatomy and diversity in the class Pentastomida. (A) *Linguatula serrata*. (B) *Cephalobaena tetrapoda*. (C) Internal anatomy of female *Pentastomum*. (D) Internal anatomy of female *Waddycephalus teretiusculus*, a parasite of Australian snakes. (E) A generalized pentastomid primary larva.

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Work on the Swedish Orsten fauna indicates that pentastomid-like animals had appeared as early as the late Cambrian (500 Ma), long before the land vertebrates had evolved. What might the original hosts of these parasites have been? Conodont fossils are common in all the Cambrian localities that have yielded pentastomids, raising the possibility that conodonts (also long a mystery, but now widely regarded as parts of early fishlike vertebrates) may have been at least one of the original hosts of these early Pentastomida.

Superclass Altocrustacea: Clade Multicrustacea

Class Malacostraca

Body of 19–20 segments, including 6-segmented cephalon/head, 8-segmented thorax (anterior-most somites often fused with head), and 6-segmented pleon (7-segmented in leptostracans), plus telson; with or without caudal rami; carapace covering part or all of thorax, or reduced, or absent; 0–3 pairs of maxillipeds; thoracopods primitively biramous, uniramous in some groups, phyllopodous only in members of the subclass Phyllocarida; antennules and antennae usually biramous; abdomen (pleon) usually with 5 pairs of biramous pleopods and 1 pair of biramous uropods; eyes usually present, compound, stalked or sessile. Mainly gonochoristic; female gonopores on sixth, and male pores on eighth thoracomeres. When uropods are present, they are often broad and flat, lying alongside the broad telson to form a tail fan.

Most classification schemes divide the more than 40,200 species of malacostracans into three subclasses, Phyllocarida (leptostracans), Hoplocarida (stomatopods), and the megadiverse Eumalacostraca. The phyllocarids are typically viewed as representing the primitive malacostracan condition (6-8-7 body segments plus telson; Figure 21.6). The basic eumalacostracan body plan, characterized by the 6-8-6 (plus telson) arrangement of body segments, was recognized in the early 1900s by W. T. Calman, who termed the defining features of the Eumalacostraca "caridoid facies" (Figure 21.7). Much work has been done since Calman's day, but the basic elements of his caridoid facies are still present in all members of the subclass Eumalacostraca.

Subclass Phyllocarida

Order Leptostraca With typical malacostracan characteristics, except notable for presence of 7 free pleomeres (plus telson), generally taken to represent the primitive condition for the class. Also, with phyllopodous thoracopods (all similar to one another); no maxillipeds; large

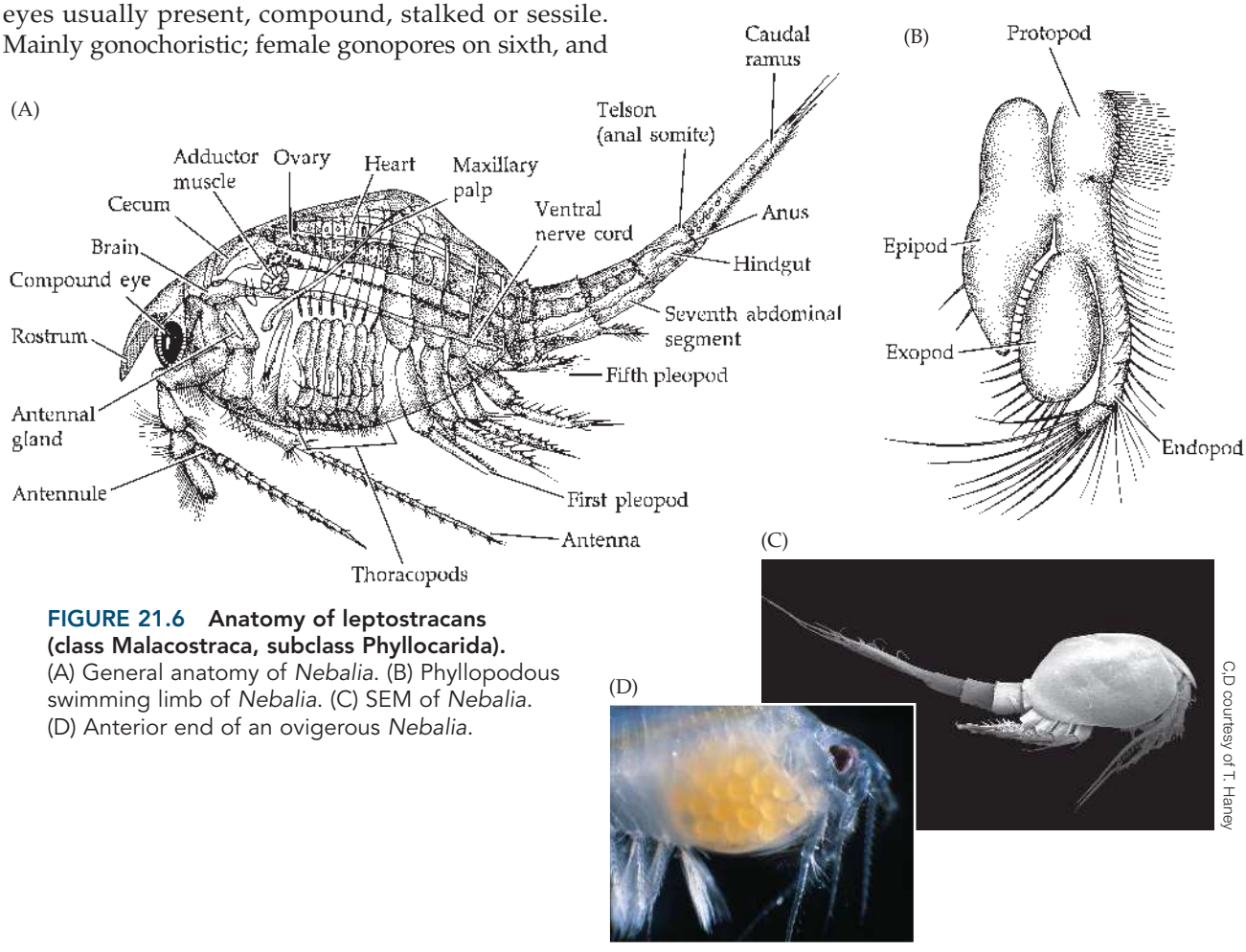

FIGURE 21.6 Anatomy of leptostracans (class Malacostraca, subclass Phyllocarida). (A) General anatomy of *Nebalia*. (B) Phyllopodous swimming limb of *Nebalia*. (C) SEM of *Nebalia*. (D) Anterior end of an ovigerous *Nebalia*.

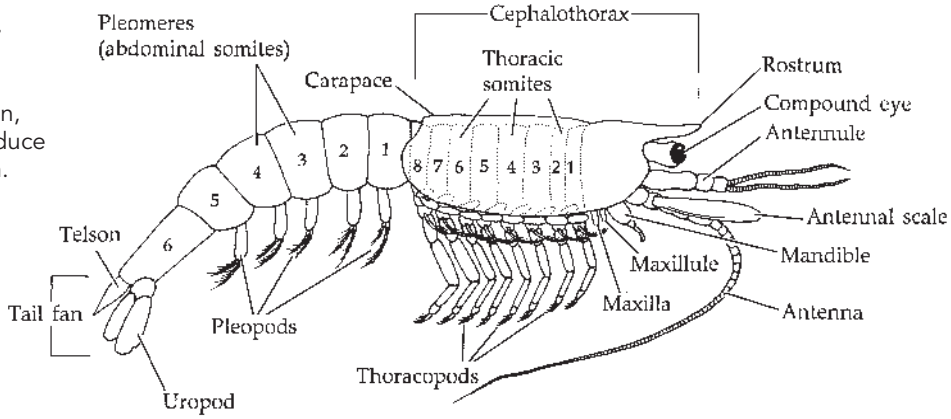

FIGURE 21.7 The basic eumalacostracan body plan and the "caridoid facies." Note the thick (muscled) abdomen and the tail fan, which work in combination to produce a powerful tail flip escape reaction.

carapace covering thorax and compressed laterally so as to form an unhinged bivalved "shell," with an adductor muscle; cephalon with a movable, articulated rostrum; pleopods 1–4 similar and biramous, 5–6 uniramous; no uropods; paired stalked compound eyes; antennules biramous; antennae uniramous; adults with both antennal and maxillary glands (Figures 21.6 and 21.21C).

The subclass Phyllocarida includes about 40 species in 10 genera. Most are 5–15 mm long, but *Nebaliopsis typica* is a giant at nearly 5 cm in length. The leptostracan body form is distinctive, with its loose bivalved carapace covering the thorax, a protruding rostrum, and an elongate abdomen. All leptostracans are marine, and most are epibenthic from the intertidal zone to a depth of 400 m; *Nebaliopsis typica* is bathypelagic. Most species seem to occur in low-oxygen environments. One species, *Dahlella caldariensis*, is associated with the hydrothermal vents of the Galapagos and the East Pacific Rise. *Speonebalia cannoni* is known only from marine caves.

Most leptostracans suspension feed by stirring up bottom sediments. They are also capable of grasping relatively large bits of food directly with the mandibles. Some are carnivorous scavengers, and some are known to aggregate in areas on the seafloor where large amounts of detritus accumulate. In many species the antennae or antennules of males are modified to hold females during copulation.

Subclass Hoplocarida

Order Stomatopoda Carapace covering portion of head and fused with thoracomeres 1–4; head with movable, articulated rostrum; thoracopods 1–5 uniramous and subchelate, second pair massive and raptorial (all 5 are sometimes called "maxillipeds" or gnathopods because they are involved in feeding); thoracopods 6–8 biramous, ambulatory; pleopods biramous, with dendrobranchiate-like gills on exopods; antennules triramous; antennae biramous, with large, paired, stalked compound eyes that are unique in the animal kingdom (Figures 21.8A–C, 21.27D, and 21.33K). Stomatopods are one of only two groups of malacostracans that possess pleopodal gills. Only the isopods share this trait, but the pleopods are quite different in the two groups. The tubular, thin, highly branched gills of stomatopods provide a large surface area for gas exchange in these active animals.

All 500 or so living hoplocarids are placed in the order Stomatopoda, known as mantis shrimps. They are relatively large crustaceans, ranging in length from 2 to 30 cm. Compared with that of most malacostracans, the muscle-filled abdomen is notably robust. Most stomatopods are found in shallow tropical or subtropical marine environments. Nearly all of them live in burrows excavated in soft sediments or in cracks and crevices, among rubble, or in other protected places. All species are raptorial carnivores, preying on fishes, molluscs, cnidarians, and other crustaceans. The large, distinctive subchelae of the second thoracopods act either as crushers or as spears (Figure 21.8C).

Stomatopods crawl about using the posterior thoracopods and the flaplike pleopods. They also can swim by metachronal beating of the pleopods (the "swimmerets"). For these relatively large animals, living in narrow burrows requires a high degree of maneuverability. The short carapace and the flexible, muscular abdomen allow these animals to twist double and turn around within their tunnels or in other cramped quarters. This ability facilitates an escape reaction whereby a mantis shrimp darts into its burrow rapidly head first, then turns around to face the entrance.

Subclass Eumalacostraca

Head, thorax, and abdomen of 6-8-6 somites respectively (plus telson); with 0, 1, 2, or 3 thoracomeres fused with head, their respective appendages usually modified as maxillipeds; antennules and antennae primitively biramous (but often reduced to uniramous); most with well-developed carapace, secondarily reduced in syncarids and some peracarids; gills primitively as thoracic epipods; tail fan composed of telson plus paired uropods; abdomen long and muscular. Three superorders: Syncarida, Peracarida, Eucarida, although the monophyly of the last has been contested in morphological and molecular analyses.

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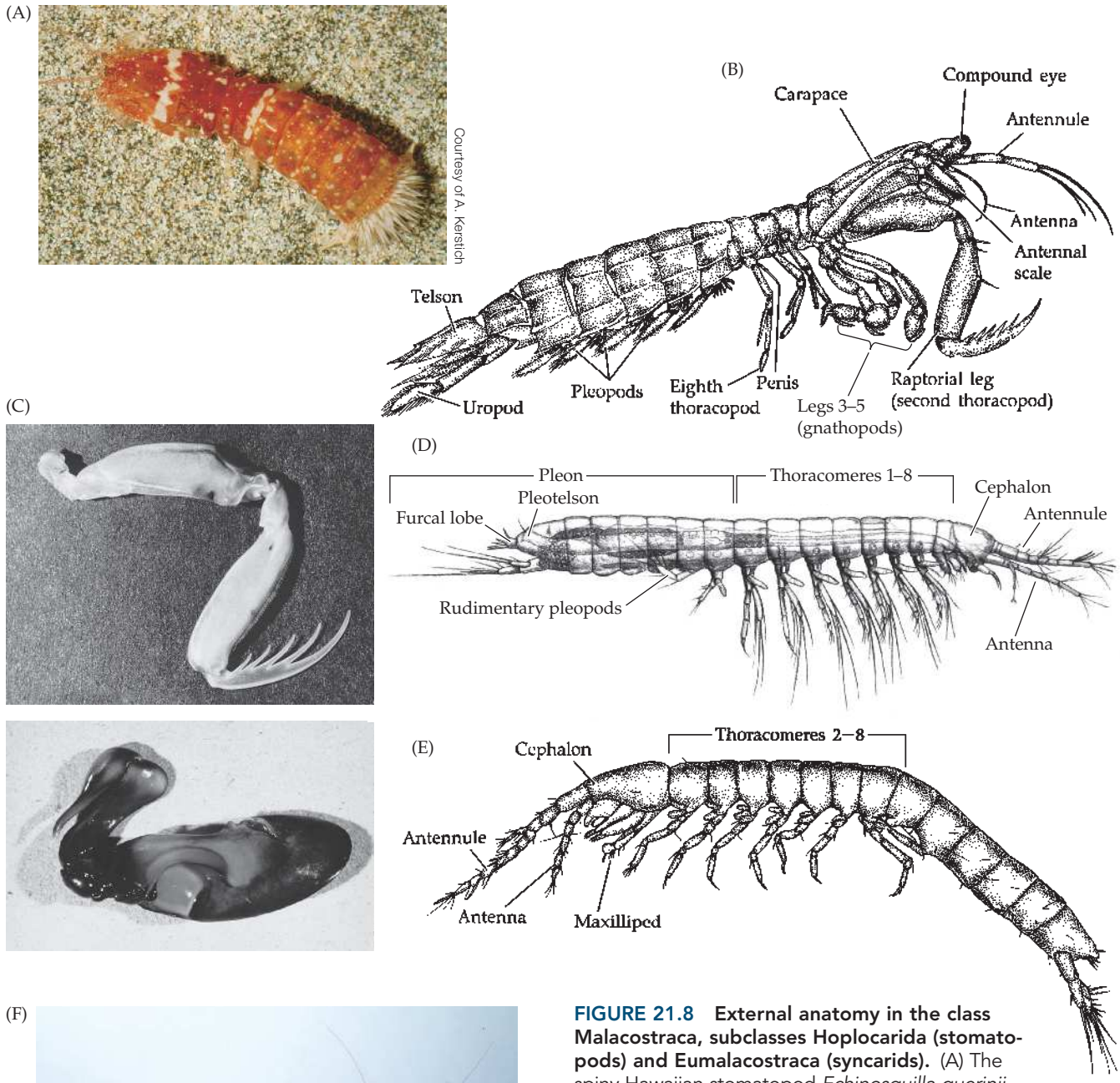

FIGURE 21.8 External anatomy in the class Malacostraca, subclasses Hoplocarida (stomatopods) and Eumalacostraca (syncarids). (A) The spiny Hawaiian stomatopod *Echinosquilla guerinii*. (B) External anatomy of the stomatopod *Squilla*. (C) "Spearing" claw and "clubbing" claw (second thoracopod) of stomatopods. (D) A bathynellacean, *Bathynella*. (E) An anaspidacean, *Stygocarella*. (F) An anaspidacean, *Paranaspides lacustris*.

Superorder Syncarida Without maxillipeds (Bathynellacea) or with 1 pair of maxillipeds (Anaspidacea, including Stygocarididae); no carapace; pleon bears telson with or without furcal lobes; at least some thoracopods biramous; pleopods variable; compound eyes present (stalked or sessile) or absent (Figure 21.8D–F). There are about 285 described species of syncarids in 2 orders, Anaspidacea and Bathynellacea. Syncarids might be an ancient relictual taxon now restricted to refugial habitats. Through studies of the fossil record and extant members of the order Anaspidacea (e.g., *Anaspides*), it has been suggested that syncarids may

encompass the most primitive living eumalacostracan body plan. Bathynellaceans occur worldwide in interstitial or groundwater habitats, whereas the anaspidaceans are strictly Gondwanan in distribution. Many Anaspidacea are endemic to Tasmania, where they inhabit freshwater environments, such as open lake surfaces, streams, ponds, and crayfish burrows. No syncarids are marine. These reclusive eumalacostracans show various degrees of characteristics of what some have regarded as paedomorphism, including small size (Anaspidacea includes members to 5 cm, whereas most others are less than 1 cm long), eyelessness, and reduction or loss of pleopods and some posterior pereopods. Bathynellaceans are small (1–3 mm long), possess 6 or 7 pairs of long, thin swimming legs, and have a pleotelson formed by the fusion of the telson to the last pleonite.

Syncarids either crawl or swim. Little is known about the biology of most species, although some are considered omnivorous. Unlike most other crustaceans, which carry the eggs and developing early embryos, syncarids lay their eggs or shed them into the water following copulation.

Superorder Eucarida Telson without caudal rami; 0, 1, or 3 pairs of maxillipeds; carapace present, covering and fused dorsally with head and entire thorax; usually with stalked compound eyes; gills thoracic. Although members of this group are highly diverse, they are united by the presence of a complete carapace that is fused with all thoracic segments, forming a characteristic cephalothorax. Most species (several thousand) belong to the order Decapoda. The other order is Euphausiacea (krill). The formerly monotypic order Amphionidacea (*Amphionides reynaudii*) has been shown to be a larval caridean decapod.

Order Euphausiacea Euphausiaceans (**krill**) are distinguished among the eucarids by their shrimplike appearance, absence of maxillipeds, exposure of the thoracic gills external to the carapace, and possession of biramous pereopods (the last 1 or 2 pairs sometimes being reduced). Adults have antennal glands. Most of them have photophores on the eyestalks, the bases of the second and seventh thoracopods, and between the first 4 pairs of abdominal limbs.

The 86 known species of euphausiaceans are all pelagic, range in length from 4 to 15 cm, and are known from all oceanic environments to depths of 5,000 m. Most species are distinctly gregarious, and species that occur in huge schools provide a major source of food for larger nektonic animals (baleen whales, squids, fishes) and even some marine birds. Northern krill has been a significant fishery in Japan and Canada, but the largest commercial stock is from the Southern Ocean, where the annual catch can exceed a half-million tons. Krill densities, particularly for *Euphausia superba*, often exceed 1,000 animals/m^3 (614 g wet weight/m^3).[5] The high concentrations of omega-3 fatty acids in krill make them popular for use in dietary supplements. Generally, euphausiaceans are suspension feeders, although predation and detritivory also occur (Figures 21.9A,B and 21.21E).

Order Decapoda With over 15,000 named species, the decapods are among the most familiar eumalacostracans. They possess a well-developed carapace enclosing a branchial chamber, but they differ from other eucarid orders in always possessing 3 pairs of maxillipeds, leaving 5 pairs of functional uniramous or weakly biramous pereopods (hence the name Decapoda); 1 or more pairs of anterior pereopods are usually clawed (chelate). Adults have antennal glands. In vernacular terms, nearly every decapod may be recognized as some sort of shrimp, crab, lobster, or crayfish.

We do not want to belabor the issue of decapod gill nomenclature. However, the gills play a prominent role in the taxonomy of this group; thus, we provide brief descriptions of the basic types. All decapod gills arise as thoracic coxal exites (epipods), but their final placement varies. Those that remain attached to the coxae are **podobranchs** (= "foot gills"), but others eventually become associated with the articular membrane between the coxae and body and are thus called **arthrobranchs** (= "joint gills"). Some actually end up on the lateral body wall, or side-surface of the thorax, as **pleurobranchs** (= "side gills"). The sequence by which some of these gills arise ontogenetically varies. For example, in the Dendrobranchiata and the Stenopodidea, arthrobranchs appear before pleurobranchs, whereas in members of the Caridea the reverse is true. In most of the other decapods the arthrobranchs and pleurobranchs tend to appear simultaneously. These developmental differences may be minor heterochronic dissimilarities and of less phylogenetic importance than actual gill anatomy.

Among the decapods, the gills can also be one of three basic structural types, described as dendrobranchiate, trichobranchiate, and phyllobranchiate (Figure 21.28B–D). All three of these gill types include a main axis carrying afferent and efferent blood vessels, but they differ markedly in the nature of the side filaments

[5]Where krill densities exceed about 100 g/m^3, they are often fished commercially. Krill schools can extend for tens of miles, contain millions of tons of krill, and stain the ocean red with their surface swarms in coastal waters. Large baleen whales can eat a ton of krill in one mouthful. Seals, fish, squid, and humans also eat krill. Krill fishing has been banned in most of North America, but it continues in Japan, where tens of thousands of tons are landed annually and used mainly as feed for farmed fish. The largest krill fishery is in the ocean surrounding Antarctica, where they have been harvested commercially since the 1970s. In the 1980s, large fleets from the Soviet Union caught up to 400,000 tons of Antarctic krill annually, but by 2015 the annual catch was down to 120,000 tons (taken by Argentina, Chile, Japan, Korea, Norway, Poland, the Ukraine, and the United States).

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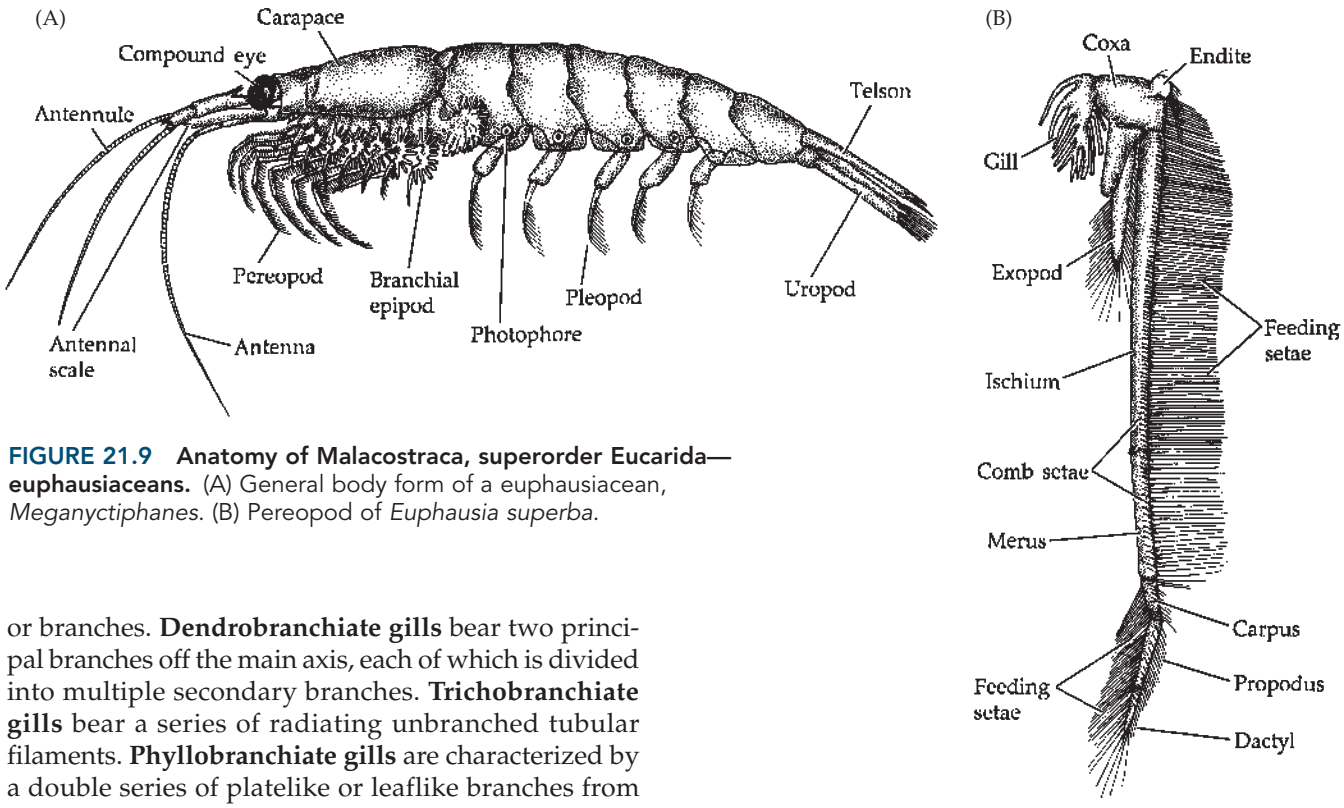

FIGURE 21.9 Anatomy of Malacostraca, superorder Eucarida—euphausiaceans. (A) General body form of a euphausiacean, *Meganyctiphanes*. (B) Pereopod of *Euphausia superba*.

or branches. **Dendrobranchiate gills** bear two principal branches off the main axis, each of which is divided into multiple secondary branches. **Trichobranchiate gills** bear a series of radiating unbranched tubular filaments. **Phyllobranchiate gills** are characterized by a double series of platelike or leaflike branches from the axis. Within each gill type, there may be considerable variation. The occurrences of these three major gill types among various taxa are presented below.

Close inspection of the proximal parts of the pereopods usually reveals another decapod feature: in most forms, the basis and ischium are fused (as a basi-ischium), with the point of fusion often indicated by a suture line (see Figure 21.21E-I). Tegumental glands are also a ubiquitous feature among the Decapoda. These glands originate below the epidermal cells and produce a fluid that opens on the surface of the cuticle. They have been reported from gills, legs, pleopods, and uropods. The roles of tegmental glands are not well known, and they have been suspected to be involved in cuticular tanning, the production of mucus by the mouthparts, the production of cement substance involved with egg attachment, and possibly also grooming.

Decapods occur in all aquatic environments at all depths, and a few spend most of their lives on land. Many are pelagic, but others have adopted benthic sedentary, errant, or burrowing lifestyles. Decorating of the exoskeleton is frequently seen among the decapods, especially in spider crabs (Brachyura: Majoidea), which use Velcro-like hooked setae to attach dead or living seaweeds and animals; decorating has been shown to reduce predation through camouflage and/or chemical deterrence. Decapod feeding strategies include suspension feeding, predation, herbivory, scavenging, and more. Two suborders are recognized: Dendrobranchiata and Pleocyemata. Recent phylogenetic research supports the monophyly of the suborders and infraorders.

Suborder Dendrobranchiata This group includes over 500 species of decapods, most of which are penaeid (Penaeoidea) and sergestid (Sergestoidea) shrimps. As the name indicates, these decapods possess dendrobranchiate gills (see Figure 21.28B), a unique synapomorphy of the taxon. One genus, *Lucifer*, has secondarily lost the gills completely. The dendrobranchiate shrimps are further characterized by chelae on the first 3 pereopods, copulatory organs modified from the first pair of pleopods in males, and ventral expansions of the abdominal tergites (called pleural lobes). Generally, none of the chelipeds is greatly enlarged. In addition, females of this group do not brood their eggs. Fertilization is external, and the embryos hatch as nauplius larvae. Many of these animals are quite large, over 30 cm long. The sergestids are pelagic and all marine, whereas the penaeids are pelagic or benthic, and some occur in brackish water. Some dendrobranchiates (e.g., *Penaeus, Sergestes, Acetes, Sicyonia*) are of major commercial importance in the world's shrimp fisheries, most of which are now being exploited beyond sustainable levels and often with fishing techniques that are highly habitat destructive (Figures 21.10A and 21.33G).

Suborder Pleocyemata All of the remaining decapods belong to the suborder Pleocyemata, divided among 10 infraorders (see below). Members of this taxon never possess dendrobranchiate gills. The embryos are brooded on the female's pleopods and hatch at some stage later than the nauplius larva.

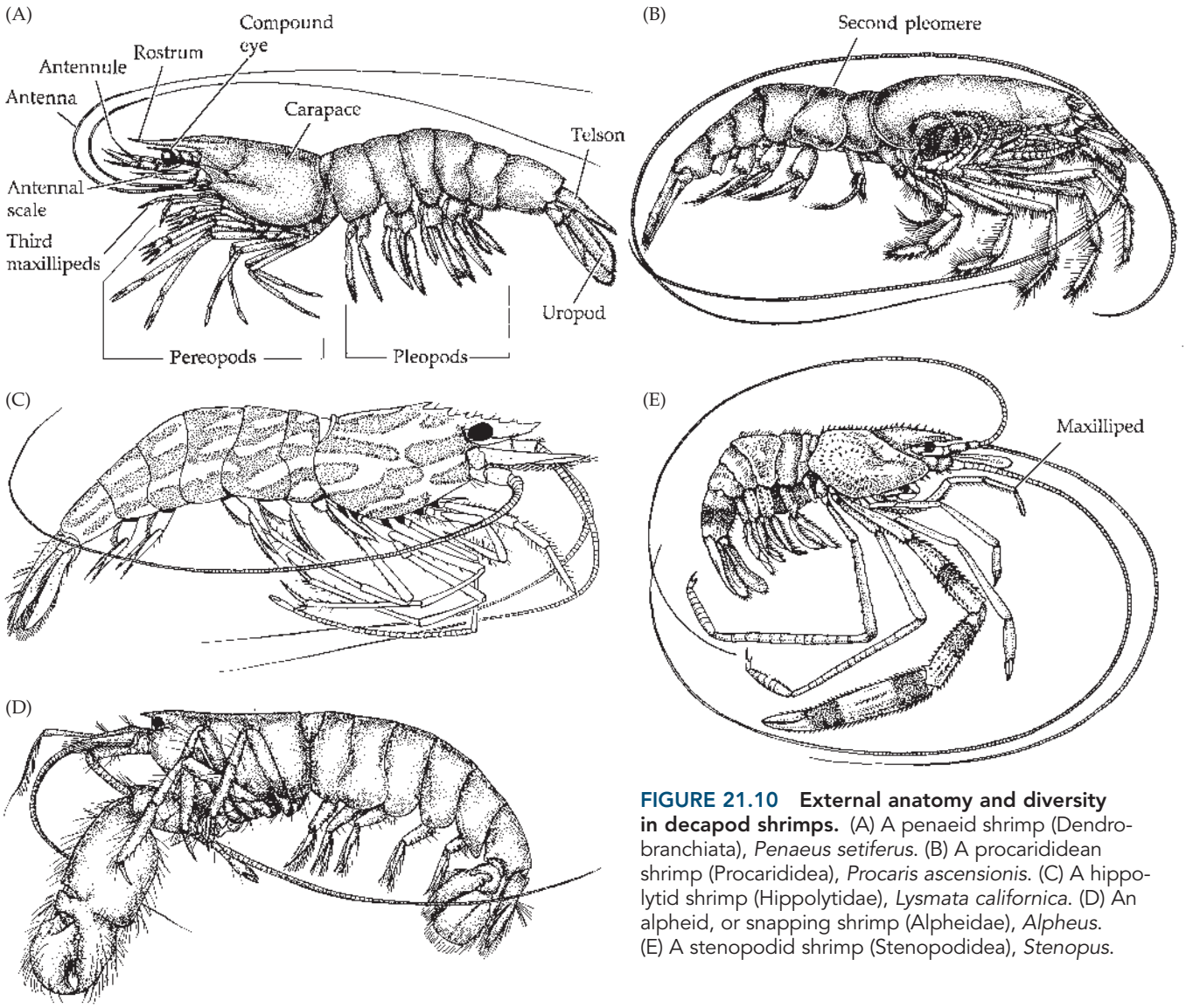

FIGURE 21.10 External anatomy and diversity in decapod shrimps. (A) A penaeid shrimp (Dendrobranchiata), *Penaeus setiferus*. (B) A procaridid shrimp (Procaridida), *Procaris ascensionis*. (C) A hippolytid shrimp (Hippolytidae), *Lysmata californica*. (D) An alpheid, or snapping shrimp (Alpheidae), *Alpheus*. (E) A stenopodid shrimp (Stenopodidea), *Stenopus*.

Included in this suborder are several kinds of shrimps, the crabs, crayfish, lobsters, and a host of less familiar forms. De Grave et al. (2009) divide the Pleocyemata into 10 infraorders (below). One older approach divided decapods into 2 large groups, called the Natantia and Reptantia—the swimming and walking decapods, respectively. Although these terms have largely been abandoned as formal taxa, recent molecular phylogenetic work finds support for a monophyletic Reptantia (pleocyemates with dorsoventrally flattened pleons). In any case, the terms still serve a useful descriptive purpose, and one continues to see references to natant decapods and reptant decapods.

Infraorder Caridea Caridean and procaridid shrimps; about 3,270 species (e.g., *Alpheus*, *Ambidexter*, *Atya*, *Betaeus*, *Crangon*, *Hippolyte*, *Hymenocera*, *Hymenodora*, *Leander*, *Lysmata*, *Macrobrachium*, *Ogyrides*, *Palaemon*, *Pandalus*, *Pasiphaea*, *Periclimenes*, *Procaris*, *Processa*, *Syncaris*, *Thor*, *Typton*, *Typhlocaris*, *Vetericaris*). Swimming decapods with phyllobranchiate gills. The first 1 or 2 pairs of pereopods may be chelate and variably enlarged. The second abdominal pleurae (side walls) are distinctly enlarged to overlap both the first and third pleurae (Figures 21.1K, 21.10C,D, 21.24E, and 21.31D). *Procaris* and *Vetericaris* are known from anchialine habitats—inland pools with brackish water on top and seawater below, with connections to the ocean (Figure 21.10B).

Infraorder Stenopodidea Stenopodidean shrimps; about 70 species (e.g., *Odontozona*, *Spongicola*, *Stenopus*). The first 3 pairs of pereopods are chelate, and the third pair is significantly larger than the others. The gills are trichobranchiate. The second abdominal pleurae are not expanded as they are in carideans (Figures 21.10E and 21.31B).

These colorful shrimps are usually only a few centimeters long (2–7 cm). Most species are tropical and

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associated with shallow benthic environments, especially with coral reefs; some are known from the deep sea. Many are commensal, and the group includes the cleaner shrimps (e.g., *Stenopus*) of tropical reefs, which are known to remove parasites from fishes. Stenopodids often occur as male-female couples. Perhaps the most noted example of this bonding is associated with the glass sponge (*Euplectella*) shrimp, *Spongicola venusta*: a young male and female shrimp enter the atrium of a host sponge, eventually growing too large to escape and thus spending the rest of their days together.

Infraorder Brachyura The so-called "true crabs" (about 7,000 species). Abdomen symmetrical but highly reduced and flexed beneath the thorax. Body hidden beneath well-developed carapace and distinctly flattened dorsoventrally. Gills typically phyllobranchiate, but exceptions occur. First pereopods chelate, usually enlarged and larger in males (usually used in contesting mating rights with other males). Pereopods 2 to 5 typically simple stenopodous walking legs. Eyes positioned lateral to the antennae. Males lack pleopods 3 to 5. Always gonochoristic. The distinctive larval stage is called a zoea; its carapace is spherical and bears a ventrally directed rostral spine (or no spine). Common brachyuran genera include *Calappa*, *Callinectes*, *Cancer*, *Cardisoma*, *Dromia*, *Ebalia*, *Epialtus*, *Eriphia*, *Fabia*, *Gecarcinus*, *Geryon*, *Goneplax*, *Grapsus*, *Hepatus*, *Herbstia*, *Libinia*, *Loxorhynchus*, *Maja*, *Menippe*, *Microphrys*, *Ocypode*, *Ozius*, *Panopeus*, *Percnon*, *Pinnixa*, *Portunus*, *Pugettia*, *Thoe*, *Trapezia*, *Uca*, and *Xanthias* (Figures 21.1E, 21.11, 21.27H, 21.28F,G, 21.29C, 21.32, and 21.33H,I).

Brachyuran crabs are mostly marine, but freshwater, semiterrestrial, and terrestrial species occur in the

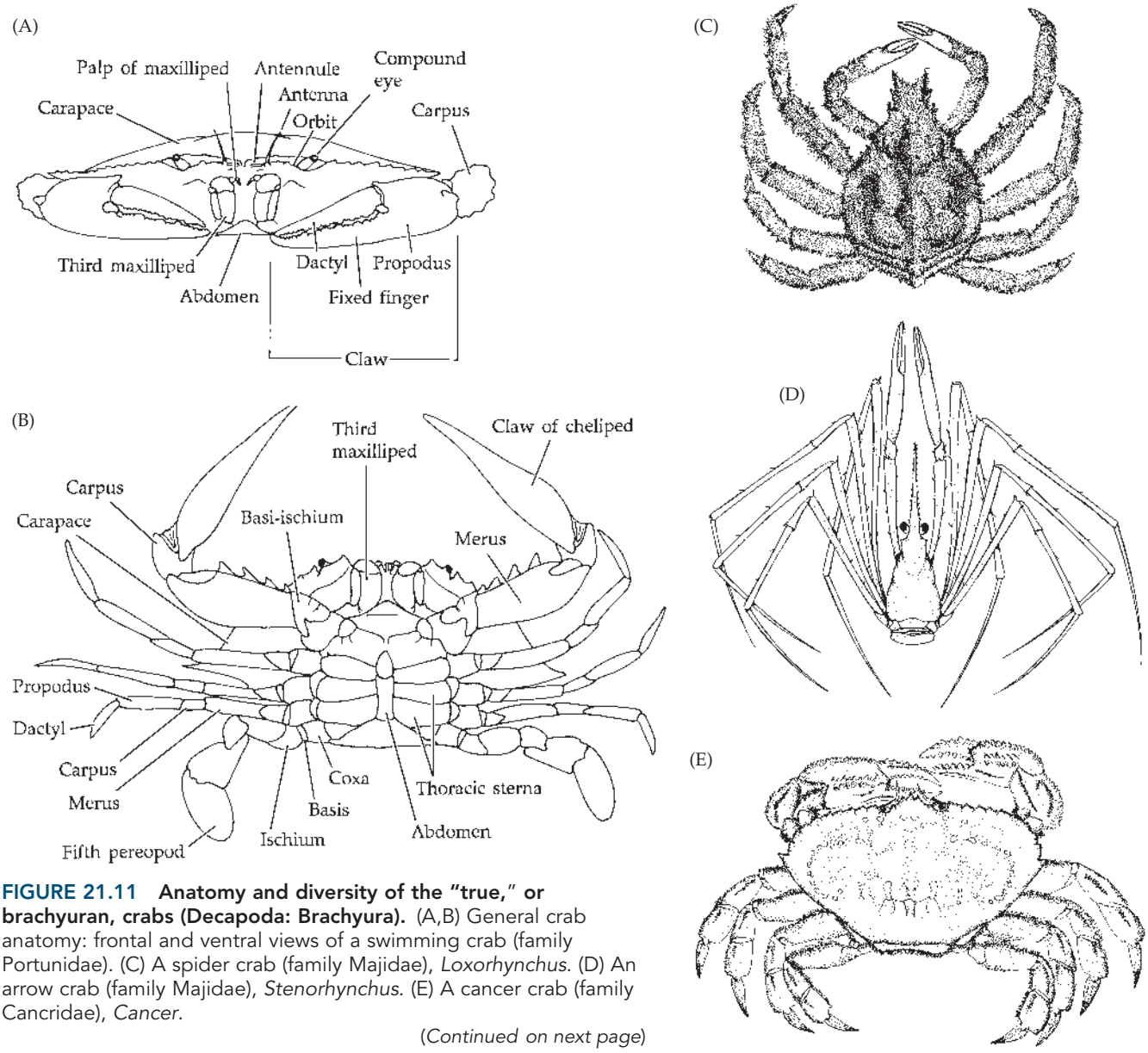

FIGURE 21.11 Anatomy and diversity of the "true," or brachyuran, crabs (Decapoda: Brachyura). (A,B) General crab anatomy: frontal and ventral views of a swimming crab (family Portunidae). (C) A spider crab (family Majidae), *Loxorhynchus*. (D) An arrow crab (family Majidae), *Stenorhynchus*. (E) A cancer crab (family Cancridae), *Cancer*.

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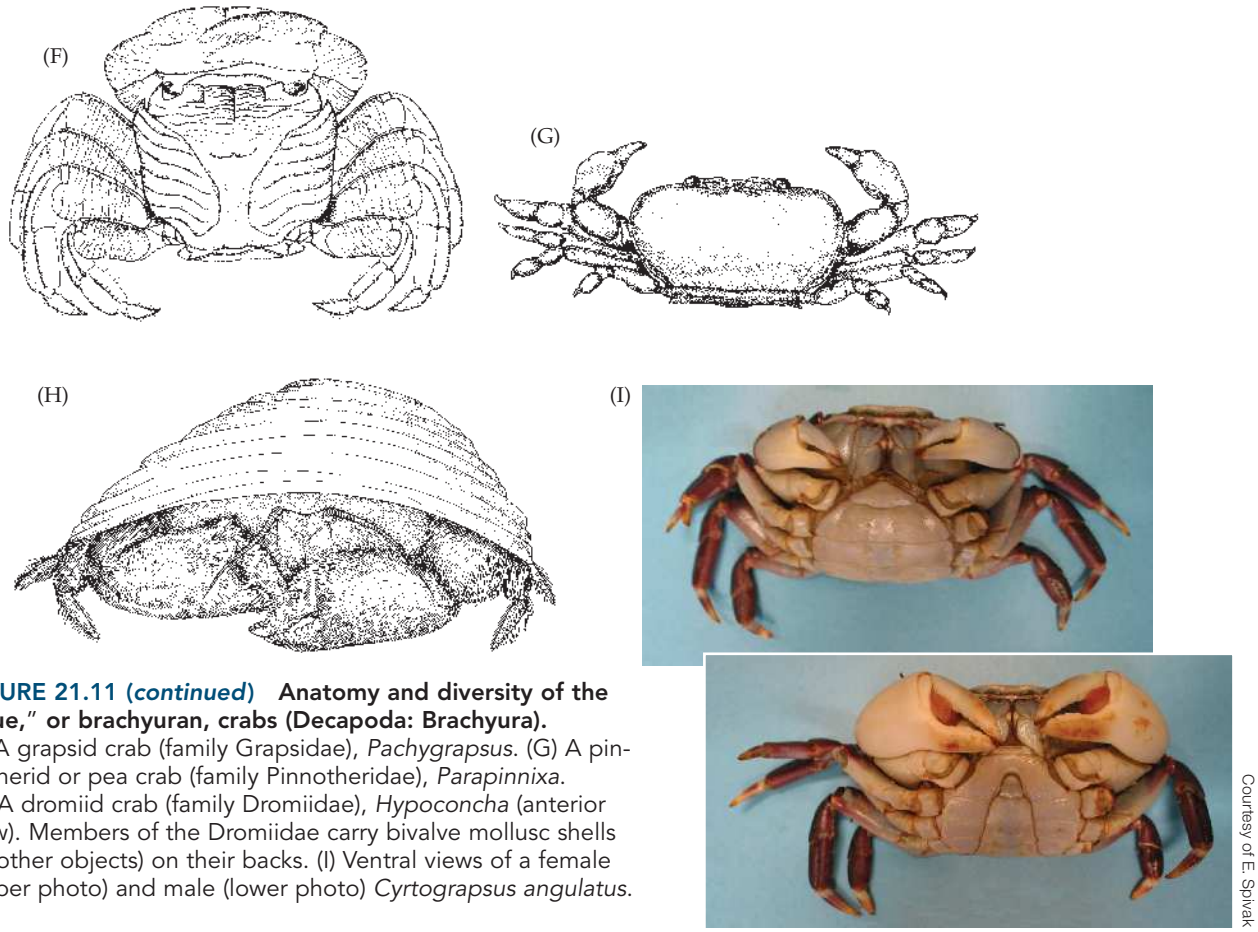

FIGURE 21.11 (*continued*) Anatomy and diversity of the "true," or brachyuran, crabs (Decapoda: Brachyura). (F) A grapsid crab (family Grapsidae), *Pachygrapsus*. (G) A pinnotherid or pea crab (family Pinnotheridae), *Parapinnixa*. (H) A dromiid crab (family Dromiidae), *Hypoconcha* (anterior view). Members of the Dromiidae carry bivalve mollusc shells (or other objects) on their backs. (I) Ventral views of a female (upper photo) and male (lower photo) *Cyrtograpsus angulatus*.

tropics. The land crabs (certain species in the families Gecarcinidae, Ocypodidae, Grapsidae, etc.) are still dependent on the ocean for breeding and larval development. The surprisingly large number of freshwater crabs (about 3,000 species, classified into about a dozen families) all have direct development, incubate their embryos, and are independent of seawater. Some freshwater crabs are intermediate hosts of *Paragonimus*, a cosmotropical parasitic human lung fluke, and others are obligate phoretic hosts of larval black flies (*Simulium*), the vector for *Onchocerca volvulus* (the causative agent of river blindness). A number of crab species carry other invertebrates on their carapace (e.g., sponges, tunicates) or on their claws (e.g., anemones); these associations are generally thought to be mutualistic, providing camouflage or predator deterrence for the crab while their partner is moved about in the environment and may feed off debris from their host's feeding activities. In the northeast Pacific, megalopae and juveniles of the crab *Metacarcinus gracilis* ride (and feed) on the bell of certain jellyfish; individuals of *Phacellophora camtschatica* (Scyphozoa) have been found with hundreds of *M. gracilis* megalopae. Evidence suggests Brachyura and Anomura are sister groups (a clade known as Meiura).

Infraorder Anomura This group includes about 2,500 species of hermit crabs, galatheid crabs, king crabs, porcelain crabs, mole crabs, and sand crabs. The abdomen may be soft and asymmetrically twisted (as in hermit crabs) or symmetrical, short, and flexed beneath the thorax (as in porcelain crabs and others). Those with twisted abdomens typically inhabit gastropod shells or other empty "houses" not of their own making. Carapace shape and gill structure vary among the Anomura. The first pereopods are chelate; the third pereopods are never chelate. The second, fourth, and fifth pairs are usually simple, but occasionally they are chelate or subchelate. The fifth pereopods (and sometimes the fourth) are generally much reduced and do not function as walking limbs; the fifth pereopods function as gill cleaners and often are not visible externally. The pleopods are reduced or absent. The eyes are positioned medial to the antennae. The zoea larva is similar to that of the true crabs but is typically longer than broad, with the rostral spine directed anteriorly. Most anomurans are marine, but a few freshwater and semiterrestrial species are known. The so-called "yeti crab" (*Kiwa hirsuta*) was discovered in 2005 at a depth of 2,200 m in hydrothermal vents south of Easter Island. It is remarkable for its "garden" of filamentous bacteria that grow on the long setae of the exoskeleton; the bacteria are heterotrophic, utilizing sulfides in the deep environment (the precise role of the bacteria, of several species, in the life history of the yeti crab is not yet well understood).

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Several additional *Kiwa* species have been described since 2011. Common anomuran genera include *Aegla*, *Birgus*, *Blepharipoda*, *Calcinus*, *Clibanarius*, *Coenobita*, *Dardanus*, *Diogenes*, *Emerita*, *Hapalogaster*, *Hippa*, *Kiwa*, *Lepidopa*, *Lithodes*, *Lomis*, *Pagurus*, *Petrocheles*, *Petrochirus*, and *Pleuroncodes* (Figures 21.1F–J, 21.12C–G, 21.24A–C, 21.31A, and 21.33I).

Infraorder Astacidea Freshwater crayfish and clawed lobsters; 685 species (e.g., *Astacus*, *Cambarus*, *Cherax*, *Faxonella*, *Homarus*, *Nephrops*, *Pacifastacus*). As in most other decapods, the dorsoventrally flattened abdomen terminates in a strong tail fan (Figure 21.2). The gills are trichobranchiate. The first 3 pairs of pereopods are always chelate, and the first pair is greatly enlarged. *Homarus americanus*, the American or Maine lobster, is strictly marine and is the largest living crustacean by weight (the record weight being over 20 kg). Most crayfish live in fresh water, but a few species live in damp soil, where they may excavate extensive and complex burrow systems. The 670+ species of freshwater crayfish (in 5 families) comprise a monophyletic group that is sister group to clawed lobsters, the crayfish originating around 330 million years ago. Over 425 species of

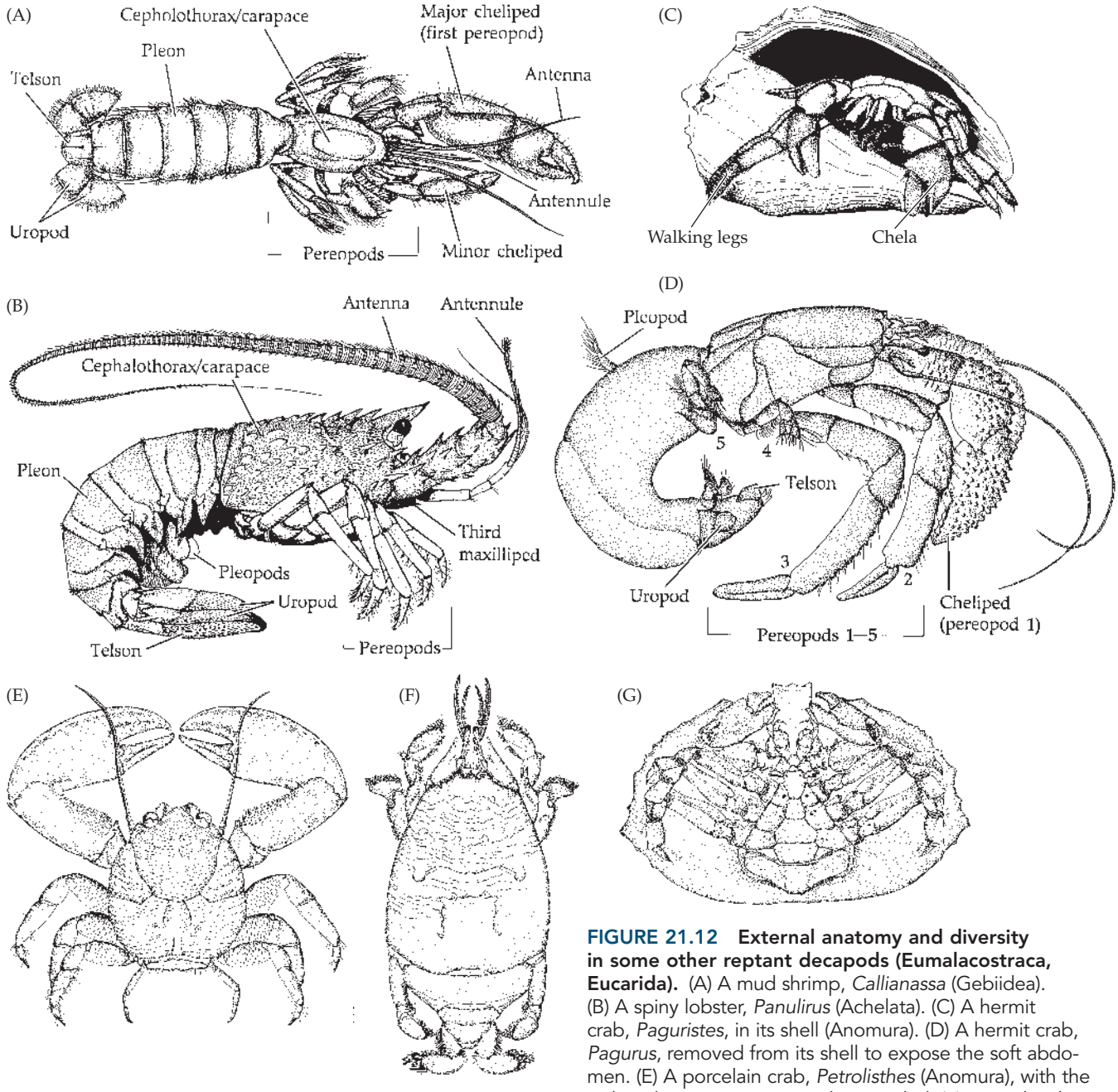

FIGURE 21.12 External anatomy and diversity in some other reptant decapods (Eumalacostraca, Eucarida). (A) A mud shrimp, *Callianassa* (Gebiidea). (B) A spiny lobster, *Panulirus* (Achelata). (C) A hermit crab, *Paguristes*, in its shell (Anomura). (D) A hermit crab, *Pagurus*, removed from its shell to expose the soft abdomen. (E) A porcelain crab, *Petrolisthes* (Anomura), with the reduced posterior pereopods extended. (F) A sand crab, *Emerita* (Anomura). (G) The umbrella crab *Cryptolithodes* (Anomura), in ventral view.

crayfish occur in North America alone, where they show high levels of endemicity to particular regions or river drainages (Figures 21.27E,G and 21.29B). Many of these are among the most invasive freshwater crustaceans.

Infraorder Achelata This group includes 140 species of spiny and slipper lobsters, many of economic importance (e.g., *Arctides*, *Evibacus*, *Ibacus*, *Panulirus*). The name Achelata comes from the fact that they lack chelae on all pereopods as adults (except for a small grooming claw on pereopod 5 in some females). The flattened abdomen bears a tail fan; the carapace may be cylindrical or flattened dorsoventrally; the gills are trichobranchiate. The large, flattened larvae, called phyllosomas because of their leaflike appearance, are unique and distinctive. All species are marine, and they are found in a variety of habitats throughout the tropics. Many species produce sounds by rubbing a process (the plectrum) at the base of the antennae against a "file" on the head (Figures 21.1M, 21.12B, 21.30A,C, and 21.33L).

Infraorders Axiidea and Gebiidea The lobster shrimps (Axiidea, 423 species, e.g., *Axius*, *Callianassa*, *Neotrypaea*, *Upogebia*) and mud/ghost shrimps (Gebiidea, 192 species, e.g., *Axianassa*, *Naushonia*). These 2 infraorders, formerly combined as Thalassinidea, have recently been recognized as distinct (the vernacular term "thalassinid" is still sometimes used to refer to them together) though they are very similar in appearance. The phylogenetic relationships of these shrimps remain unsettled. The symmetrical abdomen is flattened dorsoventrally and extends posteriorly as a well-developed tail fan. The carapace is somewhat compressed laterally, and the gills are trichobranchiate. The first 2 pairs of pereopods are chelate, and the first pair is generally much enlarged. Most of these animals are marine burrowers or live in coral rubble. They generally have a rather thin, lightly sclerotized cuticle, but some (e.g., members of the family Axiidae) have thicker skeletons and are more lobsterlike in appearance. Gebiideans often occur in huge colonies on tidal flats, where their burrow holes form characteristic patterns on the sediment surface (Figures 21.1L and 21.12A).

Infraorders Glypheidea and Polychelida The glypheids are something of a relict group, represented by 2 living genera (*Neoglyphea* and *Laurentaeglyphea*), each with a single species, of a formerly diverse group known from the fossil record. Polychelids are a group of about 38 blind deep-sea lobsters (e.g., *Polycheles*), notable for having chelae on all of their pereopods and unusual, large, globate larvae (called eryoneicus larvae) unique among the decapods.

Superorder Peracarida Telson without caudal rami; 1 pair (rarely 2–3) of maxillipeds; maxilliped basis typically produced as a bladelike endite; mandibles with articulated accessory process in adults, between molar and incisor process, called the **lacinia mobilis**; carapace, when present, not fused with posterior pereonites and usually reduced in size; gills thoracic or abdominal; with unique, thinly flattened thoracic coxal endites, called oostegites, that form a ventral brood pouch or marsupium in females of all species except members of the order Thermosbaenacea (the latter using the carapace to brood embryos); young hatch as **mancas**, a prejuvenile stage lacking the last pair of thoracopods (no free-living larvae occur among the Peracarida) (Figures 21.13–21.16).

The roughly 25,000 species of peracarids are divided among ten orders. The peracarids are an extremely successful group of malacostracan crustaceans known from many habitats. Although most are marine, many also occur on land and in fresh water, and several species live in hot springs at temperatures of 30°C–50°C. Aquatic forms include planktonic as well as benthic species at all depths. The group includes the most successful terrestrial crustaceans—the pillbugs and sowbugs of the order Isopoda—and a few amphipods that have invaded land and live in damp forest leaf litter or gardens. Peracarids range in size from tiny interstitial forms only a few millimeters long to planktonic amphipods over 12 cm long (*Cystisoma*), deep-sea necrophagous amphipods exceeding 34 cm (*Alicella gigantea*), and benthic isopods growing to 50 cm in length (*Bathynomus giganteus*; Cirolanidae). These animals exhibit all sorts of feeding strategies; a number of them, especially isopods and amphipods, are commensals or parasites.

Order Mysida Carapace well developed, covering most of thorax, but never fused with more than 4 anterior thoracic segments; maxillipeds (1–2 pairs) not associated with cephalic appendages; thoracomere 1 separated from head by internal skeletal bar; abdomen with well-developed tail fan; pereopods biramous, except last pair, which are sometimes reduced; pleopods reduced or, in males, modified; compound eyes stalked, sometimes reduced; gills absent; usually with a statocyst in each uropodal endopod; adults with antennal glands (Figures 21.13A,B, 21.30B, and 21.33C).

There are more than 1,050 species of mysidans, ranging in length from about 2 mm to 8 cm, in two families: Mysidae and Petalophthalmidae. Most swim by action of the thoracic exopods. These are shrimplike crustaceans that are often confused with the superficially similar euphausiaceans (which lack oostegites and uropodal statocysts). Mysidans are pelagic or demersal and are known from all ocean depths; a few species occur in fresh water. Some species are intertidal and burrow into the sand during low tides. Most are omnivorous suspension feeders, eating algae, zooplankton, and suspended detritus. In the past, mysidans were combined with lophogastridans, stygiomysidans, and the extinct Pygocephalomorpha as the "Mysidacea." Phylogenetic studies show these groups to be very closely related to one another.

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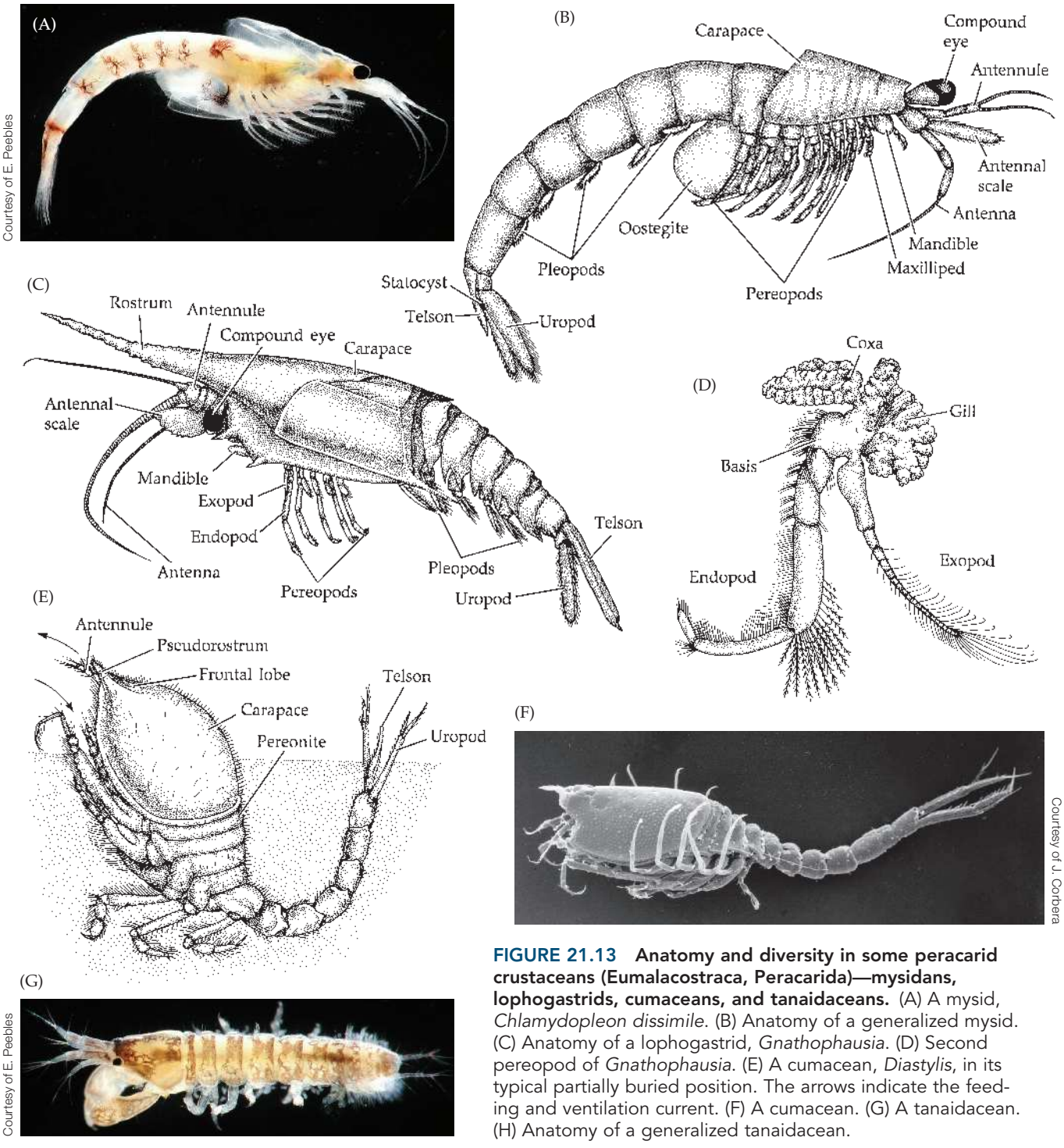

FIGURE 21.13 Anatomy and diversity in some peracarid crustaceans (Eumalacostraca, Peracarida)—mysidans, lophogastrids, cumaceans, and tanaidaceans. (A) A mysid, *Chlamydopleon dissimile*. (B) Anatomy of a generalized mysid. (C) Anatomy of a lophogastrid, *Gnathophausia*. (D) Second pereopod of *Gnathophausia*. (E) A cumacean, *Diastylis*, in its typical partially buried position. The arrows indicate the feeding and ventilation current. (F) A cumacean. (G) A tanaidacean. (H) Anatomy of a generalized tanaidacean.

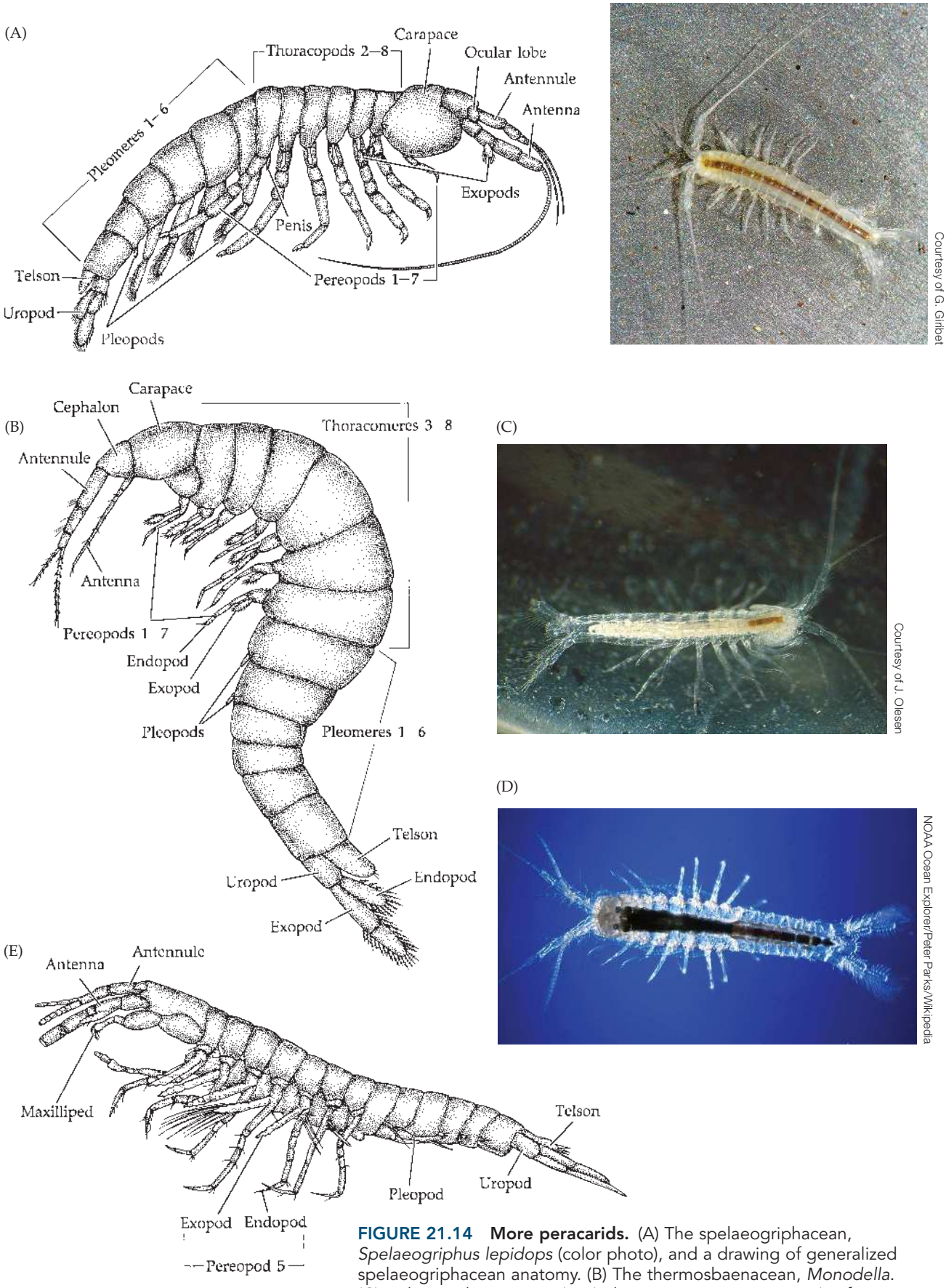

FIGURE 21.14 More peracarids. (A) The spelaeogriphacean, *Spelaeogriphus lepidops* (color photo), and a drawing of generalized spelaeogriphacean anatomy. (B) The thermosbaenacean, *Monodella*. (C) A thermosbaenacean. (D,E) The mictacean, *Mictocaris*. (E after T. E. Bowman and T. M. Iliffe. 1985. *J Crust Biol* 5: 58–73.)

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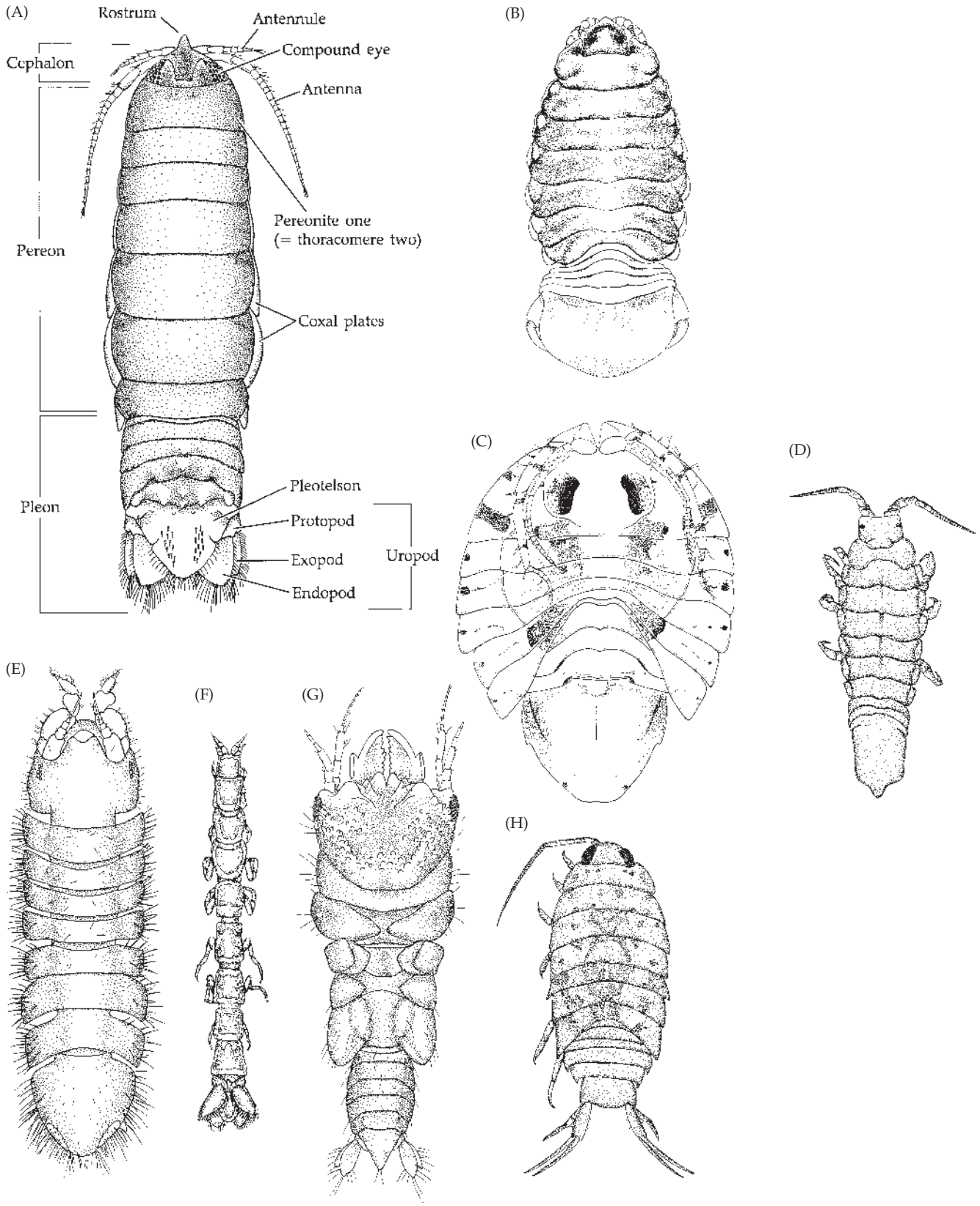
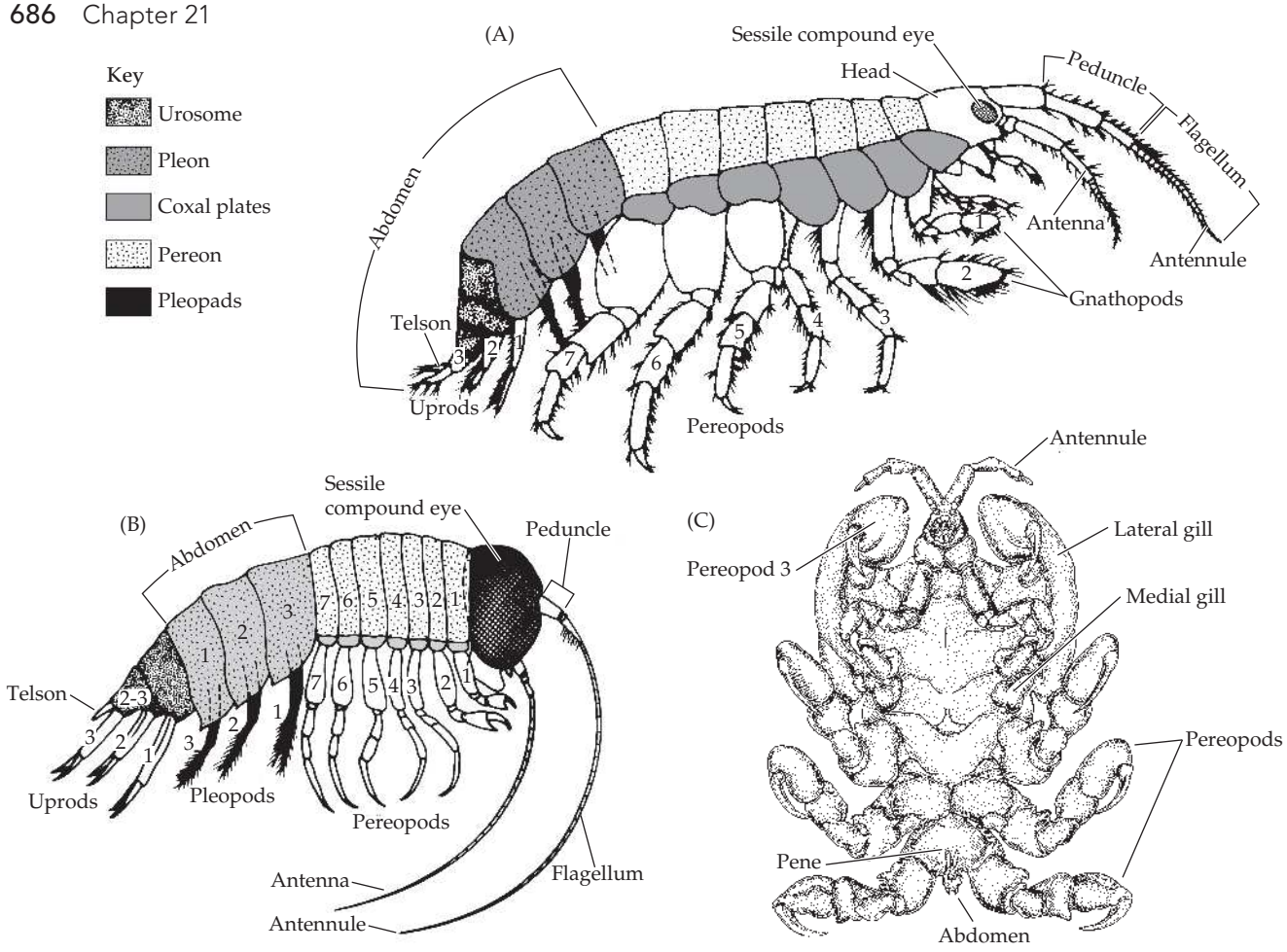


FIGURE 21.15 More peracarids: the order Isopoda. (A) *Excorallana* (Cymothooidea: Corallanidae). (B) A flabelliferan, *Codonophilus* (family Cymothoidae). Members of this genus are parasites that attach to the tongues of various marine fishes. (C) A flabelliferan, *Heteroserolis* (family Serolidae). (D) A valviferan, *Idotea* (family Idoteidae). (E) An asellote, *Joeropsis* (family Joeropsididae). (F) An anthurid, *Mesanthura* (family Anthuridae). (G) A gnathiidean, *Gnathia* (family Gnathiidae). Note the grossly enlarged mandibles characteristic of male Gnathiidae. (H) An oniscidean, *Ligia* (the common seashore "rock louse").



Courtesy of E. Peebles

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FIGURE 21.16 And still more peracarids: amphipods and ingolfiellidans. (A) General anatomy of an amphipod. (B) General anatomy of a hyperiidean amphipod. (C) General anatomy of a cyamid amphipod (*Cyamus monodontis*). (D) A senticaudatan amphipod, *Melita*. (E) A caprellid amphipod. (F) A cyamid amphipod, *Cyamus erraticus*, parasitic on right whales. (G,H) Two senticaudatan amphipods: (G) *Hyale*, a beach hopper, and (H) *Heterophlias*, an unusual, dorsoventrally flattened species. (I–K) Three hyperiidean amphipods: (I) *Primno*, (J) *Leptocottis*, and (K) a hyperiid on its host medusa. (L) A free-living caprellid, *Caprella*. (M) The ingolfiellidan *Ingolfiella*.

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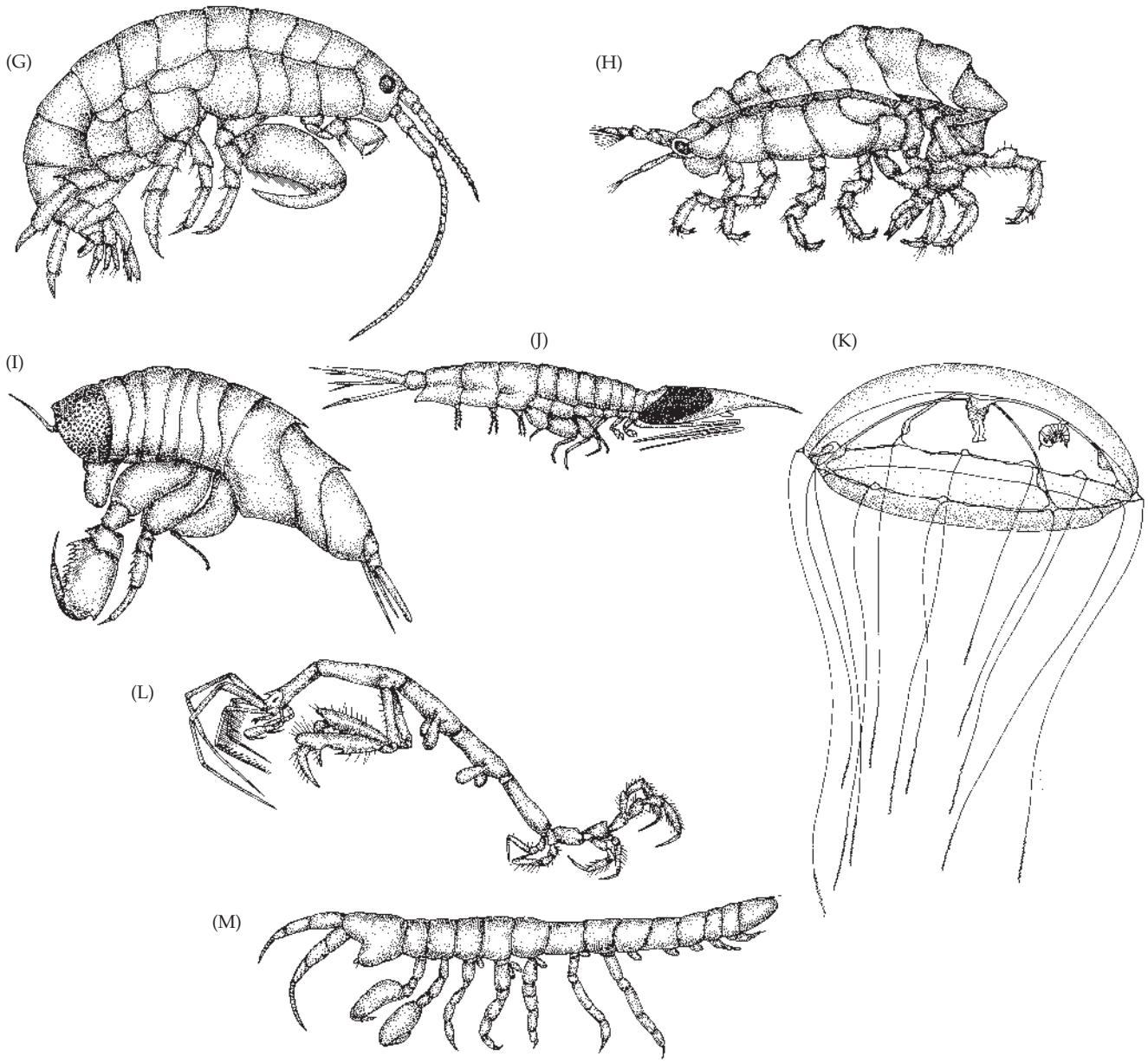

Order Stygiomysida Similar to mysidans. With biramous male and female pleopods, reduced to 1-segmented endopods and 3-segmented exopods; elongated uropod protopodites; uropods lacking statocysts; lack of podobranchs; thoracopods 2–4 modified as gnathopods; marsupium formed of 4 pairs of oostegites arising from thoracopods 3–6. Found primarily in subterranean waters with a marine influence, including anchialine caves, land crab burrows, and shrimp culture fields. Endemic species are known from anchialine caves in Caribbean Sea and Italy. Two families, fewer than 20 described species.

Order Lophogastrida Similar to mysidans, except for the following: maxillipeds (1 pair) associated with the cephalic appendages; thoracomere 1 not separated from head by internal skeletal bar; pleopods well developed; gills present; adults with both antennal and maxillary glands; without uropodal statocysts; all 7 pairs of pereopods well developed and similar (except among members of the family Eucopiidae, in which their structure varies) (Figures 21.13C,D and 21.21G).

There are three families and about 55 known species of lophogastridans, most of which are 1–8 cm long, although the giant *Neognathophausia ingens* reaches 35 cm. All are pelagic swimmers, and the group has a cosmopolitan oceanic distribution. Lophogastridans are primarily predators on zooplankton.

Order Cumacea Carapace present, covering and fused to first 3 thoracic segments, whose appendages are modified as maxillipeds, the first with modified branchial apparatus associated with branchial cavity formed by carapace; pereopods 1–5 ambulatory and simple, 1–4 may be biramous; pleopods usually absent

in females and present in males; telson sometimes fused with sixth pleonite, forming pleotelson; uropods styliform; compound eyes absent, or sessile and usually fused (Figures 21.1P and 21.13E,F).

Cumaceans are small, odd-looking crustaceans with a large, bulbous anterior end and a long, slender posterior—resembling a horizontal comma! The great carcinologist Waldo Schmitt referred to them as "little wonders and queer blunders." They occur worldwide and include about 1,500 species, most of which are between 0.1 and 2 cm long, though some species in cold waters reach 3 cm in length. Most are marine, although a few brackish-water species are known. They live in association with bottom sediments but are capable of swimming and probably leave the bottom to breed. Most are deposit feeders or predators on the meiofauna; others eat the organic film on sand grains. The oldest known fossil cumacean, *Eobodotria muisca*, is from an exquisite, mid-Cretaceous (90–95 Ma), sedimentary deposit in tropical Colombia, and it has modern familial affinities.

Order Tanaidacea Carapace present and fused with first 2 thoracic segments, forming a cephalothorax; thoracopods 1–2 are maxillipeds, the second being chelate; thoracopods 3–8 are simple, ambulatory pereopods; pleopods present or absent; uropods biramous or uniramous; telson and last 1 or 2 pleonites fused as pleotelson; adults with maxillary and (vestigial) antennal glands; compound eyes absent, or present and on cephalic lobes. Members of this order are known worldwide from benthic marine habitats; a few live in brackish or nearly fresh water. Most of the 1,500 or so species are small, ranging from 0.5 to 2 cm in length. They often live in burrows or tubes and are known from all ocean depths. Many are suspension feeders, others are detritivores, and still others are predators (Figure 21.13G,H).

Order Mictacea Without a carapace, but with a well-developed head shield fused with first thoracomere and produced laterally over bases of mouthparts; 1 pair of maxillipeds; pereopods simple, 1–5 or 2–6 biramous, exopods natatory; gills absent; pleopods reduced, uniramous or biramous; uropods biramous, with 2–5 segmented rami; telson not fused with pleonites; stalked eyes present (*Mictocaris*) but lacking any evidence of visual elements, or absent (*Hirsutia*) (Figure 21.14D–E).

The order was erected to accommodate two species of unusual crustaceans: *Mictocaris halope* (from marine caves in Bermuda) and *Hirsutia bathyalis* (from a benthic sample 1,000 m deep in the Guyana Basin off northeastern South America). A third species of Mictacea was described in 1988 from Australia, and a fourth from the Bahamas in 1992; there are now six species known. Mictaceans are small, 2–3.5 mm in length. *Mictocaris halope* is the best known of these species because many specimens have been recovered and some have been studied alive. It is pelagic in cave waters and swims by using its pereopodal exopods. Some workers recognize the family Hirsutiidae (containing *Hirsutia*, *Montucaris,* and *Thetispelecaris*) as a separate order, the Bochusacea (male pleopods biramous).

Order Spelaeogriphacea Carapace short, fused with first thoracomere; 1 pair of maxillipeds; pereopods 1–7 simple, biramous, with shortened exopods; exopods on legs 1–3 modified for producing currents, on legs 4–7 as gills; pleopods 1–4 biramous, natatory; pleopod 5 reduced; tail fan well developed; compound eyes nonfunctional or absent, but eyestalks persist (Figures 21.14A and 21.21H). The order Spelaeogriphacea is currently known from only four living species. These rare, small (less than 1 cm) peracarids were long known only from a single species living in a freshwater stream in Bat Cave on Table Mountain, South Africa (*Spelaeogriphus lepidops*; Figure 21.14A). A second species is known from a freshwater cave in Brazil, and a third and fourth species were described from an aquifer in Australia. Little is known about the biology of these animals, but they are suspected to be detritus feeders. Like thermosbaenaceans, spelaeogriphaceans are thought to be relicts of a more widespread shallow-water marine Tethyan fauna stranded in interstitial and ground-water environments during periods of marine regression.

Order Thermosbaenacea Carapace present, fused with first thoracomere and extending back over 2–3 additional segments; 1 pair of maxillipeds; pereopods biramous, simple, lacking epipods and oostegites; carapace forms dorsal brood pouch (unlike all other peracarids, which form the brood pouch from ventral oostegites); 2 pairs of uniramous pleopods; uropods biramous; telson free or forming pleotelson with last pleonite; eyes absent (Figure 21.14B,C). About 35 species of thermosbaenaceans are recognized in 7 genera. *Thermosbaena mirabilis* is known from freshwater hot springs in North Africa, where it lives at temperatures in excess of 40°C. Several species in other genera occur in much cooler fresh waters, typically in groundwater or in caves. Other species are marine or inhabit underground anchialine pools. Limited data suggest that thermosbaenaceans feed on plant detritus.

Order Isopoda Carapace absent; first thoracomere fused with head; 1 pair of maxillipeds; 7 pairs of uniramous pereopods, the first of which is sometimes subchelate, others usually simple (gnathiids have only 5 pairs of pereopods, as thoracopod 2 is a maxillipedal "pylopod" and thoracopod 8 is missing); pereopods variable, modified as ambulatory, prehensile, or swimming; in the more derived suborders pereopodal coxae are expanded as lateral side plates

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(coxal plates); pleopods biramous and well developed, natatory and for gas exchange (functioning as gills in aquatic taxa, and with air sacs called pseudotrachea in most terrestrial Oniscidea); adults with maxillary and (vestigial) antennal glands; telson fused with 1 to 6 pleonites, forming pleotelson; eyes usually sessile and compound, absent from some, pedunculate in most Gnathiidea; with biphasic molting (posterior region molts before anterior region) (Figures 21.1Q, 21.15, 21.21I, 21.28H,I, and 21.33M).

The isopods comprise about 10,000 marine, freshwater, and terrestrial species, ranging in length from 0.5 to 500 mm, the largest being species of the benthic genus *Bathynomus* (Cirolanidae). They are common inhabitants of nearly all environments, and some groups are exclusively (e.g., Bopyridae, Cymothoidae) or partly (e.g., Gnathiidae) parasitic.

The suborder Oniscidea includes about 3,600 species that have invaded land (pillbugs and sowbugs); they are the most successful terrestrial crustaceans. Their direct development, osmoregulatory capabilities, thickened cuticle, and aerial gas exchange organs (pseudotrachea) allow most oniscideans to live completely divorced from aquatic environments. However, recent molecular phylogenies suggest Oniscidea is not a monophyletic group, invasion of land from the sea happened more than once, and the first land isopods appeared about 290 million years ago (coincident with the formation of Pangaea and the diversification of vascular plants on land). Males of several species of Oniscidea are reported to have tegumental glands; the glands comprise secretory cells and ducts to the cuticle surface, and they are suspected to produce peptides or glycoproteins involved in mating.

Isopod feeding habits are extremely diverse. Many are herbivorous or omnivorous scavengers, but direct plant feeders, detritivores, and predators are also common. The wood-boring marine gribbles, *Limnoria* (Oniscidea), comprise one of the few animal groups able to survive on a diet of cellulose without relying on resident gut microbiota. Some isopods are parasites (e.g., on fishes or on other crustaceans) that feed on the tissue fluids of their hosts. Overall, grinding mandibles and herbivory seem to represent the primitive state, with slicing or piercing mandibles and predation appearing later in the evolution of several isopod clades.

Order Amphipoda Carapace absent; first thoracomere fused to head; 1 pair of maxillipeds; 7 pairs of uniramous pereopods, with first, second, and sometimes others frequently modified as chelae or subchelae; pereopodal coxae expanded as lateral side plates (coxal plates); gills thoracic (medial pereopodal epipods); adults with antennal glands; abdomen "divided" into 2 regions of 3 segments each, an anterior "pleon" and posterior urosome, with anterior appendages as typical pleopods and urosomal appendages modified as uropods; telson free or fused with last urosomite; other urosomites sometimes fused; compound eyes sessile, absent in some, huge in many (but not all) members of the suborder Hyperiidea (Figures 21.1N,O, 21.16, 21.23, 21.27F, and 21.29D). Our classification follows Lowry and Myers (2013, 2017) who recognize 6 suborders.

The roughly 10,000 species of amphipods range in length from tiny 1 mm forms to giant deep-sea benthic species reaching 30 cm, and some planktonic forms exceed 10 cm. They have invaded most marine and freshwater habitats and often constitute a large portion of the biomass in many areas. Some are common in subterranean groundwater ecosystems, the majority being stygobionts (e.g., *Niphargus*, *Stygobromus*)—obligatory groundwater species characterized by reduction or loss of eyes, pigmentation, and occasionally appendages. There are many intertidal species, and a great many of these live in association with other invertebrates and with algae. Domicolous gammaridean amphipods in at least three families spin silk from their legs that is used for consolidating the walls of their tube or shelter. The largely terrestrial superfamily Talitroidea alone comprises 117 genera, some of which are common in moist gardens and greenhouses (e.g., *Arcitalitrus sylvaticus*). The largest known amphipod is *Alicella gigantea*, a cosmopolitan marine species living at depths of up to 7,000 m.

The suborder Hyperiidea includes exclusively pelagic amphipods that have escaped the confines of benthic life by becoming associated with other plankters, particularly gelatinous zooplankton such as medusae, ctenophores, and salps. The hyperiideans are usually characterized by transparent bodies and huge eyes (and a few other inconsistent features), but several groups bear eyes no larger than those of most other amphipods. The Hyperiidea are almost certainly a polyphyletic group, and it is thought that several lineages are derived independently from various ancestors, although a modern phylogenetic analysis has yet to be attempted. The precise nature of the relationships between hyperiideans and their zooplankton hosts remains controversial. Some appear to eat host tissue, others may kill the host to fashion a floating "home," and still others may utilize the host merely for transport or as a nursery for newly hatched young. Specimens of the scyphozoan *Phacellophora camtschatica* have been found with nearly 500 *Hyperia medusarum* riding (and feeding) on them. Species of *Phronima* are famous for their habit of hollowing out the bodies of salps (pelagic tunicates) to reside inside, propelling themselves around like miniature submersible vehicles. Their extraordinarily large eyes are said to have inspired the look of the creature in the legendary science fiction film *Alien*.

The 300 or so species of caprelloidean amphipods, or "skeleton shrimp" (a clade within the suborder Senticaudata), are highly modified for clinging to other

organisms, including filamentous algae and hydroids. In most species the body and appendages are very narrow and elongated. In one family of Caprelloidea, the Cyamidae (with 28 species), individuals are obligate symbionts on cetaceans (whales, dolphins, and porpoises) and have flattened bodies and prehensile legs.

In addition to parasitism, amphipods exhibit a vast array of feeding strategies, including scavenging, herbivory, carnivory, and suspension feeding.

Order Ingolfiellida Head with vestigial pedunculate eyes; gnathopods 1–2 eucarpochelate; pleosome with 6 relatively undifferentiated segments, without epimera, with reduced pleopods and uropods. Formerly placed within Amphipoda; 45 species in 2 families distributed worldwide, from deep waters to underground fresh waters in all sorts of habitats.

Class Copepoda

Without a carapace, but with a well-developed cephalic shield; single, median, simple maxillopodan eye (sometimes lacking); 1 or more thoracomeres fused to head; thorax of 6 segments, the first always fused to the head and with maxillipeds; abdomen of 5 segments, including anal somite (= telson); well-developed caudal rami; abdomen without appendages, except an occasional reduced pair on the first segment, associated with the gonopores; point of main body flexure varies among major groups; antennules uniramous, antennae uniramous or biramous; 4–5 pairs of natatory thoracopods, most locked together for swimming; posterior thoracopods always biramous; many species with myelin-like sheaths on some nerves (Figures 21.1U, 21.4B–L, 21.27A, 21.30D, and 21.33D).

There are more than 14,500 described species of copepods. They can be incredibly abundant in the world's seas, and also in some lakes, and they compete with euphausiaceans and ants for the title of most numerous of all animals on Earth. Some estimates suggest that copepods account for 80% of all mesozooplankton biomass in the ocean. Most are small, 0.5–10 mm long, but some free-living forms exceed 1.5 cm in length, and certain highly modified parasites may reach 25 cm. The bodies of most copepods are distinctly divided into three tagmata, the names of which vary among authors. The first region includes the fused head segments and one or two additional fused thoracic somites; it is called a cephalosome (= cephalothorax) and bears the usual head appendages and maxillipeds. All of the other limbs arise on the remaining thoracic segments, which together constitute the metasome. The abdomen, or urosome, bears no limbs. The appendage-bearing regions of the body (cephalosome and metasome) are frequently collectively called the prosome. The majority of the free-living copepods, and those most frequently encountered, belong to the orders Calanoida, Harpacticoida, and Cyclopoida, although even some of these are parasitic. We focus here on these three groups and then briefly discuss some of the other, smaller orders and their modifications for parasitism.

The calanoids are characterized by a point of major body flexure between the metasome and the urosome, marked by a distinct narrowing of the body. They possess greatly elongate antennules. Most of the calanoids are planktonic, and as a group they are extremely important as primary consumers in freshwater and marine food webs. The point of body flexure in the orders Harpacticoida and Cyclopoida is between the last two (fifth and sixth) metasomal segments. (Note: Some authors define the urosome in harpacticoids and cyclopoids as that region of the body posterior to this point of flexure.) Harpacticoids are generally rather vermiform, with the posterior segments not much narrower than the anterior; cyclopoids generally narrow abruptly at the major body flexure. Both the antennules and the antennae are quite short in harpacticoids, but the latter are moderately long in cyclopoids (although never as long as the antennules of calanoids). Most harpacticoids are benthic, and those that have adapted to a planktonic lifestyle show modified body shapes. Harpacticoids occur in all aquatic environments; encystment is known to occur in at least a few freshwater and marine species. Cyclopoids are known from fresh and salt water, and most are planktonic.

The nonparasitic copepods move by crawling or swimming, using some or all of the thoracic limbs. Many of the planktonic forms have very setose appendages, offering a high resistance to sinking. Calanoids are predominantly planktonic feeders. Benthic harpacticoids are often reported as detritus feeders, but many feed predominantly on microorganisms living on the surface of detritus or sediment particles (e.g., diatoms, bacteria, and protists).

Of the seven remaining orders, the Mormonilloida are planktonic; the Misophrioida are known from deep-sea epibenthic habitats as well as anchialine caves in both the Pacific and Atlantic; and the Monstrilloida are planktonic as adults, but the larval stages are endoparasites of certain gastropods, polychaetes, and occasionally echinoderms. Members of the orders Ergasilida and Siphonostomatoida are exclusively parasitic and often have modified bodies; some form galls on their hosts (e.g., lamippids on sea pens). Siphonostomatoids are endo- or ectoparasites of various invertebrates as well as marine and freshwater fishes; they are often very tiny and show a reduction or loss of body segmentation. Ergasilidans parasitize invertebrates and marine fishes and may also show a reduced number of body segments. The Platycopioida are benthic forms known primarily from marine caves; the Gelyelloida are known only from European groundwaters. Huys and Boxshall (1991) estimated that nearly half of all known copepod species are parasites.

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Class Thecostraca

This group includes the barnacles, parasitic ascothoracidans, and the mysterious Facetotecta (so far, known only from their larvae). The thecostracan clade is defined by several rather subtle synapomorphies of cuticular fine structure, including cephalic chemosensory structures known as lattice organs. The group is also supported by molecular phylogenetic analyses. All taxa have pelagic larvae, the terminal instar of which is a unique larva, the **cypris larva (or cyprid)**, with prehensile antennules specialized for locating and attaching to the substratum of the sessile adult state.

Subclass Facetotecta Monogeneric (*Hansenocaris*): The "y-larvae," a half dozen small (250–620 mm) marine nauplii and cyprids (Figure 21.17I). Although known since Hansen's original description in 1899, the adult stage of these animals has still not been identified. However, a stage subsequent to the cypris larva, the sluglike ypsigon stage, has been induced by treating y-larvae with molting hormones. The prehensile antennules and hooked labrum of the y-cyprids and the degenerative nature of the ypsigon suggest that the adults are parasitic in yet-to-be-identified hosts.

Subclass Ascothoracida About 125 described species of parasites of cnidarians and echinoderms. Although greatly modified, they retain a bivalved carapace and the full complement of thoracic (11 segments) and abdominal (5 segments) somites. Ascothoracidans generally have mouthparts modified for piercing and sucking body fluids, but some live inside other animals and absorb the host's tissue fluids. In at least one species, *Synagoga mira*, males retain the ability to swim throughout their lives, attaching only temporarily while feeding on corals (Figure 21.17F).

Subclass Cirripedia Primitively with tagmata as in the class, but in most groups the adult body is modified for sessile or parasitic life. Thorax of 6 segments with paired biramous appendages; abdomen strongly reduced or absent; telson absent in most, although caudal rami persist on abdomen in some; unique nauplius larva with frontolateral horns (which house nerves and large unicellular glands). All begin life with a series of free-swimming naupliar instars (planktotrophic or lecithotrophic) terminating in a unique, "bivalved," nonfeeding cypris larva (modified for settlement and subsequent metamorphosis into an adult); cyprid with articulating telson bearing 2 caudal (furcal) rami. Adult carapace "bivalved" (folded) or forming fleshy mantle; first thoracomere often fused with cephalon and bearing maxilliped-like oral appendages; female gonopores near bases of first thoracic limbs, male gonopore on median penis on last thoracic or first abdominal segment; compound eyes lost in adults (Figures 21.1S,T, 21.17A–E, 21.25, 21.26, 21.27B,C, 21.32E, and 21.33F).

The 1,300 or so described cirripede species are mostly free-living barnacles, but this group also includes some strange parasitic "barnacles" rarely seen except by specialists. The common acorn and goose barnacles belong to the superorder Thoracica. Some acorn barnacles are known to transform from their oval-shaped aperture to a narrow or bent aperture when exposed to predatory snails, making them better able to withstand predator assaults. The superorder Acrothoracica consists of minute animals that burrow into calcareous substrata, including corals and mollusc shells (Figure 21.17G). The superorder Rhizocephala are exceptionally modified parasites of other crustaceans, especially decapods (Figure 21.17H).

In cyprids the carapace is always present and "bivalved," the two sides being held by a transverse cypris adductor muscle; in adults the carapace may be lost (Rhizocephala) or modified as a membranous, saclike mantle (thoracicans and acrothoracicans). In the barnacles (Thoracica), it is this mantle that produces the familiar, hard, calcareous plates that enclose the body. Cyprids and adult acrothoracicans share a unique tripartite crystalline cone structure in the compound eye, a feature not known from any other crustacean group. Most species of barnacles are hermaphrodites, although separate sexes are the rule in acrothoracicans and rhizocephalans, and some androgonochoristic species (males + hermaphrodites; e.g., *Scalpellum*) have also been reported.

Locomotion in barnacles is generally confined to the larval stages, although adults of a few species are specifically adapted to live attached to floating objects (e.g., seaweeds, pumice, logs) or nektonic marine animals (e.g., whales, sea turtles). Cyprids can both swim and walk (on the antennules) to locate a suitable site for settlement, whereupon they cement themselves to the substratum; the paired cement glands constitute a synapomorphy for cirripedes (ascothoracidan cyprids attach by mechanical means). Others are often found on the shells and exoskeletons of various errant invertebrates (e.g., crabs and gastropods), which inadvertently provide a means of transportation from one place to another. Thoracican and acrothoracican barnacles use their feathery thoracopods (called **cirri**) to suspension feed. Barnacles in the family Coronulidae are suspension feeders that attach to whales and turtles (e.g., *Chelonibia, Platylepas, Stomatolepas, Coronula, Xenobalanus*). The 300 or so known species of rhizocephalans are all endoparasitic in other Crustacea, and they are the most highly modified of all cirripedes. They mainly inhabit decapod crustaceans, but a few are known from isopods, cumaceans, stomatopods, and even thoracican barnacles. Some even parasitize freshwater and terrestrial crabs. The body consists of a reproductive part (the **externa**) positioned outside the host's body, and an internal, ramifying, nutrient-absorbing part (the **interna**). Most of the externa is female and contains the ovary as well as the male "organs" in the form of one or several dwarf males that are implanted into the virginal female.

(A)

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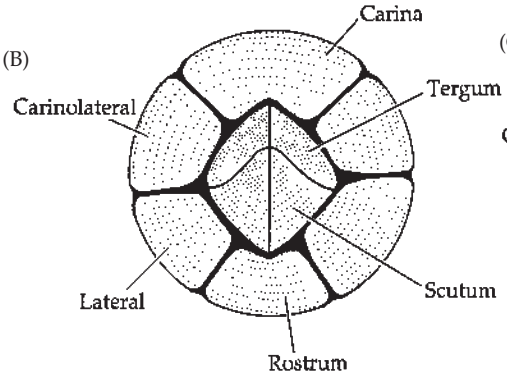
(B)



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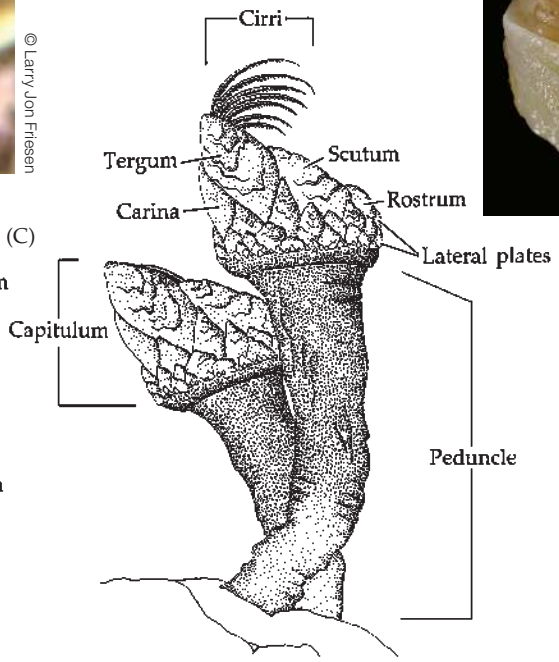

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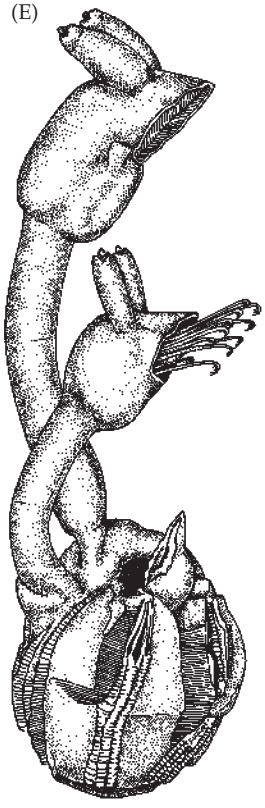

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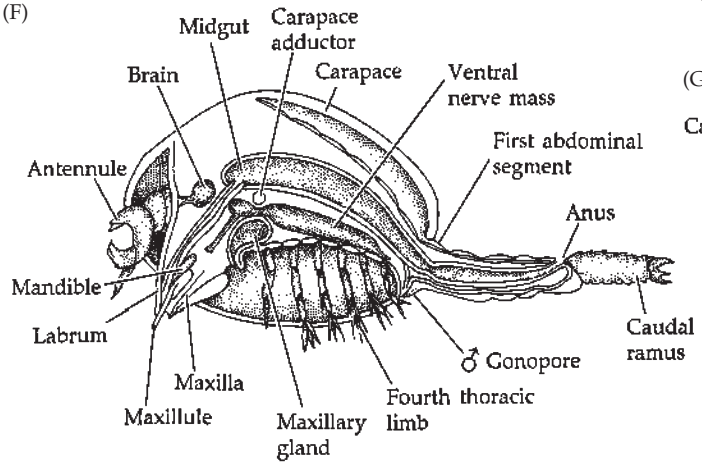

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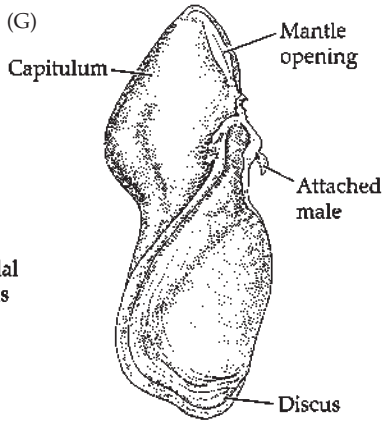

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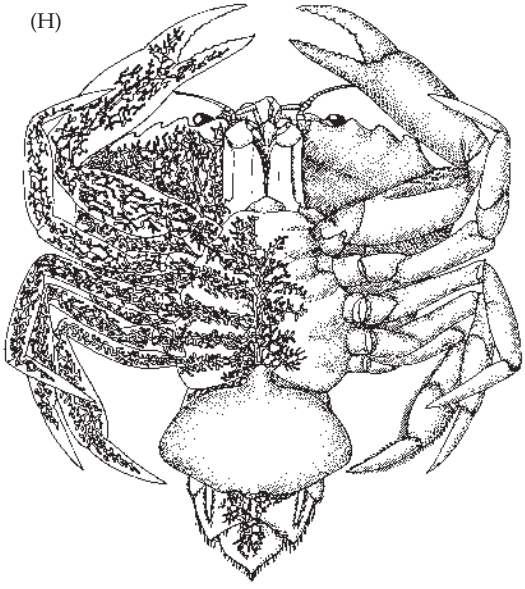

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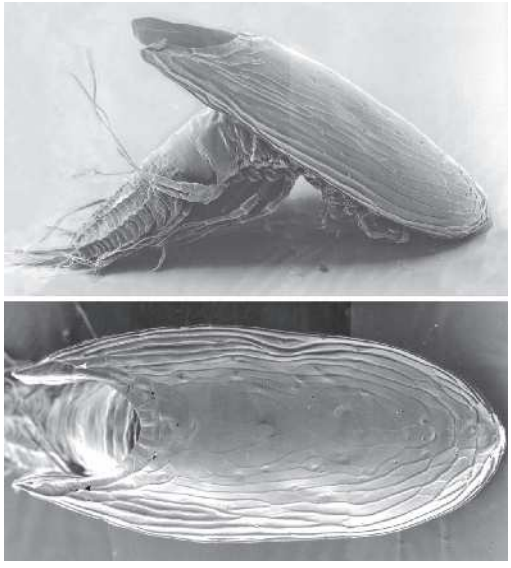

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◀ **FIGURE 21.17 Anatomy and diversity in the class Thecostraca—barnacles and their kin.** (A–E) Thoracican barnacles. (A) A sessile (acorn) barnacle with its cirri extended for feeding. (B) Plate terminology in a balanomorph (acorn) barnacle. (C) The lepadomorph (stalked) barnacle *Pollicipes polymerus*. (D) *Verruca*, the "wart" barnacle. (E) Two thoracican barnacles that live in association with each other and with whales. The stalked barnacle *Conchoderma* attaches to the sessile barnacle *Coronula*, which in turn attaches to the skin of certain whales. (F) Anatomy of the ascothoracidan *Ascothorax ophioctenis*, a parasite that feeds periodically on echinoderms (longitudinal section). (G) An acrothoracican barnacle, *Trypetesa*. Note the highly modified female and the tiny attached male. This species bores into calcareous substrata such as coral skeletons. (H) A crab (*Carcinus*) infected with the rhizocephalan *Sacculina carcini*. The crab's right side is shown as transparent, exposing the ramifying body of the parasite. (I) A cypris y-larva, in lateral and dorsal views. (E after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, Oxford.)

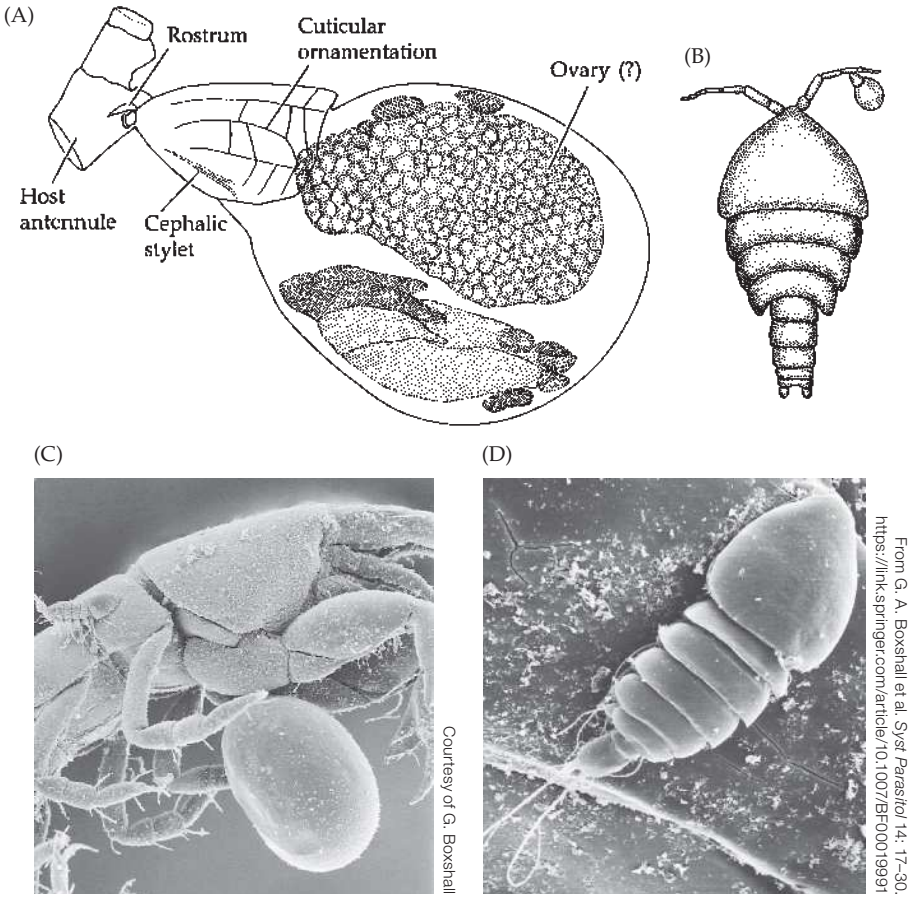
All stages, including the nauplii and cyprids, lack any trace of an alimentary canal, and the parasitic stages lack any segmentation or appendages.[6]

Class Tantulocarida

A small group of about 3 dozen bizarre parasites of mostly deep-water crustaceans, although some are known from the intertidal zone and from anchialine pools and hydrothermal vents (Figures 21.1V and 21.18). Tantulocarids are the smallest living crustaceans, at least in the juvenile or "larval" stage (the **tantulus**), which ranges from just 70 to 150 μm (comparable in size to some protists). The unique tantulus stage is adapted to both free swimming (through sediments) and an attached parasitic mode of life. In the free-swimming phase there is a cephalon, 6-segmented thorax, and abdomen with up to 7 segments. The cephalon lacks appendages (except for unsegmented antennules in sexual females; absent in larvae) but has an internal median stylet. Natatory thoracopods 1–5 are biramous, 6 is uniramous; the abdomen lacks appendages but bears caudal rami. Paired bundles of longitudinal muscles run along the midline in the thoracic somites and partly into the abdomen. There is emerging molecular and morphological evidence that tantulocarids are closely related to thecostracans, and they might one day be moved into that class.

Tantulocarids have a most remarkable life cycle. Atypically, the tantulus is able to switch its lifestyle from one of mobility to that of a sessile parasite without further molting. Thus, this one stage represents adaptations for both motile and attached/sessile lifestyles, and the transformation from one to the other involves dramatic changes in the animal's physiology and anatomy. When the free-swimming tantulus finds a proper host, a unique cuticular organ, the proboscis (sometimes called the "funnel-shaped organ"), is everted from an oral disc to establish an attachment, likely using a type of glue. The proboscis is then retracted back into the tantulus,

[6]Rhizocephalans of the family Sacculinidae infest only decapod crustaceans and have been suggested as biological control agents for invasive exotics such as the green crab (*Carcinus maenas*), which are upsetting coastal ecosystems worldwide. Sacculinds have the ability to take control over such major host functions as molting and reproduction, and also to compromise the host's immune system.



Courtesy of G. Boxshall

From G. A. Boxshall et al. *Syst Parasitol* 14: 17–30. https://link.springer.com/article/10.1007/BF00019991

FIGURE 21.18 Anatomy in the class Tantulocarida. (A) An adult *Basipodella atlantica*. Note the absence of an abdomen and the modifications for parasitic life. (B) *Basipodella* attached to the antenna of a copepod host. (C,D) *Microdajus pectinatus* on a crustacean host, adult (C), and juvenile (D) (SEM). (A,B after G. A. Boxshall and R. J. Lincoln. 1983. *J Crust Biol* 3: 1–16.)

and a permanent attachment is made by the oral disc. To access the host's nutrients, the tantulus pierces the victim's cuticle with a stylet (which has protractor and retractor muscles), which is subsequently withdrawn back into the larval head. The tip of the stylet is solid, and the organ apparently does not inject anything into the host. The tiny hole left from this puncture serves as an entrance for a unique rootlet system that grows into the host to absorb nutrients. Once attached to a host, the tantulus loses its attachment organs, including the cement glands, and all of the musculature degenerates and is resorbed. It then either sheds the whole trunk and forms a cuticular sac containing a developing parthenogenetic tantulus or female, or retains the trunk somites but expands to form a cuticular sac in which a male develops. Thus, the tantulus either enters a parthenogenetic phase (becoming a so-called parthenogenetic female, which produces more tantuli) or develops into a sexually reproducing adult. In both cases, the next stage develops inside the cuticular sac of the tantulus itself. Progeny are released into the environment.

Superclass Altocrustacea: Clade Allotriocarida

Class Cephalocarida

Head followed by 8-segmented thorax with each segment bearing limbs, an 11-segmented limbless abdomen, and a telson with caudal rami; common gonopore on protopods of sixth thoracopods; carapace absent but head covered by cephalic shield; thoracopods 1–7 biramous and phyllopodous, with large flattened exopods and epipods (exites) and stenopodous endopods; thoracopods 8 reduced or absent; maxillae resemble thoracopods; no maxillipeds; eyes absent; nauplii with antennal glands, adults with maxillary glands and (vestigial) antennal glands; with long and gradual (anamorphic) larval development (Figures 21.1B 21.19A–C, and 21.21A).

Cephalocarids are tiny, elongate crustaceans ranging in length from 2 to 4 mm. There are 12 species in five genera. All are benthic marine detritus feeders, although many seem to have commensal relationships with sedentary polychaetes. Most are associated with sediments covered by a layer of flocculent organic detritus, although some have been found in clean sands. They occur from the intertidal zone to depths of over 1,500 m, from the North and South Pacific to the North and South Atlantic and in the Mediterranean. Hatching is at a slightly advanced naupliar stage (called a metanauplius).

Class Branchiopoda

Numbers of segments and appendages on thorax and abdomen vary, the latter usually lacking appendages; carapace present or absent; telson usually with caudal rami; body appendages generally phyllopodous; maxillules and maxillae reduced or absent; no maxillipeds (Figures 21.1C,D, 21.20, 21.21B, 21.31C, and 21.35B).

The branchiopods are difficult to describe in a general way. The majority are small freshwater forms with leaflike legs and minimal body tagmosis. Most are short-lived, and those inhabiting ephemeral waters complete their life cycle in just a few weeks. Because of their short life cycle and predilection for temporary pools (e.g., vernal pools), many groups produce drought-resistant eggs or zygotes, called cysts, which can survive years or decades until the next adequate rains appear. As diverse as the branchiopods might appear, both morphological and molecular analyses indicate that they comprise a monophyletic group. Development is remarkably uniform across the group, with naupliar larvae distinguishable by several unique features. A few groups have conquered the world oceans secondarily (e.g., marine cladocerans). Most species are filter feeders, but predators are known both within Anostraca and Cladocera. About 1,130 extant species have been described (around half of which are cladocerans), and at least one fossil branchiopod (*Rehbachiella*) is known from the middle Cambrian, confirming that they are an ancient group. Although branchiopod taxonomy is still in a bit of flux, the group is generally divided into two subclasses, Anostraca (the carapaceless fairy shrimps) and Phyllopoda (the carapaced branchiopods).

Subclass Anostraca

Postcephalic trunk divisible into appendage-bearing thorax of 11 segments (or, rarely, 10, 17, or 19) and abdomen of 8 segments plus telson with caudal rami; gonopores on genital region of abdomen; trunk limbs biramous and phyllopodous; small cephalic shield present, though fully developed carapace lacking; paired, large, stalked compound eyes and a single median simple (naupliar) eye.

Anostracans are primitive-looking crustaceans commonly called fairy shrimps and brine shrimps that differ from all other branchiopods in lacking a carapace. There are just over 300 living species, worldwide, most of which are less than 1 cm in length, although a few giants attain lengths of 10 cm. Anostracans inhabit ephemeral ponds (including snowmelt ponds and desert pools), hypersaline lakes, and marine lagoons. In many areas they are an important food resource for water birds. Anostracans are sometimes united with the extinct Lipostraca as the "Sarsostraca." Their fossil record dates back to the Devonian.

Anostracans swim ventral side up by metachronal beating of the trunk appendages. Many use these limb movements for suspension feeding. Some other species scrape organic material from submerged surfaces, and at least two species (*Branchinecta gigas, B. raptor*) are specialized as predators on other fairy shrimps. Although most anostracans live in isolated ponds, their eggs are transported on the feathers of birds and feet of mammals

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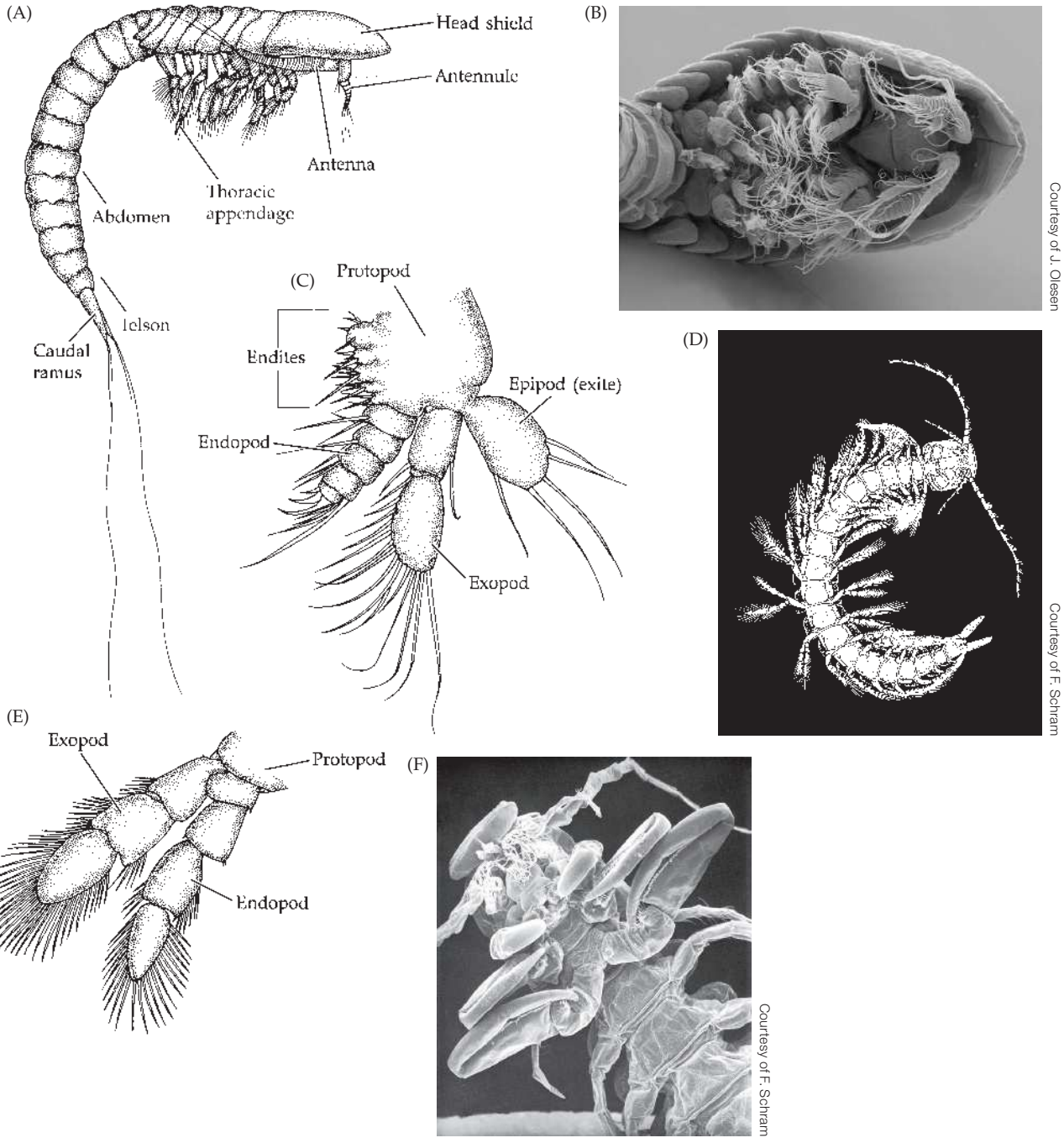

FIGURE 21.19 Anatomy in the classes Remipedia and Cephalocarida. (A) The cephalocarid *Hutchinsoniella macracantha* (lateral view). (B) SEM of head and thorax of a cephalocarid. (C) First trunk limb of the cephalocarid *Lightiella*. (D) The remipede *Morlockia ondinae* (ventral view). (E) Tenth trunk limb of the remipede *Lasionectes*. (F) The anterior end of a remipede (ventral view). In both the cephalocarids and the remipedes, the trunk is a long, homonomous series of somites with biramous swimming appendages. In cephalocarids the first trunk appendages are like all the others, which bear large swimming epipods (exites). In remipedes the first trunk somite is fused to the head, and its appendages are maxillipeds. See chapter opener photo of *Xibalbanus tulumensis*.

and might also be transported during passage through the gut of predatory diving beetles (Dytiscidae).

Subclass Phyllopoda

The tadpole shrimps (Notostraca) and "bivalved" branchiopods (Diplostraca).

Order Notostraca Thorax of 11 segments, each with 1 pair of phyllopodous appendages; abdomen of "rings," each formed of more than 1 true segment; each anterior ring with several pairs of appendages; posterior rings lack appendages; telson with long caudal rami; gonopores on last thoracomere; broad, shield-like carapace fused only with head, but extending to

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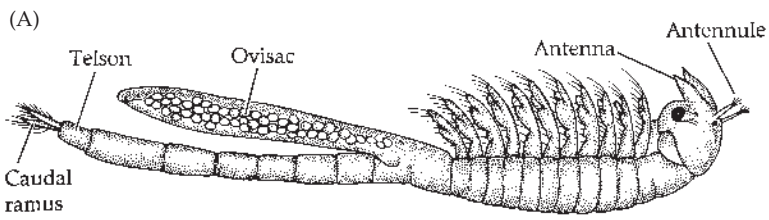

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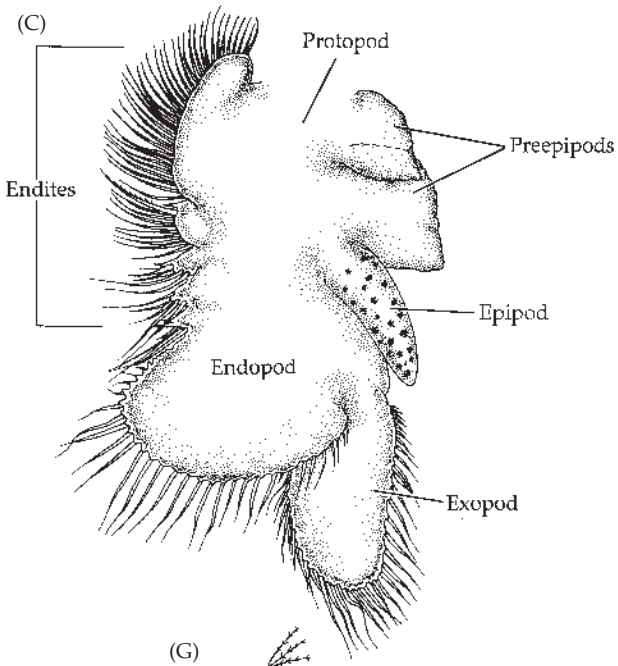

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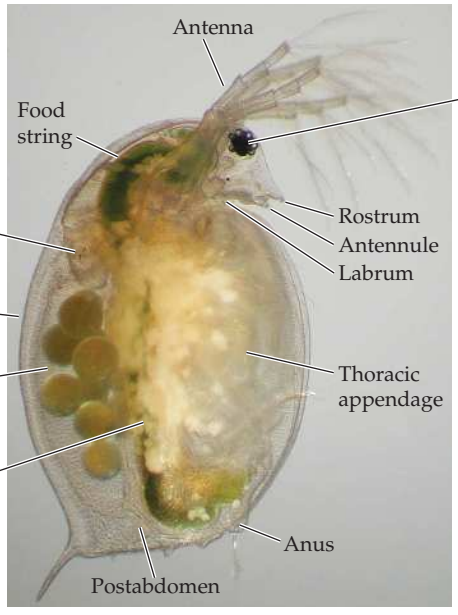

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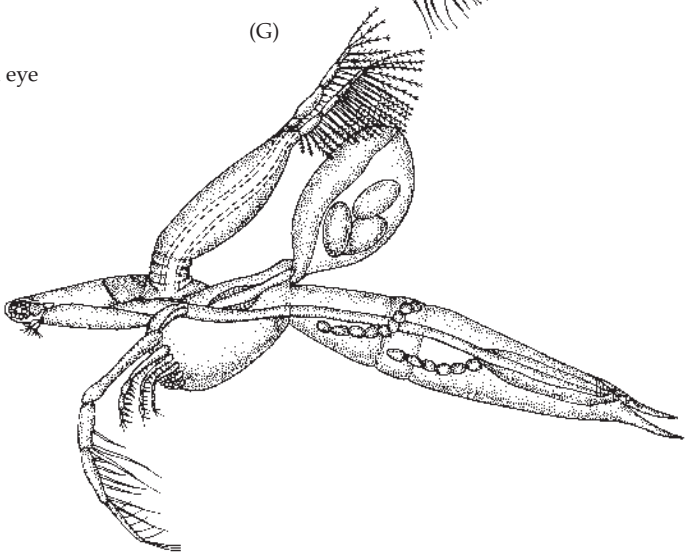

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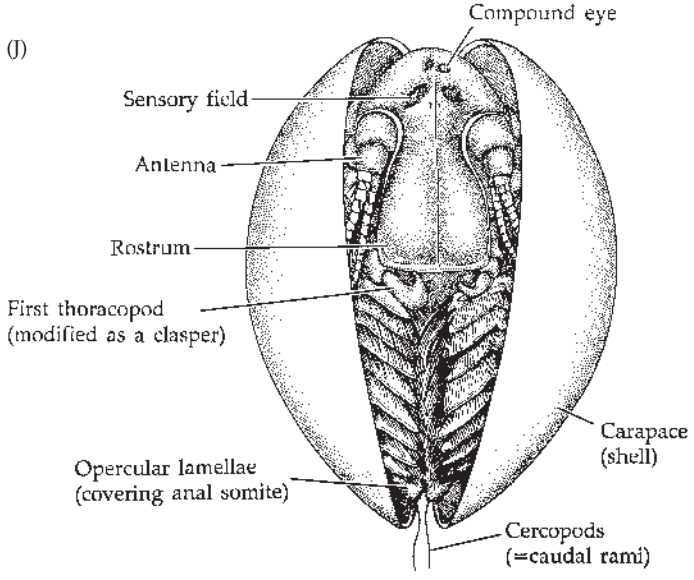

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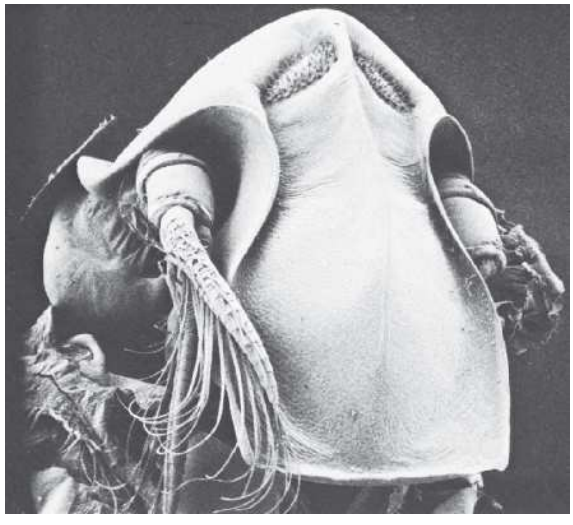

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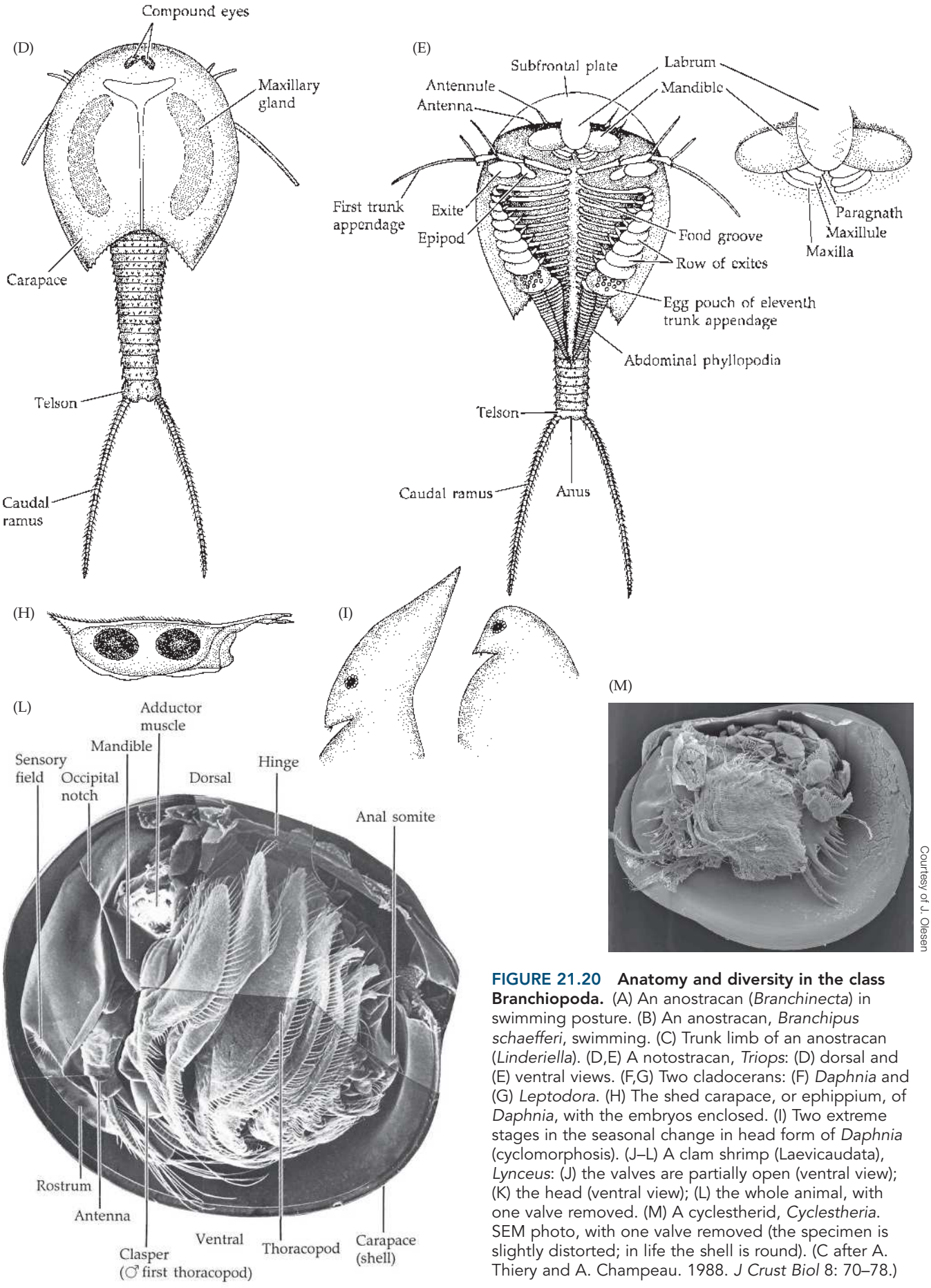

From J. W. Martin et al. 1986. *Zool Scripta* 15: 221–232

Courtesy of J. Olesen

FIGURE 21.20 Anatomy and diversity in the class Branchiopoda. (A) An anostracan (*Branchinecta*) in swimming posture. (B) An anostracan, *Branchipus schaefferi*, swimming. (C) Trunk limb of an anostracan (*Linderiella*). (D,E) A notostracan, *Triops*: (D) dorsal and (E) ventral views. (F,G) Two cladocerans: (F) *Daphnia* and (G) *Leptodora*. (H) The shed carapace, or ephippium, of *Daphnia*, with the embryos enclosed. (I) Two extreme stages in the seasonal change in head form of *Daphnia* (cyclomorphosis). (J–L) A clam shrimp (Laevicaudata), *Lynceus*: (J) the valves are partially open (ventral view); (K) the head (ventral view); (L) the whole animal, with one valve removed. (M) A cyclestherid, *Cyclestheria*. SEM photo, with one valve removed (the specimen is slightly distorted; in life the shell is round). (C after A. Thiery and A. Champeau. 1988. *J Crust Biol* 8: 70–78.)

loosely cover thorax and part of abdomen; paired, sessile compound eyes and a single simple eye near anterior midline on carapace.

There are only about a dozen living species of tadpole shrimps, in two genera (*Triops* and *Lepidurus*) placed in a single family, Triopsidae. Most species are 2–10 cm long. The common name derives from the general body shape: the broad carapace and narrow "trunk" give the animals a superficial tadpolelike appearance.

Notostracans inhabit inland waters of all salinities, but none occur in the ocean. Of the two known genera, *Triops* (Figure 21.20D,E) lives only in temporary waters, and its eggs are capable of surviving extended dry periods. Most species of *Lepidurus* live in temporary ponds, but at least one species (*L. arcticus*) inhabits permanent ponds and lakes. However, all species are short-lived, and most complete their life cycle in just 30 to 40 days. *Triops* is of some economic importance in that large populations often occur in rice paddies and destroy the crop by burrowing into the mud and dislodging young plants. Tadpole shrimps mostly crawl, but they are also capable of swimming for short periods by beating the thoracic limbs. They are omnivorous, feeding mostly on organic material stirred up from the sediments, although many species scavenge or prey on other animals, including molluscs, other crustaceans, frog eggs, and even frog tadpoles and small fishes. Some species of notostracans are exclusively gonochoristic, but others may include hermaphroditic populations (often those populations living at high latitudes). Earlier reports of parthenogenetic populations have been questioned.

Order Diplostraca The "bivalved" branchiopods: clam shrimps and cladocerans (water fleas) (Figure 21.20J–L). Large "bivalved" carapace covers all or most of the body; body divided into cephalon and trunk, the latter with 10–32 segments, all with appendages, and with no regionalization into thorax and abdomen; trunk limbs phyllopodous, decreasing in size posteriorly; males with trunk limbs 1, or 1–2, modified for grasping females during mating; trunk typically terminates in spinous anal somite or telson, usually with robust caudal rami (cercopods); gonopores on eleventh trunk segment; bivalved carapace completely encloses body; valves folded (Onychocaudata) or hinged (Laevicaudata) dorsally; usually with a pair of sessile compound eyes and a single, median, simple eye.

Most diplostracans are benthic, but many swim during reproductive periods. Some are direct suspension feeders, whereas others stir up detritus from the substratum and feed on suspended particles, and others scrape pieces of food from the sediment. There are two suborders, Laevicaudata and Onychocaudata.

The suborder Laevicaudata, or flat-tailed clam shrimps, contains the single family Lynceidae with close to 40 freshwater species. They are characterized by a hinged, globular carapace that encloses the entire animal. This carapace gives them a superficial resemblance to cladocerans and ostracods, and lack of obvious growth lines on the carapace quickly distinguishes them from Spinicaudata and Cyclestherida. The suborder Onychocaudata contains the spiny-tailed or "true" clam shrimp (Spinicaudata), the monotypic Cyclestherida (*Cyclestheria hislopi*), and the cladocerans (the water fleas). *Cyclestheria* is also sometimes called a clam shrimp, though it is more closely related to the Cladocera than to Spinicaudata. Despite the confused taxonomy of *Daphnia* (only a quarter of the >360 named species are valid), it has become a model genus for ecological, toxicological, and evolutionary studies.

The common name "clam shrimp" derives from the clamlike appearance of the valves, which usually bear concentric growth lines reminiscent of bivalved molluscs. The approximately 200 species of clam shrimps (including laevicaudatans, spinicaudatans, and *Cyclestheria*) live primarily in ephemeral freshwater habitats worldwide. *Cyclestheria hislopi* inhabits permanent freshwater habitats throughout the world's tropics and is one of the most widespread animals on Earth. *Cyclestheria* is also the only clam shrimp with direct development, the larval and juvenile stages being passed within the brood chamber, one of the features allying it with the cladocerans in the infraorder Cladoceromorpha.

In cladocerans, the carapace is never hinged (only folded dorsally, like a taco) and never covers the entire body, and appendages do not occur on all the trunk somites. The body segmentation is generally reduced. The thorax and abdomen are fused as a "trunk" bearing 4–6 pairs of appendages anteriorly and terminating in a flexed "postabdomen" with clawlike caudal rami. The trunk appendages are usually phyllopodous. The carapace typically encloses the entire trunk, but not the cephalon, serving as a brood chamber (and greatly reduced to this function) in some species; a single median compound eye is always present.

The cladocerans, or water fleas, include about 400 species of predominantly freshwater crustaceans. Several American marine genera and species are known (e.g., *Evadne*, *Podon*). Although there are relatively few species, the group exhibits great morphological and ecological diversity. Most cladocerans are 0.5–3 mm long, but *Leptodora kindtii* reaches 18 mm in length. Except for the cephalon and large natatory antennae, the body is enclosed by a folded carapace, which is fused with at least some of the trunk region. The carapace is greatly reduced in members of the families Polyphemidae and Leptodoridae, in which it forms a brood chamber.

Cladocerans are distributed worldwide in nearly all inland waters. Most are benthic crawlers or burrowers, while others are planktonic and swim by means of their large antennae. One genus (*Scapholeberis*) is typically found in the surface film of ponds, and another (*Anchistropus*) is ectoparasitic on *Hydra*. Most of the benthic forms feed by scraping organic material from sediment particles or other objects; the planktonic

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species are suspension feeders. Some, such as *Leptodora* and *Bythotrephes*, are predators on other cladocerans.

In sexual reproduction, fertilization generally occurs in a brood chamber between the dorsal surface of the trunk and the inside of the carapace. Most species have direct development. In the family Daphniidae the developing embryos are retained by a portion of the shed carapace, which functions as an egg case called an **ephippium** (Figure 21.20H), whereas in the Chydoridae the ephippium remains attached to the entire shed carapace. *Leptodora* exhibits a heterogenous life cycle, alternating between parthenogenesis and sexual reproduction, the latter of which results in free-living larvae (metanauplii hatch from the shed resting eggs).

Cladoceran life histories are often compared with those of animals such as rotifers and aphids. Dwarf males occur in many species in all three groups, and parthenogenesis is common. Members of two cladoceran families that undergo parthenogenesis (Moinidae and Polyphemidae) produce eggs with very little yolk. In these groups the floor of the brood chamber is lined with glandular tissue that secretes a fluid rich in nutrients, which is absorbed by the developing embryos. Periods of overcrowding, adverse temperatures, or food scarcity can induce parthenogenetic females to produce male offspring. Occasional periods of sexual reproduction have been shown to occur in most parthenogenetic species. Many planktonic cladocerans undergo seasonal changes in body form through succeeding generations of parthenogenetically produced individuals (Figure 21.20I), a phenomenon known as cyclomorphism.

Class Remipedia

Body of 2 regions, a short cephalon and an elongate homonomous trunk of up to 32 segments, each with a pair of flattened limbs. Cephalon with a pair of sensory preantennular frontal processes; first antennae (antennules) biramous; trunk limbs laterally directed, biramous, paddlelike, but without large epipods; rami of trunk limbs (exopod and endopod) each of 3 or more articles; without a carapace, but with cephalic shield covering head; midgut with serially arranged digestive ceca; first trunk segment fused with head and bearing 1 pair of prehensile maxillipeds; labrum very large, forming a chamber (atrium oris) in which reside the "internalized" mandibles; maxillules function as hypodermic fangs, injecting venom from associated venom glands; last trunk segment partly fused dorsally with telson; telson with caudal rami; segmental double ventral nerve cord; eyes absent in living species; male gonopore on trunk limb 15, female on 8; up to 45 mm in length. The above diagnosis is for the 27 known living remipedes (order Nectiopoda); the fossil record is currently based on a single poorly preserved specimen (order Enantiopoda) (chapter opener and Figures 21.1A, 21.19D–F, 21.21D, 21.22F, and 21.31E,F).

The discovery of living remipedes in 1981 by Jill Yager, strange vermiform crustaceans first collected from a cavern in the Bahamas, gave the carcinological world a turn. The combination of features distinguishing these creatures is puzzling, for they possess characteristics long thought to be primitive (e.g., long, homonomous trunk; double ventral nerve cord; segmental digestive ceca; cephalic shield) as well as some attributes traditionally recognized as advanced (e.g., maxillipeds; nonphyllopodous [though flattened], biramous limbs). They swim about on their backs as a result of metachronal beating of the trunk appendages, similar to anostracans. The remipedes are thus reminiscent of two other classes, the branchiopods and cephalocarids. However, the laterally directed limbs are unlike those of any other crustacean, and the "internalized" mandibles and the poison-injecting hypodermic maxillules are unique (the complex venom contains neurotoxins, peptidases, and chitinases). The presence of the preantennular processes is also puzzling, although similar structures are known to occur in a few other crustaceans. Some phylogenetic analyses based on morphological data suggest that remipedes may be the most primitive living crustaceans, whereas phylogenomic data place them unambiguously as the sister group of the Hexapoda.

All of the living remipedes discovered thus far are troglobitic, found in caves, cenotes, lava tubes, and sinkholes (usually with connections to the sea) in the Caribbean Basin, Canary Islands, and Western Australia. The water in these systems is often distinctly stratified, with a layer of fresh water overlying the denser salt water in which the remipedes swim. Remipedes hatch as lecithotrophic naupliar larvae, which is also unusual given their habitat (most cave crustaceans have direct development). Postnaupliar development is anamorphic; juveniles have fewer trunk segments than do the adults. Based on the three pairs of raptorial, prehensile cephalic limbs (and direct observations), it was long thought that remipedes were strictly predators. However, studies by Stefan Koenemann and his colleagues have suggested they might also be capable of suspension feeding.

The Crustacean Body Plan

We realize that the above synopses are rather extensive, but the diversity of crustaceans demands emphasis before we attempt to generalize about their biology. The evolutionary success of crustaceans, like that of other arthropods, has been closely tied to modifications of the jointed exoskeleton and appendages, the latter having an extensive range of modifications for a great variety of functions.

The most basic crustacean body plan is a **head (cephalon)** followed by a long body (**trunk**) with many similar appendages, as seen in the class Remipedia (Figures 21.1A and 21.19D,E). In the other crustacean classes, however, various degrees of tagmosis occur, and the cephalon is typically followed by a trunk that is usually divided into two distinct regions, a **thorax** and an **abdomen**. The

first segment of the body (ocular segment) and the last segment of the body (telson) are without appendages. Many crustacean groups have a **cephalic shield** (**head shield**) or a **carapace**. The cephalic shield results from the fusion of the dorsal head tergites to form a solid cuticular plate, often with ventrolateral folds (**pleural folds**) on the sides. Head shields are found in ancient Cambrian fossil crustaceans (e.g., from the Orsten fauna), and they are characteristic of the classes Remipedia and Cephalocarida; they also occur in a few other groups. The carapace is a more expansive structure, composed of the head shield and a large fold of the exoskeleton that probably arises (primitively) from the maxillary somite. The carapace may extend over the body dorsally and laterally as well as posteriorly, and it often fuses to one or more thoracic segments, thereby producing a **cephalothorax** (Figure 21.2A). Occasionally, the carapace may grow forward beyond the head as a narrow rostrum.

Most of the differences among the major groups of crustaceans, and the basis for much of their classification, arise from variations in the number of somites in the thorax and abdomen, the form of their appendages, and the size and shape of the carapace. A brief skimming of the synopses (above) and the corresponding figures will give you some idea of the range of variation in these features.

Uniformity within the subphylum Crustacea is demonstrated particularly by the consistency of elements of the cephalon and the presence of the nauplius larva. Except for a few cases of secondary reduction, the head of all crustaceans has five pairs of appendages. From anterior to posterior, these are the **antennules** (first antennae), **antennae** (second antennae), **mandibles**, **maxillules** (first maxillae), and **maxillae** (second maxillae). The presence of two pairs of antennae is, among arthropods, unique to the Crustacea (as is the nauplius larva, although similar "head larvae" are known from other arthropod groups in the fossil record).[7] Although the eyes of some crustaceans are simple, most possess a pair of well-developed compound eyes, either set directly on the head (sessile eyes) or borne on distinct movable stalks (stalked eyes).

In many crustaceans, from one to three anterior thoracic segments (**thoracomeres**) are fused with the cephalon. The appendages of these fused segments are typically incorporated into the head as additional mouthparts called **maxillipeds**. In some cases, anterior thoracopods may not fuse with the cephalon during

[7]Cambrian crustacean-like larvae in the fossil record termed "head larvae" may be precursors to the distinctive nauplius stage seen in many modern crustaceans. See Martin et al. (2014).

TABLE 21.1 Comparison of Distinguishing Features among the 11 Crustacean Classes (and in the Subclasses of Class Eumalacostraca)

Taxon	Carapace or Cephalic Shield	Body Tagmata and Number of Segments in Each (excluding telson)	Thoracopods
Class Ostracoda	Carapace, bivalved	Subdivisions not clear; 6–8 pairs of limbs	Not phyllopodous, reduced
Class Mystacocarida	Cephalic shield	Cephalon (6), trunk (10)	Not phyllopodous
Class Branchiura	Carapace broad, covering head and trunk	Cephalon (6), thorax (6), abdomen (4?)	Not phyllopodous (but all natatory)
Class Pentastomida	None	Not distinguishable; body vermiform	None
Class Malacostraca, subclass Phyllocarida	Large, folded carapace covers thorax	Cephalon (6), thorax (8), abdomen (7)	Phyllopodous
Class Malacostraca, subclass Hoplocarida	Well-developed carapace covers thorax	Cephalon (6), thorax (8), abdomen (6)	Not phyllopodous
Class Malacostraca, subclass Eumalacostraca	Carapace well developed or secondarily reduced or lost	Cephalon (6), thorax (8), abdomen (6)	Not phyllopodous, uniramous in many
Class Copepoda	Cephalic shield	Cephalon (6), thorax (6), abdomen (5)	Not phyllopodous, natatory, often reduced
Class Thecostraca	Carapace bivalved (at some stage), often modified as a mantle	Cephalon (6), thorax (6), abdomen (4)	Not phyllopodous, often reduced
Class Tantulocarida	Cephalic shield	Cephalon (6), thorax (6), abdomen (up to 7)	Not phyllopodous, greatly reduced
Class Cephalocarida	Cephalic shield	Cephalon (6), thorax (8), abdomen (11)	Phyllopodous
Class Branchiopoda	Cephalic shield or carapace	Cephalon (6), thorax (usually 10–32), abdomen (8 to many)	Phyllopodous
Class Remipedia	Cephalic shield	Cephalon (6), trunk (up to 32)	Not phyllopodous

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development, but still become modified to move food to the mouth; these, too, are usually called maxillipeds. In the class Malacostraca, the remaining free thoracomeres are together termed the **pereon**. Each segment of the pereon is called a **pereonite** (= pereomere), and the appendages on those segments are called **pereopods**. The pereopods may be specialized for walking, swimming, gas exchange, feeding, and/or defense. Crustacean thoracic (and pleonal) appendages might be primitively biramous, although the uniramous condition is seen in a variety of taxa. The general crustacean limb is composed of a basal **protopod** (= sympod), from which may arise medial **endites** (e.g., gnathobases), lateral **exites** (e.g., **epipods**), and two rami, the endopod and exopod. Members of the classes Remipedia, Cephalocarida, and Branchiopoda and some members of the class Ostracoda possess appendages with uniarticulate (single-segment) protopods; the remaining classes usually have appendages with multiarticulate protopods (Table 21.1).[8]

[8]The term "peduncle" is a general name often applied to the basal portion of certain appendages; it is occasionally (but not always) used in a way that is synonymous with "protopod." As noted in Chapter 20, the exopod might be no more than a highly modified exite that evolved from an ancestral uniramous condition

The abdomen, called a **pleon** in malacostracans, is composed of several segments, or **pleonites** (= pleomeres), followed by a "postsegmental" plate or lobe, the **telson** or **anal somite**, bearing the anus (Figure 21.2B). In some crustaceans this anal somite bears a pair of appendage-like or spinelike processes conventionally called **caudal rami**. In the Eumalacostraca, the anal somite lacks caudal rami and is followed by a flattened flap; this flap is often referred to as the telson.

In general, distinctive abdominal appendages (**pleopods**) occur only in the malacostracans. These appendages are almost always biramous, and often they are flaplike and used for swimming (e.g., Figures 21.10–21.16). The posteriorly directed last pairs of abdominal appendages are usually different from the other pleopods and are called **uropods**. Together with the telson, the uropods form a distinct **tail fan** in many malacostracans (Figure 21.2B).

Crustaceans produce a characteristic larval stage called the **nauplius** (Figures 21.25B,C and 21.33D). Even upper Cambrian fossil nauplii (*Bredocaris admirabilis*, *Rehbachiella kinnekullensis*) are nearly indistinguishable from modern-day nauplii. In their simplest form, nauplii are oval or pear-shaped, lack external segmentation, and have three pairs of appendages

Maxillipeds	Antennules	Antennae	Compound Eyes	Abdominal Appendages
None	Uniramous	Biramous	Absent (typically)	None
1 pair	Uniramous	Biramous	Absent	None
None	Uniramous, reduced	Biramous, reduced	Present	None
None	None	None	Absent	None
None	Biramous	Uniramous	Present	Pleopods (posteriorly reduced)
5 pairs of thoracopods referred to as maxillipeds	Triramous	Biramous	Present, well developed	Well developed pleopods with gills, 1 pair of uropods
0–3 pairs	Uniramous or biramous	Uniramous or biramous	Present, well developed	Usually 5 pairs of pleopods, 1 pair of uropods
Usually 1 pair	Uniramous	Uniramous or biramous	Absent	None
None	Uniramous	Biramous	Absent (in adults)	None
None	None (paired in one stage)	None	Absent	None
None	Uniramous	Biramous	Absent	None
None	Uniramous	Uniramous, biramous, or vestigial	Present	None, or present but often posteriorly reduced
1 pair	Biramous	Biramous	Absent	All trunk appendages similar

that will become the adult antennules, antennae, and mandibles. The antennules are uniramous and primarily sensory. The antennae and mandibles are almost always biramous and usually natatory and feeding limbs. There is usually a single, anterior eye, the **nauplius eye** (= **naupliar eye**) that may persist into adulthood in some taxa. The nauplius eye is actually a cluster of three or four median eyes. The body is often covered with a dorsal cephalic (naupliar) shield, sometimes called a head shield, that commonly expands

TABLE 21.2 Summary of Crustacean Reproductive Features in Major Groups

Taxon	Development Type, or Larval Type at Hatching	Hermaphroditic (at Least Some Species)	Gonochoristic	Parthenogenesis (in at Least Some Species)
Class Ostracoda	Direct development, or with bivalved nauplius/metanauplius with anamorphic development	No	Yes	Yes
Class Mystacocarida	Metanauplius (partly anamorphic)	No	Yes	No
Class Branchiura	Metanauplius-like (partly anamorphic), or with direct development	No	Yes	No
Class Malacostraca, subclass Phyllocarida	Direct development	No	Yes	No
Class Malacostraca, subclass Hoplocarida	Zoea larva ("antizoea" or "pseudozoea") (metamorphic)	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Syncarida	Direct development	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Peracarida	Direct development	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Eucarida, order Euphausiacea	Nauplius (metamorphic)	No	Yes	No
Class Malacostraca, subclass Eumalacostraca, superorder Eucarida, order Decapoda	Prezoea or zoea larva, and with a nauplius in Dendrobranchiata (metamorphic), or direct development	Rare	Yes	No
Class Copepoda	Nauplius (metamorphic)	No	Yes	No
Class Thecostraca	?	Yes	Yes	No
Class Tantulocarida	Nauplius? + tantulus (metamorphic)	No	Yes	?
Class Cephalocarida	Metanauplius (anamorphic)	Yes	No	No
Class Branchiopoda	Nauplius or metanauplius (anamorphic), or direct development	Yes/no	Yes	Yes
Class Remipedia	Nauplius (anamorphic)	Yes	No	No

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over the thorax of the adult as a carapace. Behind the head segments is a growth zone and the telson.

In many groups (e.g., Peracarida, most Decapoda), the free-living nauplius larva is absent or suppressed. In such cases, development is either fully direct or mixed, with larval hatching taking place at some postnaupliar stage (Table 21.2). Often other larval stages follow the nauplius (or other hatching stage) as the individual passes through a series of molts, during which segments and appendages are gradually added. A recent compilation of all crustacean larval forms (Martin et al. 2014) includes keys to the distinctive naupliar larvae in all groups that hatch as a nauplius as well as synopses of larval development in all crustaceans.

Comments
Embryos usually deposited directly on substratum; many myodocopans and some podocopans brood embryos between valves until hatching as reduced adults; no metamorphosis; up to 8 preadult instars.
Little studied, but apparently the eggs are laid free and up to 7 preadult stages may occur.
Embryos are deposited; only *Argulus* is known to hatch as metanauplii; others have direct development and hatch as juveniles.
Undergo direct development in the female brood pouch, emerging as a postlarval/prejuvenile stage called a "manca."
Eggs brooded or deposited in burrow; hatch late as clawed pseudozoea larvae, or earlier as unclawed antizoea larvae. Both molt into distinct ericthus (and some into alima) larvae before settling on bottom as postlarvae or juveniles.
All free larval stages have been lost; eggs deposited on substratum.
Embryos brooded in marsupium of female, typically formed from ventral coxal plates called oostegites; usually released as mancas (subjuveniles with incompletely developed eighth thoracopods). Brood pouch (marsupium) in Thermosbaenacea formed by dorsal carapace chamber.
Embryos shed or briefly brooded; typically undergo nauplius-metanauplius-calyptopis-furcilia-juvenile developmental series.
Dendrobranchiata shed embryos to hatch in water as nauplii or prezoea larvae; all others brood embryos (on pleopods), which do not hatch until a prezoeal or zoeal stage (or later).
Usually with 6 naupliar stages leading to a second series of 5 "larval" stages called copepodites.
Six naupliar stages followed by a unique larval form called a cypris larva.
A benthic nonfeeding stage, possibly a nauplius, has been reported but not formally described. Development entails complex metamorphosis with infective "tantulus larva."
One or 2 eggs at a time are fertilized and carried on genital processes of the first pleonites.
Anostraca: embryos usually shed from ovisac early in development; resistant (cryptobiotic) fertilized eggs accommodate unfavorable conditions.
Notostraca: eggs briefly brooded, then deposited on substratum; resistant (cryptobiotic) fertilized eggs accommodate unfavorable conditions.
Diplostraca: most cladocerans undergo direct development (*Leptodora* hatches as nauplii or metanauplii). Clam shrimps carry developing embryos on the thoracopods prior to releasing them as nauplii or metanauplii.
Eight naupliar stages (2 orthonauplii and 6 metanauplii), followed by a "prejuvenile" stage, have been reported.

Locomotion

Crustaceans move about primarily by use of their limbs (Figure 21.21), and lateral body undulations are not known. They crawl or swim, or more rarely burrow, "hitchhike," or jump. Many of the ectoparasitic forms (e.g., branchiurans, certain isopods and copepods) are largely sedentary on their hosts, and most cirripedes are fully sessile.

Swimming is usually accomplished by a rowing action of the limbs. Archetypical swimming is exemplified by crustaceans with relatively undifferentiated trunks and high numbers of similar biramous appendages (e.g., remipedes, anostracans, notostracans). In general, these animals swim by posterior to anterior metachronal beating of the trunk limbs (Figure 21.22 and Chapter 20). The appendages of such crustaceans are often broad and flattened, and they usually bear fringes of setae that increase the effectiveness of the power stroke. On the recovery stroke the limbs are flexed, and the setae may collapse, reducing resistance. In members of some groups (e.g., cephalocarids, branchiopods, leptostracans), large exites or epipods arise from the base of the leg, producing broad, "leafy" limbs called **phyllopodia**. These flaplike structures aid in locomotion and may also serve as osmoregulatory (branchiopods) or gas exchange (cephalocarids and leptostracans) surfaces (Figure 21.21A–C). Although such epipods increase the surface area on the power stroke, they also are hinged so that they collapse on the recovery stroke, reducing resistance. Metachronal limb movements are retained in many of the "higher" swimming crustaceans, but they tend to be restricted to selected appendages (e.g., the pleopods of shrimps, stomatopods, amphipods, and isopods; the pereopods of euphausiaceans and mysidans). In swimming euphausiaceans and mysidans the thoracopods beat in a metachronal rowing fashion. The movements and neuromuscular coordination of crustacean limbs are deceivingly complex. In the common lophogastridan *Neognathophausia ingens*, for example, 12 separate muscles power the thoracic exopod alone (3 that are extrinsic to the exopod, 5 in the limb peduncle, and 4 in the exopodal flagellum).

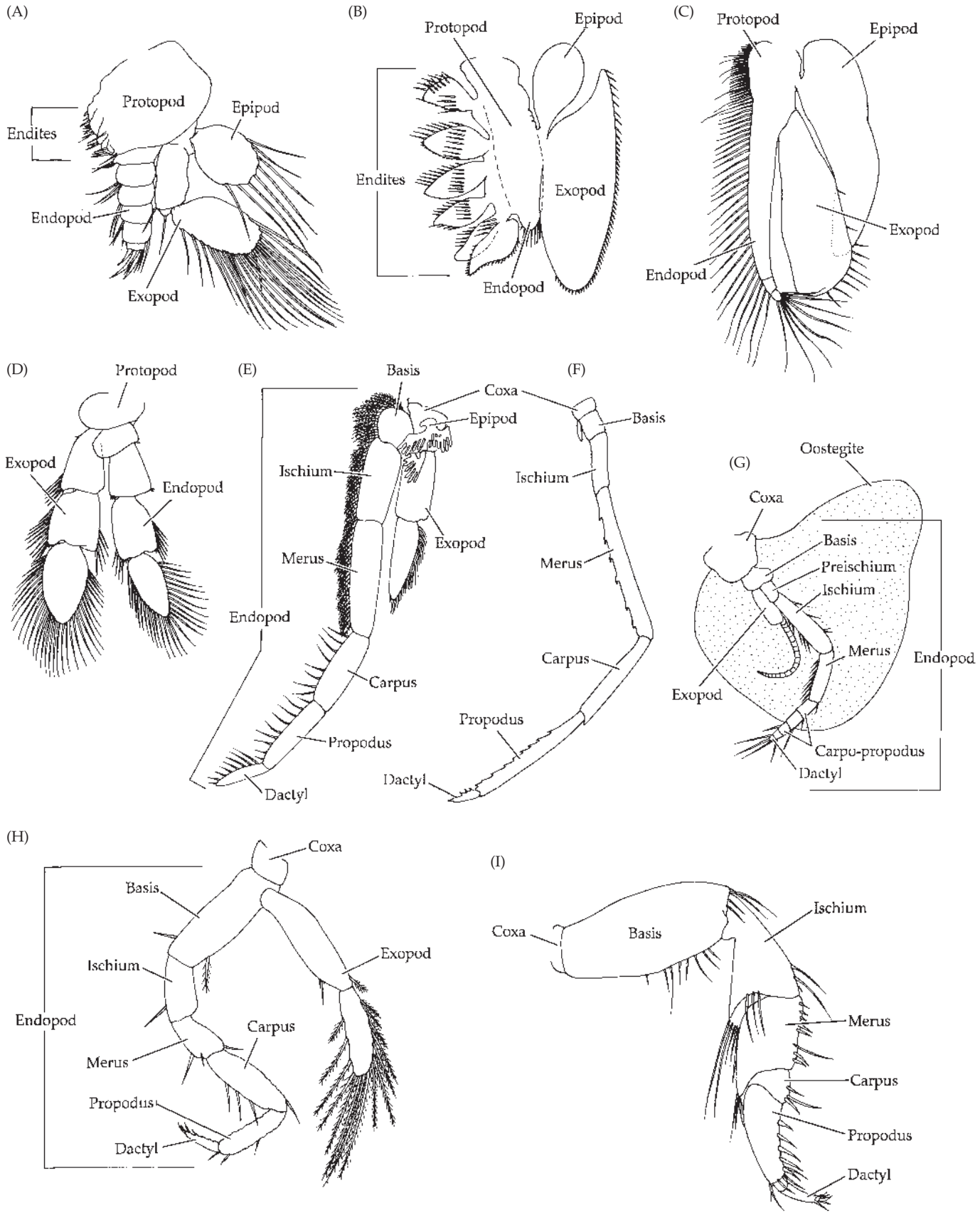
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FIGURE 21.21 Generalized thoracic appendages of various crustaceans. (A–C) Biramous, phyllopodous thoracopods. (A) Cephalocarida. (B) Branchiopoda. Dashed lines indicate fold or "hinge" lines. (C) Leptostraca (Phyllocarida). (D) A biramous, flattened, but nonphyllopodous thoracopod (Remipedia). (E–I) Stenopodous thoracopods. (E) Euphausiacea. (F) Caridea (Decapoda). (G) Lophogastrida (Peracarida). (H) Spelaeogriphacea (Peracarida). (I) Isopoda (Peracarida). Because of the presence of large epipods on the legs of the cephalocarids, branchiopods, and phyllocarids, some authors refer to them as "triramous" appendages. However, smaller epipods also occur on many typical "biramous" legs, so this distinction seems unwarranted (and confusing). Note that in four groups of crustaceans (cephalocarids, branchiopods, phyllocarids, and remipedes) the protopod is composed of a single article. And in branchiopods and leptostracans the articles of the endopod are not clearly separated from one another. In other crustaceans (Malacostraca and former "maxillopodans") the protopod comprises two or three separate articles, although in most former maxillopodans these may be reduced and not easily observed. In the lophogastridans (G), the large marsupial oostegite characteristic of most female peracarids is shown arising from the coxa. In two groups (amphipods and isopods) all traces of the exopods have disappeared, and only the endopod remains as a long, powerful, uniramous walking leg.

Recall from our discussions in Chapters 3 and 20 that at the low Reynolds numbers at which small crustaceans (such as copepods or larvae) swim about, the netlike setal appendages act not as a filtering net, but as a paddle, pushing water in front of them and dragging the surrounding water along with them due to the thick boundary layer adhering to the limb. Only in larger organisms, with Reynolds numbers approaching 1, do setose appendages (e.g., the feeding cirri of barnacles) begin to act as filters, or rakes, as the surrounding water acts less viscous and the boundary layer is relatively thinner. Of course, the closer together the setae and setules are placed, the more likely it is that their individual boundary layers will overlap; thus densely setose appendages are more likely to act as paddles.

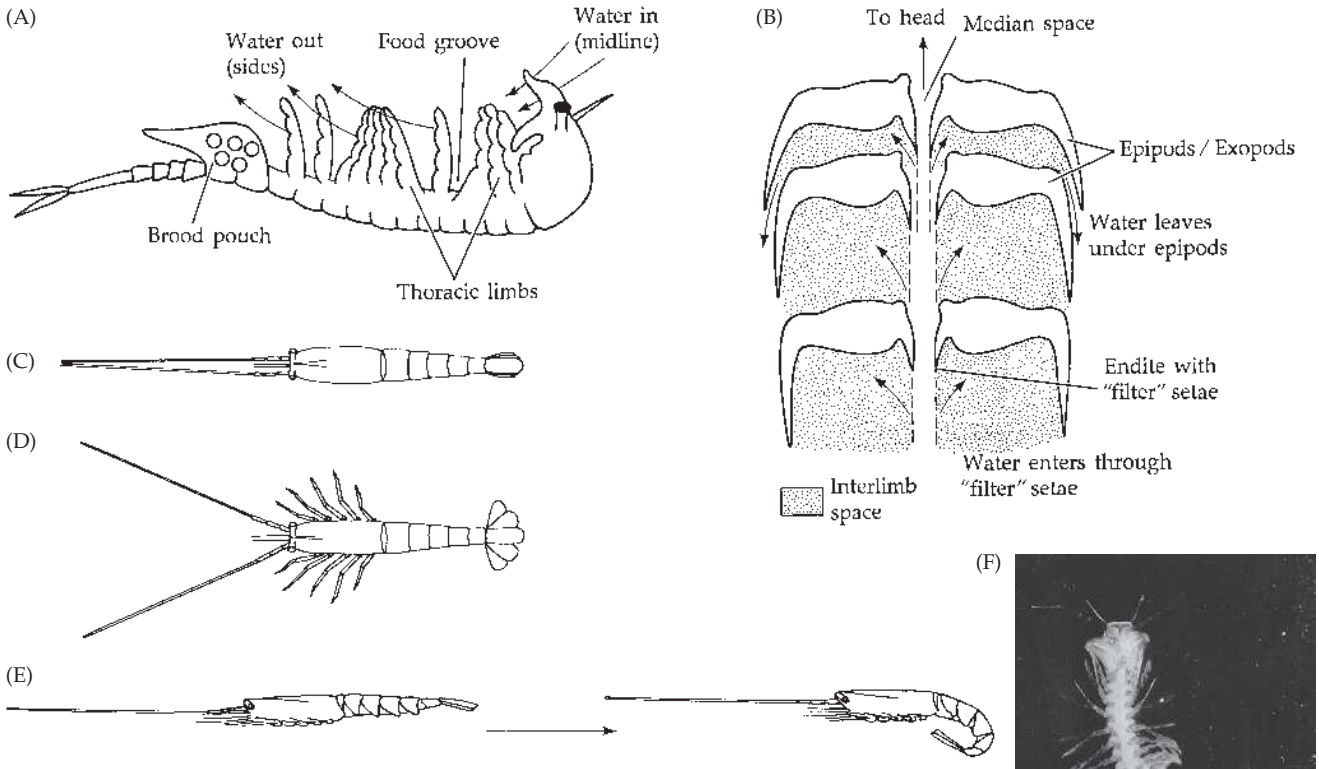

Photo by D. Williams, courtesy of J. Yager

FIGURE 21.22 Some aspects of locomotion (and feeding) in three crustaceans (also see Chapter 20). (A,B) Generation of swimming and feeding currents in an anostracan. (A) An anostracan swimming on its back by metachronal beating of the trunk limbs. The limbs are hinged to fold on the recovery stroke, thereby reducing resistance. (B) Water is drawn from anterior to posterior along the midline and into the interlimb spaces, and food particles are trapped on the medial sides of the endites; excess water is pressed out laterally, and the trapped food is moved anteriorly to the mouth. (C–E) Locomotion in the postlarva of *Panulirus argus*. (C) Normal swimming posture when moving forward slowly. (D) Sinking posture with appendages flared to reduce sinking rate. (E) A quick retreat by rapid tail flexure (the "caridoid escape reaction"), a method commonly employed by crustaceans with well-developed abdomens and tail fans. (F) A swimming remipede, *Lasionectes*. Note the metachronal waves of appendage movement. (C,E after M. D. Calinski and W. G. Lyons. 1983. *J Crust Biol* 3: 329–335.)

Not all swimming crustaceans move by metachronal waves of limb action. Certain planktonic copepods, for example, move haltingly and depend on their long antennules and dense setation for flotation between movements (Figure 21.4F). Watch living calanoid copepods, and you will notice that they may move slowly, by use of the antennae and other appendages, or in short jerky increments, often sinking slightly between these movements. The latter type of motion results from an extremely rapid and condensed metachronal wave of power strokes along the trunk limbs. Although the long antennae may appear to be acting as paddles, they actually collapse against the body an instant prior to the beating of the limbs, thus reducing resistance to forward motion. Some other planktonic copepods create swimming currents by rapid vibrations of cephalic appendages, by which the body moves smoothly through the water. Some copepods execute rapid escape responses, or jumps, when they encounter "upstream" movement that may indicate an approaching predator. These escape responses accelerate them to 200 body lengths per second within milliseconds and, in part, are due to the presence of myelin-like sheaths on key nerve fibers (notably in the antennules). "Rowing" occurs in the swimming crabs (family Portunidae) and some deep-sea asellote isopods (e.g., family Eurycopidae), both of which use paddle-shaped posterior thoracopods to scull about.

Most eumalacostracans with well-developed abdomens exhibit a form of temporary, or "burst," swimming that serves as an escape reaction (e.g., mysidans, syncarids, euphausiaceans, shrimps, lobsters, and crayfish). By rapidly contracting the ventral abdominal (flexor) muscles, such animals shoot quickly backward, the bent-down, spread tail fan providing a large propulsive surface (Figure 21.22C–E). This behavior is sometimes called a **tail flip**, or "**caridoid escape reaction**."

Surface crawling by crustaceans is accomplished by the same general sorts of leg movements seen in insects and other arthropods: by flexion and extension of the limbs to pull or push the animal forward. Walking limbs are typically composed of relatively stout, more or less cylindrical articles (i.e., stenopodous limbs), as opposed to the broader, often phyllopodous limbs of swimmers (see Figure 21.21 for a comparison of crustacean limb types). Walking limbs are lifted from the substratum and moved forward during their recovery strokes; then they are placed against the substratum, which provides purchase as they move posteriorly through their power strokes, pulling and then pushing the animal forward. Like many other arthropods, crustaceans generally lack lateral flexibility at the body joints, so turning is accomplished by reducing the stride length or movement frequency on one side of the body, toward which the animal turns (like a tractor or tank slowing one tread). Many crustaceans migrate; perhaps the most famous is the Chinese mitten crab (*Eriocheir sinensis*), which spends most of its life in fresh water but returns to the sea to breed. These crabs have been found over 1,000 km upriver from the sea—testimony to their superb locomotory ability. Not unexpectedly, *E. sinensis* is also an important (and destructive) invasive species in North America and Europe. It has been accidentally introduced into the Great Lakes several times but has not yet been able to establish a permanent population. Recent work suggests that stomatopods have the ability to accurately return to their "home" burrow using navigation similar to that seen in the terrestrial environment by social hymenopterans, spiders, rodents, fiddler crabs, etc.—through a process known as "path integration." During path integration an animal navigates back on a path previously taken by monitoring the position of the sun and overhead polarization patterns in combination with an internal "odometer."

Most walking crustaceans can also reverse the direction of leg action and move backward, and most brachyuran crabs can walk sideways. Brachyuran crabs are perhaps the most agile of all crustaceans. The extreme reduction of the abdomen in this group allows for very rapid movement because adjacent limbs can move in directions that avoid interference with one another (and much the same thing has happened, independently, in many anomurans with reduced abdomens). Brachyuran crab legs are hinged in such a way that most of their motion involves lateral extension (abduction) and medial flexion (adduction) rather than rotation frontward and backward. As a crab moves, its limbs move in various sequences, as in normal crawling, but those on the leading side exert their force by flexing and pulling the body toward the limb tips, while the opposite, trailing, legs exert propulsive force as they extend and push the body away from the tips. Still, this motion is simply a mechanical variation on the common arthropodan walking behavior. Many crustaceans move into mollusc shells or other objects, carrying these about as added protection. In most cases, the exoskeleton of the crustacean is reduced, especially the abdomen (e.g., hermit crabs). Of course, crustaceans grow in size as they go through their molts, so these mobile-home-carrying crustaceans must continually find larger shells to inhabit. Many hermit crabs assemble in congregations to exchange shells in a sort of group "passing of the shells" as they move into vacated larger abodes.

In addition to these two basic locomotor methods ("typical" walking and swimming by metachronal beating of limbs), many crustaceans move by other specialized means. Ostracods, cladocerans, and clam shrimps (Diplostraca), most of which are largely enclosed by their carapaces (Figures 21.3 and 21.20F,G,J,L,M), swim by rowing with the antennae. Mystacocarids crawl in interstitial water using various head appendages. Most semiterrestrial amphipods known as "beach hoppers" (e.g., *Orchestia* and *Orchestoidea*) execute dramatic jumps by rapidly extending the urosome and its appendages (uropods), reminiscent of the jumping of springtails described in Chapter 22. Most caprelloidean

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amphipods (Figure 21.16E) move about in inchworm fashion, using their subchelate appendages for clinging. There are also a number of crustacean burrowers, and even some that build their own tubes or "homes" from materials in their surroundings. Many benthic amphipods, for example, spin silk-lined mud burrows in which they reside. At least one species, *Pseudamphithoides incurvaria*, constructs and lives in an unusual "bivalved pod" cut from the thin blades of the same alga on which it feeds (Figure 21.23A). Another amphipod, *Photis conchicola*, actually uses empty gastropod shells in a fashion similar to that of hermit crabs (Figure 21.23B). "Hitchhiking" (phoresis) occurs in various ectosymbiotic crustaceans, including isopods that parasitize fishes or shrimps and hyperiidean amphipods that ride on gelatinous drifting plankters.

In addition to simply getting from one place to another in their usual day-to-day activities, many crustaceans exhibit various migratory behaviors, employing their locomotor skills to avoid stressful situations or to remain where conditions are optimal. A number of planktonic crustaceans undertake daily vertical migrations, typically moving upward at night and to greater depths during the day. Such vertical migrators include various copepods, cladocerans, ostracods, and hyperiid amphipods (the latter may make their migrations by riding on their gelatinous hosts). Such movements place the animals in their near-surface feeding grounds during the dark hours, when there is probably less danger of being detected by visual predators. In the daytime, they move to deeper, perhaps safer, waters. These crustaceans can form enormous shoals that contribute to the deep scattering layer seen on ships' sonar. Many intertidal crustaceans use their locomotor abilities to change their behaviors with the tides. Crab larvae in particular are known to migrate upward or downward according to

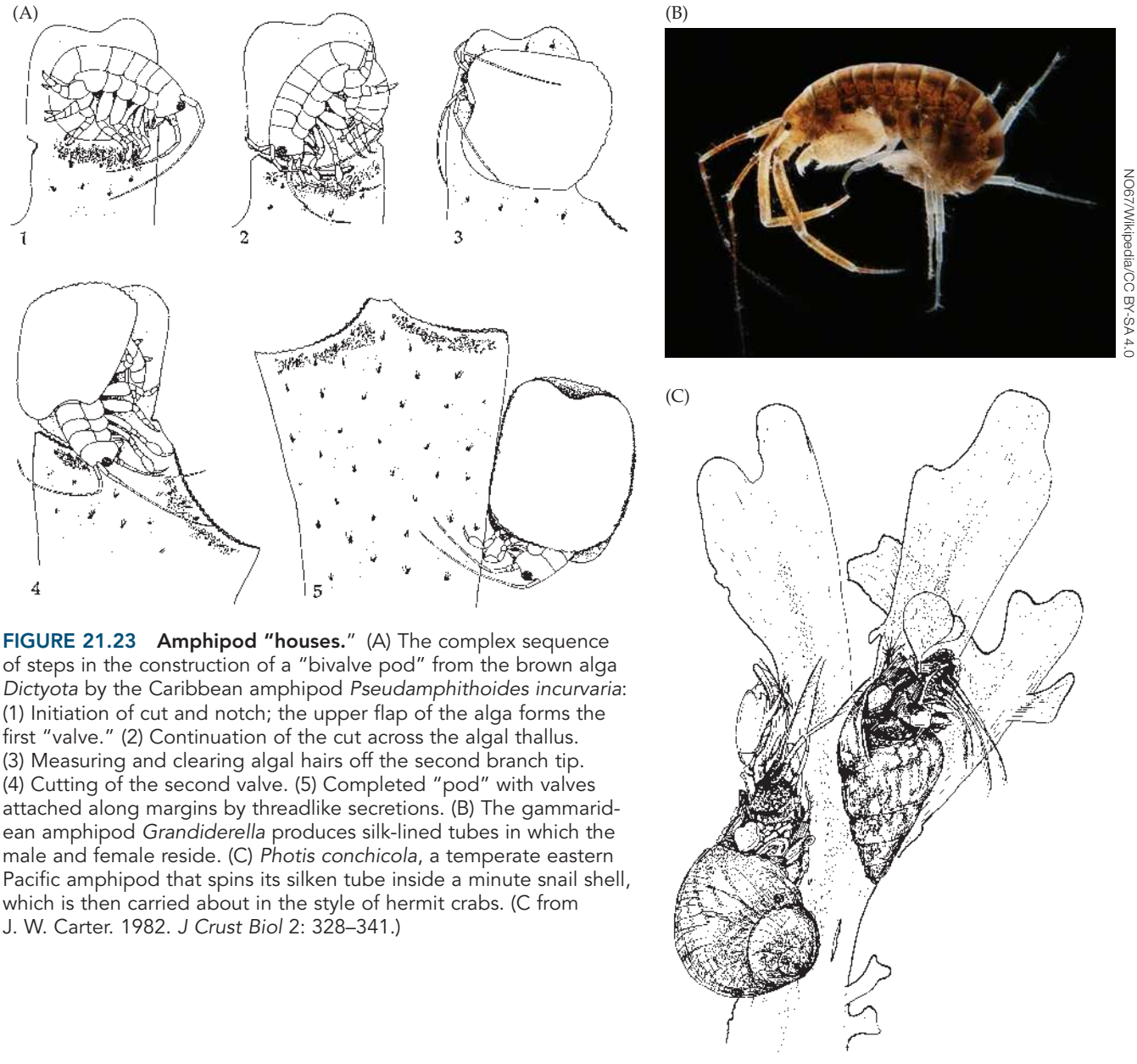

FIGURE 21.23 Amphipod "houses." (A) The complex sequence of steps in the construction of a "bivalve pod" from the brown alga *Dictyota* by the Caribbean amphipod *Pseudamphithoides incurvaria*: (1) Initiation of cut and notch; the upper flap of the alga forms the first "valve." (2) Continuation of the cut across the algal thallus. (3) Measuring and clearing algal hairs off the second branch tip. (4) Cutting of the second valve. (5) Completed "pod" with valves attached along margins by threadlike secretions. (B) The gammaridean amphipod *Grandiderella* produces silk-lined tubes in which the male and female reside. (C) *Photis conchicola*, a temperate eastern Pacific amphipod that spins its silken tube inside a minute snail shell, which is then carried about in the style of hermit crabs. (C from J. W. Carter. 1982. *J Crust Biol* 2: 328–341.)

daily rhythms, taking advantage of incoming or outgoing tides to move in and out of estuaries. Some anomuran and brachyuran crabs simply move in and out with the tide, or seek shelter beneath rocks when the tide is out, thus avoiding the problems of air exposure. One of the most interesting locomotor behaviors among crustaceans is the mass migration of the spiny lobster, *Panulirus argus*, in the Gulf of Mexico and northern Caribbean. Each autumn, lobsters queue up in single file and march in long lines across the seafloor for several days. They move from shallow areas to the edges of deeper oceanic channels. This behavior is apparently triggered by winter storm fronts moving into the area, and it may be a means of avoiding rough water conditions in the shallows. At the beginning of the wet season, the endemic Christmas Island red crabs (*Gecarcoidea natalis*) undertake their annual mass migration from the forest to shore (up to 8 km) to deposit their eggs in the sea.

Feeding

With the exception of ciliary mechanisms, crustaceans have exploited virtually every feeding strategy imaginable (and some "unimaginable"). Even without cilia, many crustaceans generate water currents and engage in various types of suspension feeding. We have selected a few examples to demonstrate the range of feeding mechanisms that occur in this group. In most cases, suspension-feeding Crustacea capture and consume particles in the <100 μm size (unicellular algae, invertebrate eggs and larvae, bacteria, suspended organic detritus).

In some crustaceans the action of the thoracic limbs simultaneously creates the swimming and suspension-feeding currents. As the metachronal wave of appendage motion passes along the body, adjacent limb pairs are alternately moved apart and then pressed together, thus changing the size of each interlimb space (Figure 21.22A,B; see also Chapters 3 and 20). Surrounding water is drawn into an interlimb space as the adjacent appendages move away from one another, and waterborne particles are trapped by setae on the endites as the appendages then press together. From here, the trapped particles are moved to a midventral food groove and then anteriorly, toward the head. This mechanism of forming a boxlike "filter press" with setose phyllopodous limbs is the typical suspension-feeding strategy of cephalocarids, most branchiopods, and many malacostracans.

Planktonic copepods were long thought to "filter" feed by generating lateral feeding gyres or currents by movements of the antennae and mouth appendages. It was believed that these gyres swept in small particles that were directly filtered by the maxillae. This classic idea of maxillary filtration, built on work by H. G. Cannon in the 1920s, has been questioned by recent work, but the model persists and is still commonly presented in general works. As mentioned in Chapter 3, we now know that copepods and other small planktonic crustaceans live in a world of low Reynolds numbers, a world dominated by viscosity rather than by inertia. Thus, the setose mouth appendages behave more like paddles than like sieves, with a water layer near the limb adhering to it and forming part of the "paddle." As the maxillae move apart, parcels of water containing food are drawn into the interlimb space. As the maxillae press together, the "parcel" is moved forward to the endites of the maxillules, which push it into the mouth. Thus, food particles are actually not filtered from the water, but captured in small parcels of water. High-speed cinematography indicates that copepods are capable of capturing individual algal cells, one at a time, by this "hydraulic vacuum" method. In fact, copepods may be fairly selective about what they consume, which includes everything from protistan microplankton (e.g., diatoms) to other small crustaceans.

Sessile thoracican barnacles feed by using their long, feathery, biramous thoracopods, called **cirri**, to filter feed on suspended material from the surrounding water (Figure 21.17A,C,E). Studies indicate that barnacles are capable of trapping food particles ranging from 2 μm to 1 mm, including detritus, bacteria, algae, and various zooplankters. Many barnacles are also capable of preying on larger planktonic animals by coiling a single cirrus around the prey, in tentacle fashion. In slow-moving or very quiet water, most barnacles feed actively by extending the last three pairs of cirri in a fanlike manner and sweeping them rhythmically through the water. The setae on adjacent limbs and limb rami overlap to form an effective filtering net. The first three pairs of cirri serve to remove trapped food from the posterior cirri and pass it to the mouthparts. In areas of high water movement, such as wave-swept rocky shores, barnacles often extend their cirri into the backwash of waves, allowing the moving water to simply run through the "filter," rather than actively moving the cirri through the water. In such areas you will often see clusters of barnacles in which all the individuals are oriented similarly, taking advantage of this labor-saving device.

Most krill (euphausiaceans) feed in a fashion similar to that of barnacles, but while swimming. The thoracopods form a "feeding basket" that expands as the legs move outward, sucking food-laden water in from the front. Once inside the basket, particles are retained on the setae of the legs as the water is squeezed out laterally. Other setae comb the food particles out of the "trap" setae, while yet another set brushes them forward to the mouth region.

Anomuran sand crabs (e.g., *Emerita*, *Lepidopa*, *Blepharipoda*) use their long, setose antennae in a fashion similar to that of barnacle cirri that "passively" strain wave backwash (Figure 21.24; see also Chapter 3). Sand crabs are adapted to living on wave-swept sand beaches. Their compact oval shape and strong appendages facilitate burrowing in the unstable substratum. They burrow posterior end first in the area of wave wash, with the anterior end facing upward. Following

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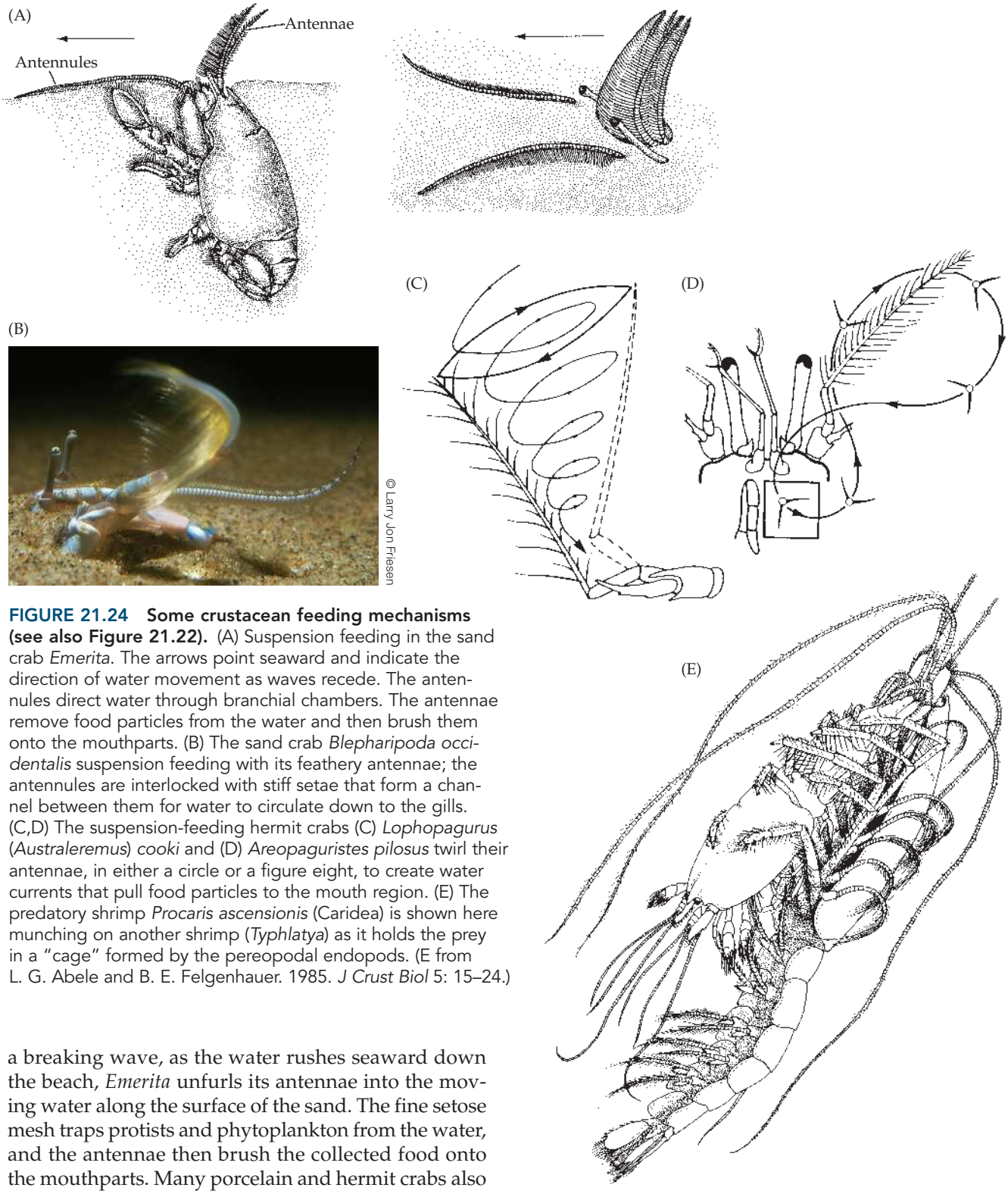

FIGURE 21.24 Some crustacean feeding mechanisms (see also Figure 21.22). (A) Suspension feeding in the sand crab *Emerita*. The arrows point seaward and indicate the direction of water movement as waves recede. The antennules direct water through branchial chambers. The antennae remove food particles from the water and then brush them onto the mouthparts. (B) The sand crab *Blepharipoda occidentalis* suspension feeding with its feathery antennae; the antennules are interlocked with stiff setae that form a channel between them for water to circulate down to the gills. (C,D) The suspension-feeding hermit crabs (C) *Lophopagurus* (*Australeremus*) *cooki* and (D) *Areopaguristes pilosus* twirl their antennae, in either a circle or a figure eight, to create water currents that pull food particles to the mouth region. (E) The predatory shrimp *Procaris ascensionis* (Caridea) is shown here munching on another shrimp (*Typhlatya*) as it holds the prey in a "cage" formed by the pereopodal endopods. (E from L. G. Abele and B. E. Felgenhauer. 1985. *J Crust Biol* 5: 15–24.)

a breaking wave, as the water rushes seaward down the beach, *Emerita* unfurls its antennae into the moving water along the surface of the sand. The fine setose mesh traps protists and phytoplankton from the water, and the antennae then brush the collected food onto the mouthparts. Many porcelain and hermit crabs also engage in suspension feeding. By twirling their antennae in various patterns, these anomurans create spiraling currents that bring food-laden water toward the mouth (Figure 21.24B,C). Food particles then become entangled on setae of the mouth appendages and are brushed into the mouth by the endopods of the third maxillipeds. Many of these animals also feed on detritus by simply picking up particles with their chelipeds.

Some mud, ghost, and lobster shrimps, such as *Callianassa* and *Upogebia* (Axiidea, Gebiidea), suspension feed within their burrows. They drive water through the burrow by beating the pleopods, and the first two pairs of pereopods remove food with medially directed setal brushes. The maxillipeds then comb the captured particles forward to the mouth.

Most other crustacean feeding mechanisms are less complicated than suspension feeding and usually involve direct manipulation of food by the mouthparts and sometimes the pereopods, especially chelate or

subchelate anterior legs. However, even in these cases of direct manipulation, the sheer number of crustacean appendages adapted for feeding makes "simple" feeding a surprisingly complex affair, with the various mouthparts taking on tasks that include tasting (via sensory setae), holding, chewing, scraping, and macerating.

Many small crustaceans may be classified as microphagous selective deposit feeders, employing various methods of removing food from the sediments in which they live. Mystacocarids, many harpacticoid copepods, and some cumaceans and gammaridean amphipods are referred to as "sand grazers" or "sand lickers." By various methods these animals remove detritus, diatoms, and other microorganisms from the surfaces of sediment particles. Interstitial mystacocarids, for example, simply brush sand grains with their setose mouthparts. On the other hand, some cumaceans pick up an individual sand grain with their first pereopods and pass it to the maxillipeds, which in turn rotate and tumble the particle against the margins of the maxillules and mandibles. The maxillules brush and the mandibles scrape, removing organic material. Some sand-dwelling isopods may employ a similar feeding behavior.

Predatory crustaceans include stomatopods, remipedes, and most lophogastridans, as well as many species of anostracans, cladocerans, copepods, ostracods, cirripedes, anaspidaceans, euphausiaceans, decapods, tanaidaceans, isopods, and amphipods. Predation typically involves grasping the prey with chelate or subchelate pereopods (or sometimes directly with the mouth appendages), or even with the antennae in the case of predatory anostracans, followed by tearing, grinding, or shearing with various mouthparts, particularly the mandibles. Perhaps the most highly adapted predatory specialists are the stomatopods (Figure 21.8), which possess greatly enlarged, raptorial subchelate limbs, which they use to stab or to club and smash prey. Some species search out prey, but many sit in ambush at their burrow entrance. The actual attack generally follows visual detection of a potential prey item, which may be another crustacean, a mollusc, or even a small fish. Once captured and stunned or killed by the raptorial claws, the prey is held against the mouthparts and shredded into ingestible pieces.

Although the cave-dwelling and often presumed "primitive" shrimp *Procaris* is omnivorous, its predatory behavior is particularly interesting. Its prey includes other crustaceans, particularly amphipods and shrimps. After *Procaris* locates a potential victim (probably by chemoreception), it moves quickly to the prey and grasps it within a "cage" formed by the pereopodal endopods (Figure 21.24E). Once captured, the prey is eaten while the shrimp swims about. Apparently the third maxillipeds press the prey against the mandibles, which bite off chunks and pass them to the mouth.

The remipedes capture prey with their raptorial mouth appendages (Figures 21.1A, 21.19D–F, and 21.22F) and then immobilize the victim with an injection of venom from the hypodermic maxillules. It is suspected that tissues are then sucked out of the prey by action of a mandibular mill and muscular foregut. Remipedes are probably also facultative suspension feeders and scavengers.

Another fascinating adaptation for predation can be seen in many species of Alpheidae (the snapping shrimps, e.g., *Alpheus, Synalpheus*) (Figure 21.10D). In such species, one of the chelipeds is much larger than the other, and the movable finger is hinged in such a way that it can be held open under muscle tension and then snapped closed quickly; this forceful closing produces a loud popping sound and a pressure or "shock" wave in the surrounding water. Some species appear to use this mechanism in ambushing prey (although most alpheids are probably omnivores and even include algae in their diet). When feeding in a predatory mode, the shrimp sits at its burrow entrance with the antennae extended. When a potential prey approaches (usually a small fish, crustacean, or annelid), the shrimp "pops" its cheliped, and the resulting pressure wave stuns the victim, which is then quickly pulled into the burrow and consumed. These shrimps typically live in male-female pairs within the burrow, and prey captured by one individual is shared with its partner. Two mechanisms have been proposed for the production of the "pop" and associated shock wave. In some species the pop seems to be created by mechanical impact of the dactylus hammering into the propodus. A second mechanism recently proposed is the collapse of cavitation bubbles, which are created by the rapid closure of the claw (in excess of 100 km/sec). Cavitation occurs in liquids when bubbles form and then implode around an object (it is a well-known phenomenon damaging ship propellers). Both mechanisms create shock waves. Cavitation shocks are also used by some stomatopods while feeding. Some boring (endolithic) alpheids even use the claw snap to break off pieces of the rock into which they are digging. In some areas of the world, populations of snapping shrimps are so large that their noise disturbs underwater communication. In the Caribbean, colonies of alpheids have been likened to those of social insects (e.g., *Synalpheus regalis* colonies in Belize inhabit sponges and contain up to 350 sibling males and females, with a single dominant breeding female).

Many crustaceans emerge from the benthos under cover of darkness to feed or mate in the water column. Many predatory isopods emerge at night to feed on invertebrates or fish, particularly weak or diseased fish (or fish caught in fishing nets).

Macrophagous herbivorous and scavenging crustaceans generally feed by simply hanging onto the food source and biting off bits with the mandibles (a feeding technique similar to that of grasshoppers and other insects). Notostracans, some ostracods, and many decapods, isopods, and amphipods are scavengers and herbivores. Isopods in several families bore into wood,

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and those in the family Limnoriidae (the gribbles) produce their own cellulase, which they use to digest woody tissues (the presence of blood hemocyanin in the hindgut appears to enhance the digestibility of the cellulose). Some species of Sphaeromatidae bore into the aerial roots of mangrove trees, and their activities often result in root breakage followed by new multiple root initiation, creating the stiltlike appearance characteristic of red mangroves (*Rhizophora*), although at an overall growth-productivity cost to the trees. A number of crustaceans are full-time or part-time detritivores; many scavenge directly on detritus, but others (e.g., cephalocarids) stir up the sediments in order to remove organic particles by suspension feeding.

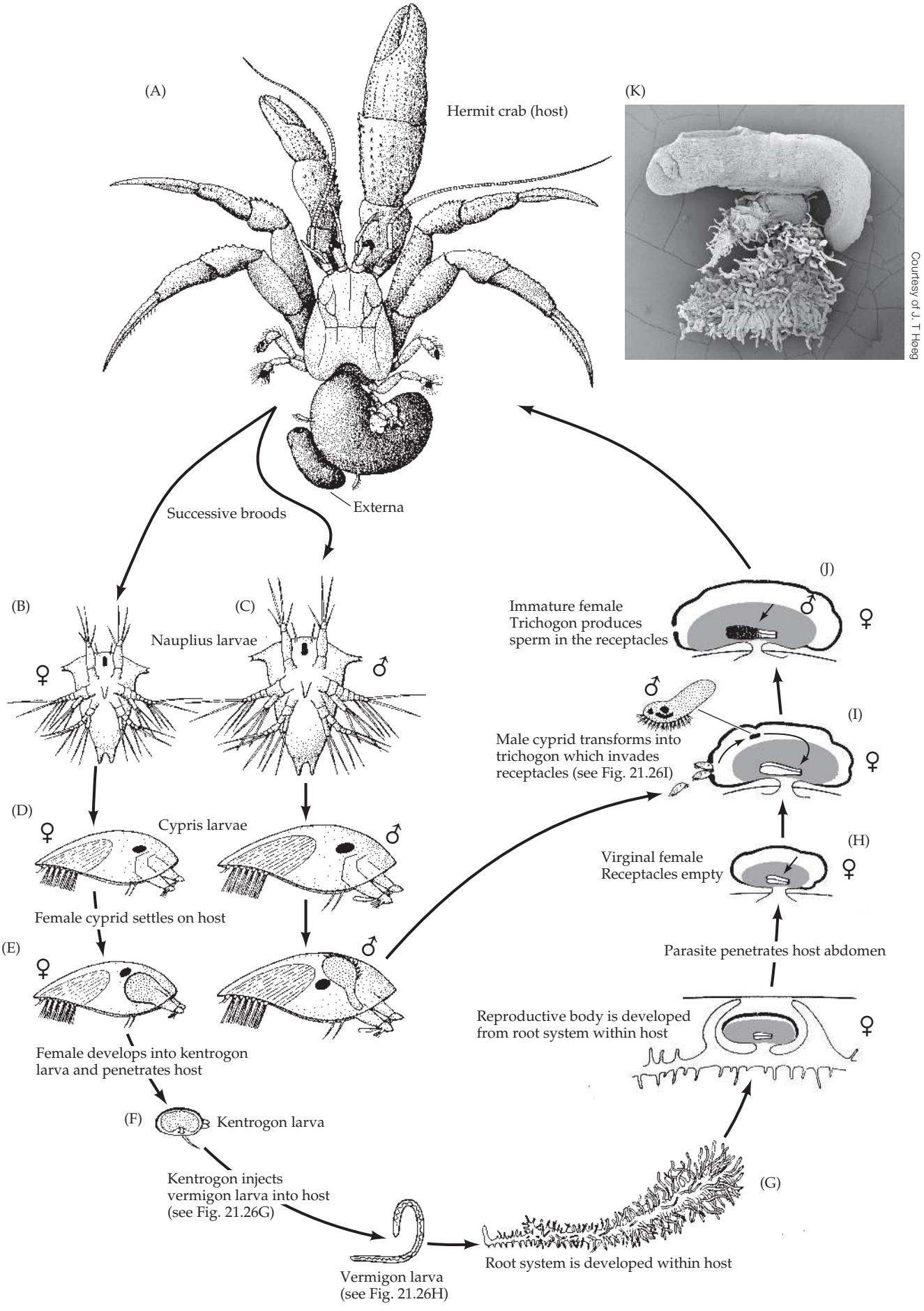
A great many crustacean species, and entire lineages are symbiotic with other organisms. Many are parasites, but others are commensals or mutualists. Some decapod mutualists are simply cases in which the crustacean defends the host against predators and/or removes detritus and potential pathogens from the host's surface. Among the true crabs (Brachyura), six families consist exclusively of obligate symbionts, and obligate symbionts are also found in at least four additional brachyuran families (and facultative symbionts occur in numerous other families). For example, the gall crabs (Cryptochiridae) comprise over 50 species of obligate symbionts of scleractinian corals. There is a range of "gall" formation, from simple pits or chambers to enclosures formed by the coral as it grows over the crab (presumably induced by the respiratory currents and scratching of the crabs on the coral). Gall crab females always inhabit pits or chambers and rarely leave; males live in separate chambers or free on the coral surface and must move into the females' chambers for copulation. Members of the brachyuran families Domeciidae and Tetraliidae are also all symbionts of zooxanthellate corals, Trapeziidae are obligate symbionts of corals and other colonial cnidarians and sponges, and the subfamily Eumedoninae (Pilumnidae) are obligate symbionts of Indo–West Pacific echinoderms.

Several groups of crustaceans have adopted various degrees of parasitism. These animals range from ectoparasites with mouthparts modified for piercing or tearing and sucking body fluids (e.g., many copepods, branchiurans, tantulocarids, several isopod families, and at least one species of ostracod), to the highly modified and fully parasitic rhizocephalans, whose bodies ramify throughout the host tissue and absorb nutrients directly (Figures 21.25 and 21.26), and pentastomids.

Rhizocephalans, which are cirripeds that have been highly modified to become internal parasites of other crustaceans, are some of the most bizarre organisms in the animal kingdom. The most complex rhizocephalan life cycle is that of the kentrogonid forms, in which a settled female cypris larva undergoes an internal reorganization that rivals that of caterpillar pupae in scope, developing an infective stage, called the **kentrogon**, beneath the cyprid exoskeleton. Once fully developed, the kentrogon forms a hollow cuticular structure, the **stylet**, which injects a motile, multicellular, vermiform stage called the **vermigon** into the host. The vermigon is the active infection stage. It has a thin cuticle and epidermis, several types of cells, and the anlage of an ovary. It invades the host's hemocoel by sending out long, branching, hollow rootlets that penetrate most of the host's body and draw nutrients directly from the hemocoel. So profound is the intrusion by the rootlets that the parasite takes over nearly complete control of the host's body, altering its morphology, physiology, and behavior. Once the parasite invades the host's gonads, parasitic castration may result (i.e., the gonads of parasitized crabs never produce mature gametes). Thus the host is transformed into a slave that serves the needs of its master. The internal root system, or **interna**, eventually develops an external reproductive body (the **externa**), where egg production occurs. A male cyprid settles on the externa, transforms into a minute sexually mature instar called a **trichogon**, and moves into the ovary-filled externa to take up residence, where its sole function is to produce sperm. It takes only one or two trichogons to stimulate the female ovaries to mature and begin releasing eggs into the chamber of the externa. An externa that fails to obtain male trichogons eventually dies. The males are thus parasitic on the female (which is itself parasitic on the crustacean host), and kentrogonids are gonochoristic. A mature externa, usually arising from the host's abdomen, will produce a succession of larval broods, molting after each larval release (it is the only part of the rhizocephalan body that molts). The larvae are lecithotrophic and develop through several nauplius stages to the cyprid (Figures 21.25 and 21.26).

The akentrogonid rhizocephalans lack a kentrogon stage in their life cycle. Instead of injecting a vermigon, the female cyprid has long, slender antennules that it uses to attach to the abdomen of the host, one of which actually penetrates the host's cuticle, becomes hollow, and serves for the passage of embryonic cells from cypris larva to host. Male cyprids somehow find infected hosts and penetrate them in the same fashion as the females, releasing their sperm in such a way that they actually enter the body of the female parasite.

The akentrogonid life cycle is similar to that of kentrogonid species, although in some cases more than one individual parasite might infect a single host, leading to multiple externas. And in at least one genus (*Thompsonia*), multiple externas can develop from a single infection. The anatomy of the externa is more variable than in kentrogonids, and the embryos develop directly into cypris larvae—there are no free-swimming nauplius stages. The extreme sexual size dimorphism of kentrogonids does not occur in akentrogonid species, and no migrating trichogon stage has been observed. These two life cycle types used to be the basis for dividing the Rhizocephala into two orders, Kentrogonida and Akentrogonida, but an elegant phylogenetic analysis by Høeg et al. (2020) showed these two groups to be


(A)
Hermit crab (host)
(K)
Courtesy of J. T Høeg
Externa
Successive broods
(B)
(C)
Nauplius larvae
(J)
Immature female
Trichogon produces
sperm in the receptacles
(D)
Cypris larvae
(I)
Male cyprid transforms into
trichogon which invades
receptacles (see Fig. 21.26I)
Female cyprid settles on host
(H)
Virginal female
Receptacles empty
(E)
Parasite penetrates host abdomen
Reproductive body is developed
from root system within host
Female develops into kentrogon
larva and penetrates host
(F)
Kentrogon larva
Kentrogon injects
vermigon larva into host
(see Fig. 21.26G)
(G)
Root system is developed within host
Vermigon larva
(see Fig. 21.26H)

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◀ **FIGURE 21.25 The life cycle of the rhizocephalan cirripede *Peltogaster paguri*, a kentrogonid parasite of hermit crabs.** (A) The mature reproductive portion of the parasite (externa) produces numerous broods of male and female larvae, which are released as nauplii (B,C) and eventually metamorphose into cypris larvae (D). Female cyprids settle on the thorax and limbs of host crabs (E) and undergo a major internal metamorphosis into the kentrogon form (F), which is provided with a pair of antennules and an injection stylet. The kentrogon's viscera metamorphoses into an infective stage, the vermigon, which is transferred to the host through the hollow stylet. Inside the host, the vermigon grows rootlets that ramify throughout much of the host's body; it is now called the interna (G). Eventually the female parasite emerges on the abdomen of the host as a virginal externa (H). When the externa acquires a mantle pore, or aperture, it becomes attractive to male cyprids (I). Male cyprids settle within the aperture, transform into a trichogon form, and implant part of their body contents in the female's receptacles (J). The deposit proceeds to differentiate into spermatozoa, which fertilize the eggs of the female. (K) The dissected externa, with its rootlets, of *Peltogaster*, removed from its host. Note the mantle aperture.

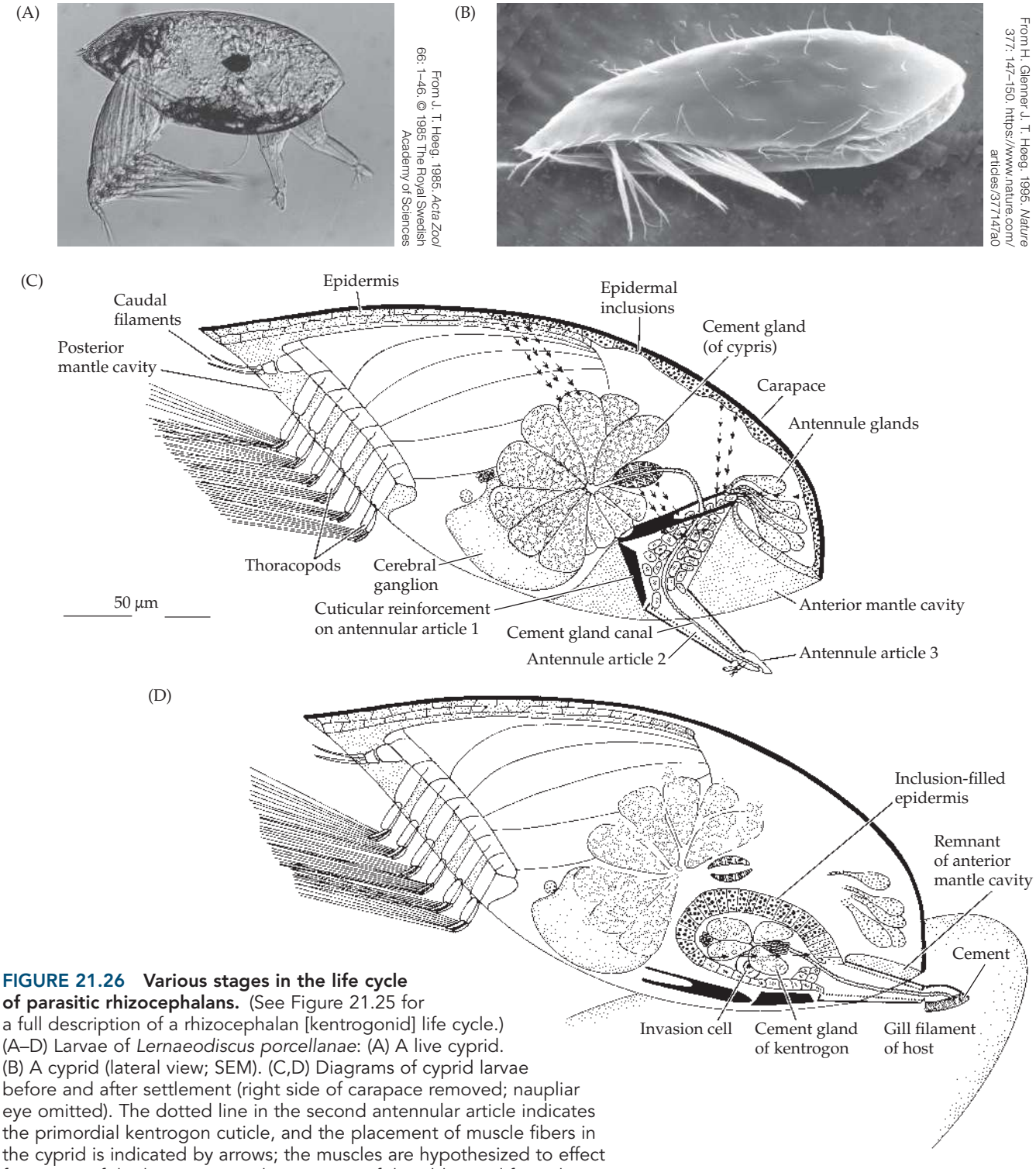

FIGURE 21.26 Various stages in the life cycle of parasitic rhizocephalans. (See Figure 21.25 for a full description of a rhizocephalan [kentrogonid] life cycle.) (A–D) Larvae of *Lernaeodiscus porcellanae*: (A) A live cyprid. (B) A cyprid (lateral view; SEM). (C,D) Diagrams of cyprid larvae before and after settlement (right side of carapace removed; naupliar eye omitted). The dotted line in the second antennular article indicates the primordial kentrogon cuticle, and the placement of muscle fibers in the cyprid is indicated by arrows; the muscles are hypothesized to effect formation of the kentrogon and separation of the old cyprid from the kentrogon. In D, kentrogon formation is complete.

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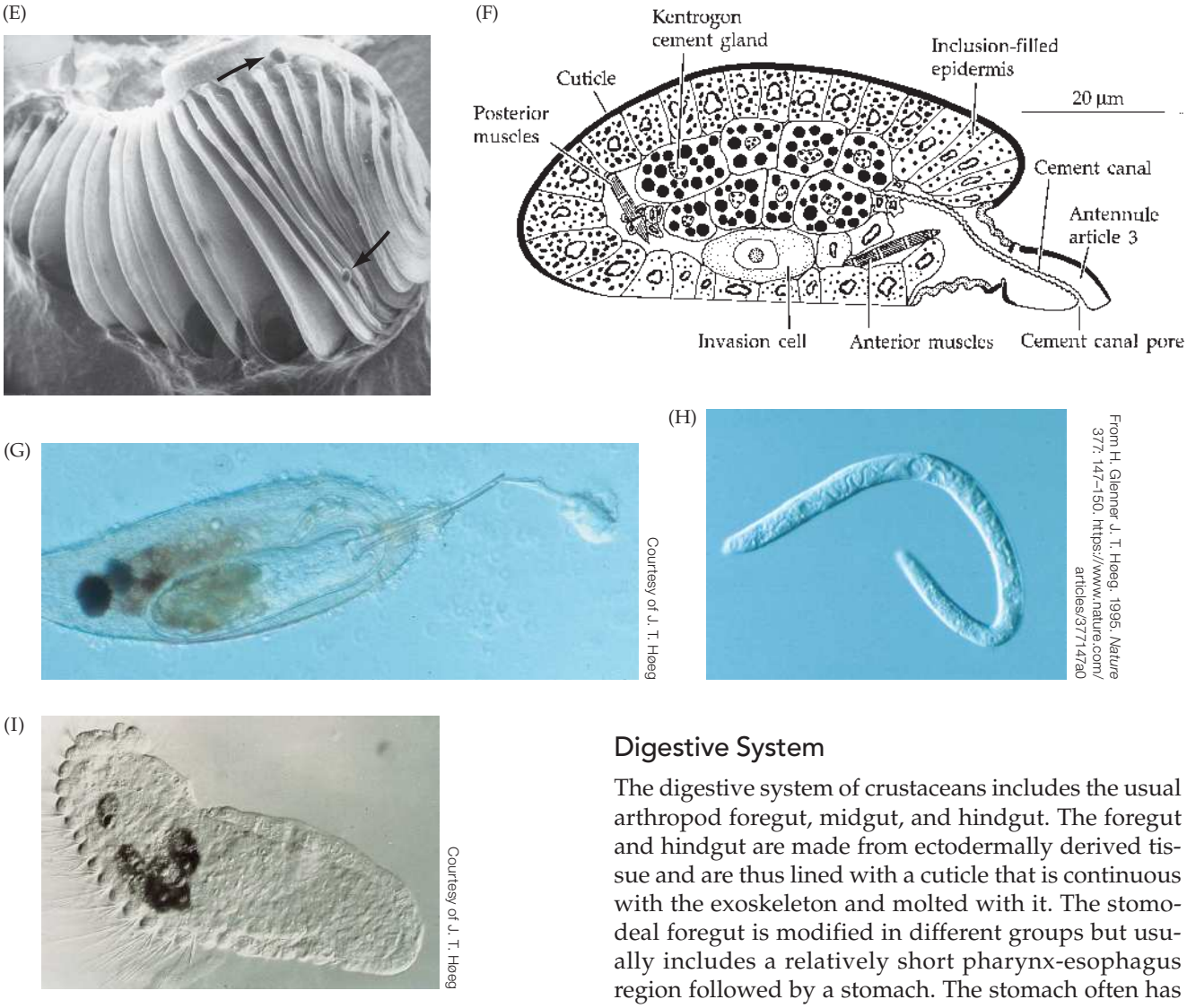

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Courtesy of J. T. Høeg

FIGURE 21.26 (*continued*) Various stages in the life cycle of parasitic rhizocephalans. (E) A whole gill (SEM) of a host crab, *Petrolisthes cabrilloi* (Anomura), with several attached kentrogons (arrows). (F) A 2-hour-old kentrogon (sagittal section). (G) A kentrogon injecting a vermigon via the stylet. (H) A vermigon. (I) A trichogon.

nonmonophyletic. The kentrogonid mode of host invasion is likely the original, whereas the akentrogonid mode has been derived at least twice.

Isopods of the family Cymothoidae use modified mouthparts to suck the body fluids of their fish hosts. They attach to their host's skin or gills or, in some genera, to the tongue. One species, *Cymothoa exigua*, sucks so much blood out of its host's tongue (the spotted rose snapper, in the Gulf of California) that the tongue completely degenerates. But, remarkably, the fish doesn't die; the isopod remains attached with its clawed legs to the basal muscles of the missing tongue, and the fish uses the crustacean as a "replacement tongue" to continue to feed. This is one of the few known cases of a parasite functionally replacing a host organ it destroys.

Digestive System

The digestive system of crustaceans includes the usual arthropod foregut, midgut, and hindgut. The foregut and hindgut are made from ectodermally derived tissue and are thus lined with a cuticle that is continuous with the exoskeleton and molted with it. The stomodeal foregut is modified in different groups but usually includes a relatively short pharynx-esophagus region followed by a stomach. The stomach often has chambers or specialized regions for storage, grinding, and sorting; these structures are best developed in the malacostracans (Figure 21.27G). The midgut forms a short or long intestine—the length depending mainly on overall body shape and size—and bears variably placed **digestive ceca**. The ceca are serially arranged only in the remipedes. In some malacostracans, such as crabs, the ceca fuse to form a solid glandular mass, best called a **digestive gland** but sometimes called a midgut gland or hepatopancreas, within which are many branched, blind tubules. The digestive gland in some crustaceans has been shown to store lipids. The hindgut is usually short, and the anus is generally borne on the anal somite or telson, or on the last segment of the abdomen (when the anal somite is reduced or lost).

Examples of some crustacean digestive tracts are shown in Figure 21.27. Generally, expansion of the esophagus and foregut creates a suction that draws food into the mouth and esophagus. Foregut contractions push the food into the midgut, where most breakdown and absorption occur. The foregut is typically elaborate with folds and ridges and can even be armed with calcareous ossicles (e.g., many decapods).

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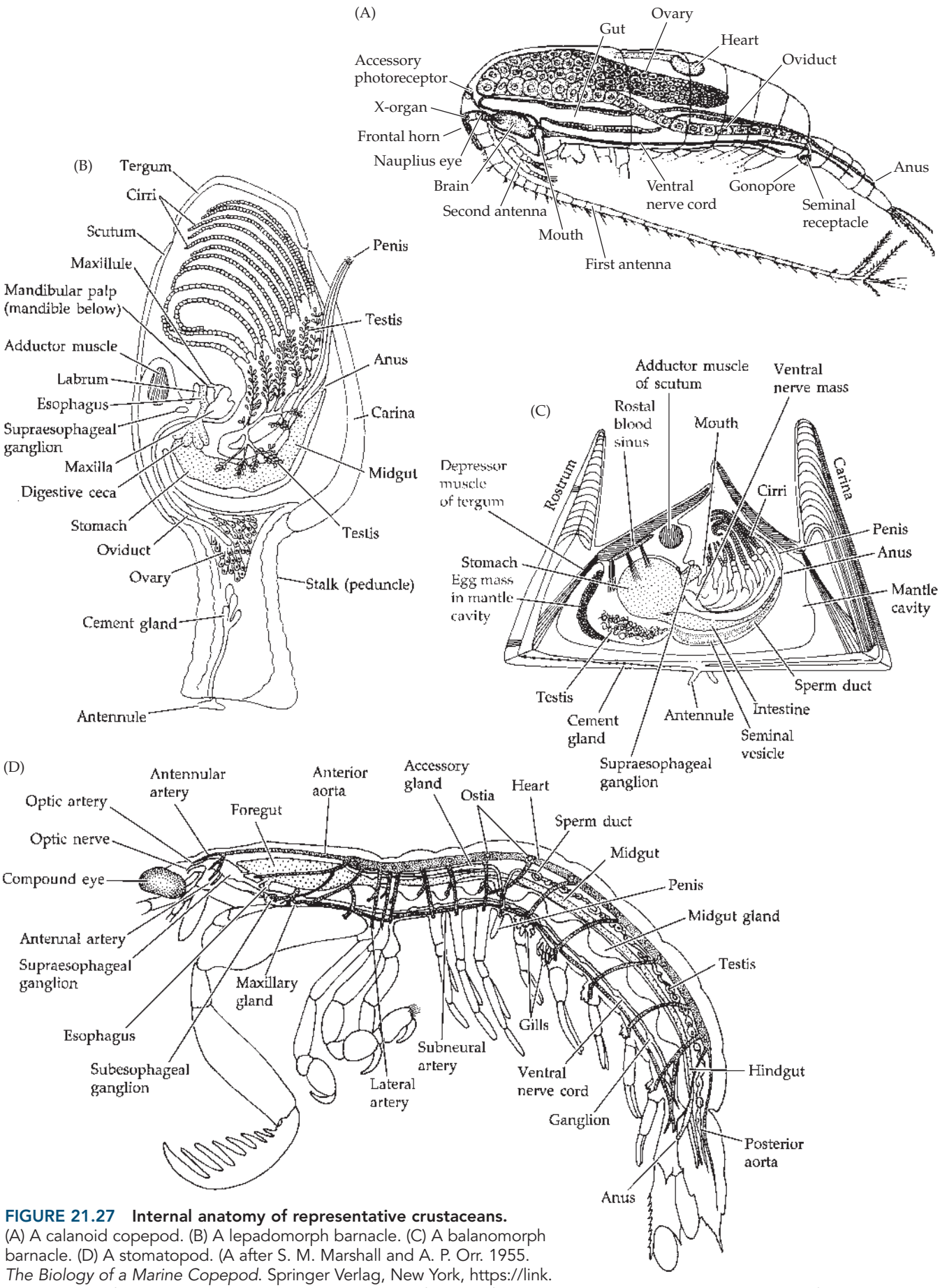

FIGURE 21.27 Internal anatomy of representative crustaceans. (A) A calanoid copepod. (B) A lepadomorph barnacle. (C) A balanomorph barnacle. (D) A stomatopod. (A after S. M. Marshall and A. P. Orr. 1955. *The Biology of a Marine Copepod*. Springer Verlag, New York, https://link.springer.com/chapter/10.1007/978-3-662-13138-1_2 [and see credits].).

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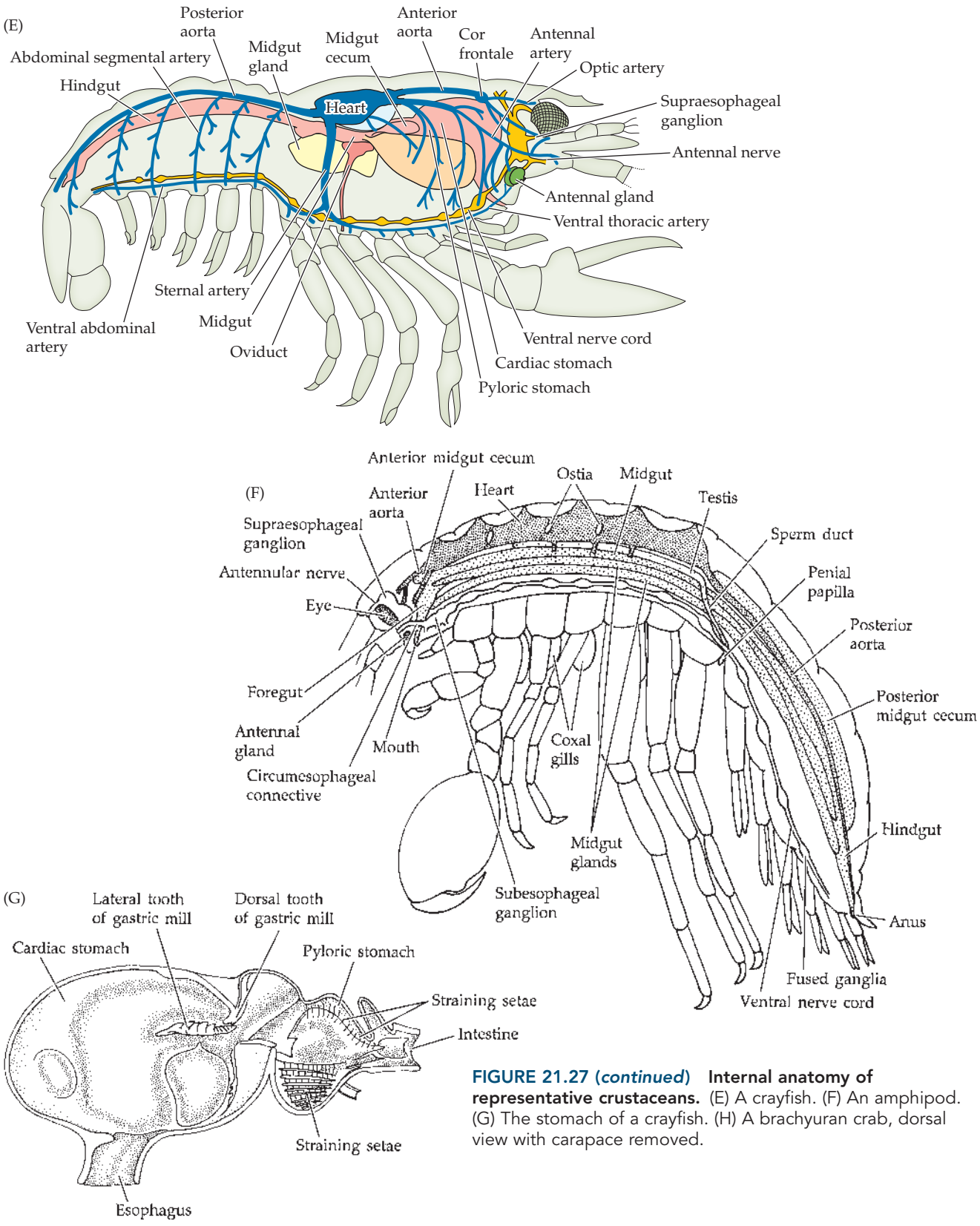

FIGURE 21.27 (*continued*) Internal anatomy of representative crustaceans. (E) A crayfish. (F) An amphipod. (G) The stomach of a crayfish. (H) A brachyuran crab, dorsal view with carapace removed.

After ingestion, the food material is usually handled mechanically by the foregut. This may involve simply transporting the food to the midgut or, more commonly, processing the food in various ways prior to chemical digestion. For example, the complex foregut of decapods (Figure 21.27G) is divided into an anterior cardiac stomach and a posterior pyloric stomach. Food is stored in the enlarged portion of the cardiac stomach

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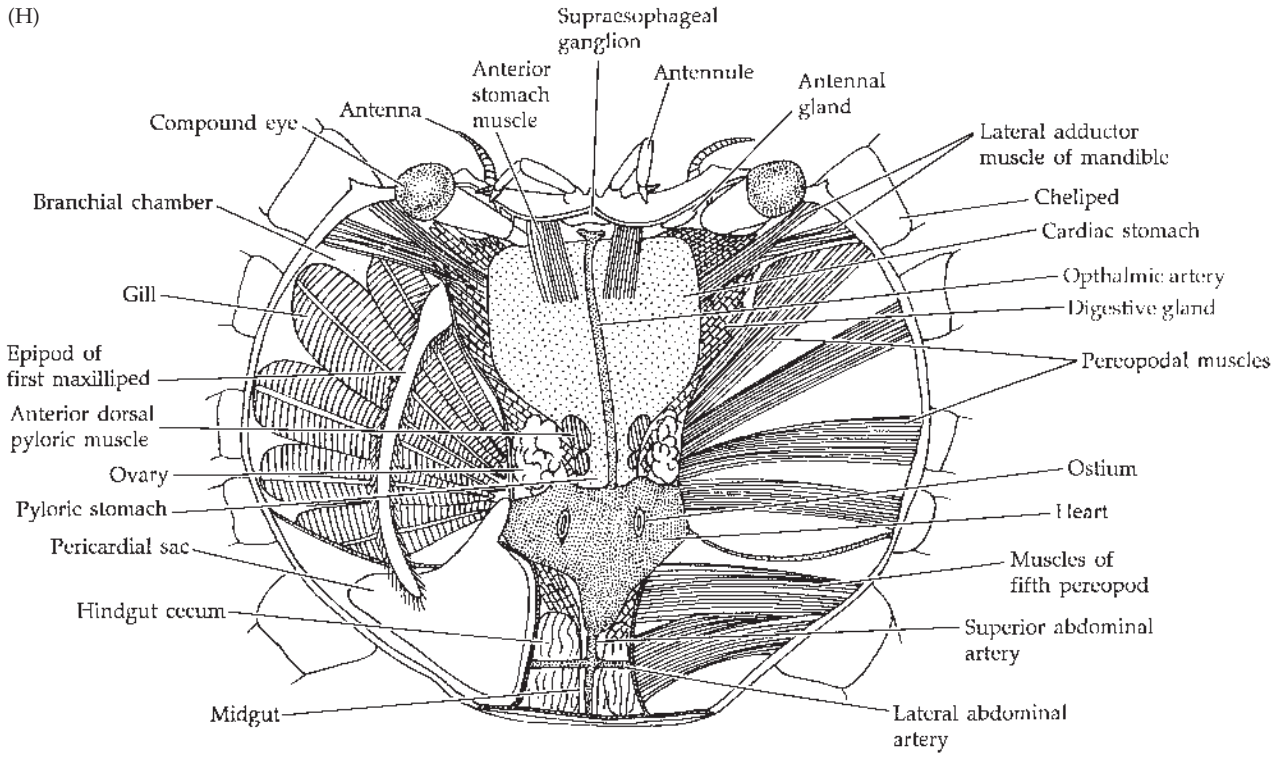

and then moved a bit at a time to a region containing a gastric mill, which usually bears heavily sclerotized teeth. Special muscles associated with the stomach wall move the teeth, grinding the food into smaller particles. The macerated material then moves into the back part of the pyloric stomach, where sets of filtering setae prevent large particles from entering the midgut. This type of foregut arrangement is best developed in macrophagous decapods (scavengers, predators, and some herbivores). Thus the food can be taken in quickly, in big bites, and mechanically processed afterward.

Circulation and Gas Exchange

The basic crustacean circulatory system usually consists of an elongate, dorsal, ostiate heart within a pericardial cavity and variously developed vessels emptying into an open hemocoel (Figure 21.28). But the open hemocoel, which in the past led to descriptions of crustaceans as having an open circulatory system, has become highly modified in many groups, and in most there is a complex and intricate arrangement of true vessels (arteries) and lacunar canals that has only recently begun to be recognized. A distinct heart is absent in most ostracods, many copepods, and many cirripedes. In some groups the heart is replaced or supplemented by accessory pumping structures derived from muscular vessels. But in all cases, the organs and tissues are exposed to the hemolymph, which fills the body cavities. The circulating hemolymph helps regulate pH and inorganic ions, and it transports amino acids, proteins, carbohydrates and lipids, and other nutrients, as well as waste products and oxygen (via hemocyanin or hemoglobin). Hemolymph also contributes to wound healing through the clotting of hemocytes and other cells.

The primitive heart structure in crustaceans is a long tube with segmental ostia, a condition retained in part in cephalocarids and in some branchiopods, leptostracans, and stomatopods. However, the general shape of the heart and the number of ostia are closely related to body form and the location of gas exchange structures. The heart may be relatively long and extend through much of the postcephalic region of the body, as it does in the remipedes, anostracans, and leptostracans, or it may tend toward a globular or box shape and be restricted to the thorax (e.g., as in cladocerans), where it may be associated with the thoracic gills (e.g., as in decapods). The intimate coevolution of the circulatory system with body form and gill placement is best exemplified when closely related groups are compared. Although isopods and amphipods, for instance, are both peracarids, their hearts are located largely in the pleon and in the pereon, respectively, corresponding to the pleopodal and pereopodal gill locations.

The number and length of blood vessels and the presence of accessory pumping organs are related to body size and to the extent of the heart itself. In most nonmalacostracans, for example, there are no arterial vessels at all; the heart pumps blood directly into the hemocoel from both ends. These animals tend to have short bodies, long hearts, or both, an arrangement that facilitates circulation of the blood to all body parts. Sessile forms, such as most cirripedes, have lost the heart

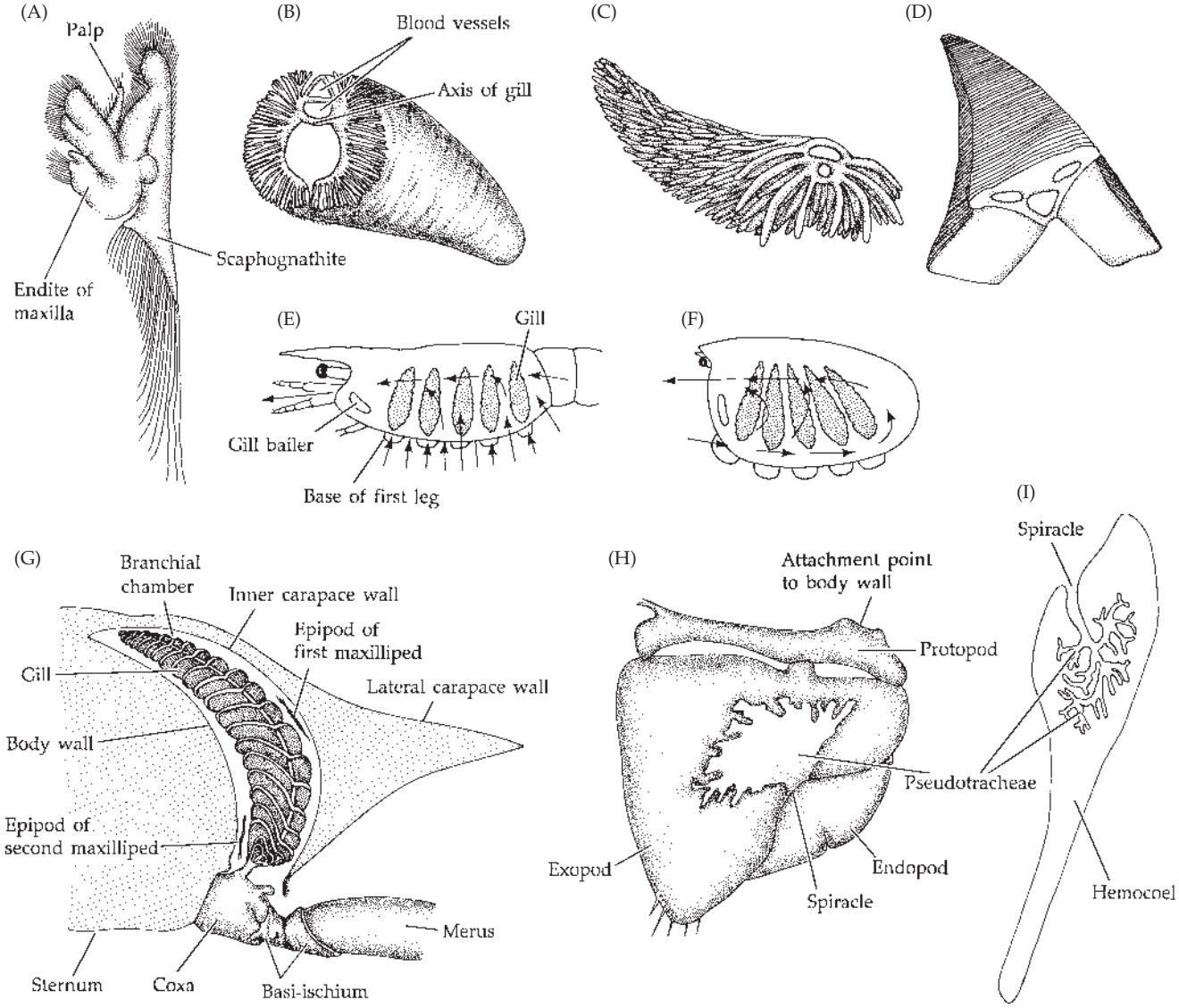

FIGURE 21.28 Gas exchange structures. (A) Maxilla of the shrimp *Pandalus*. Note the setose scaphagnathite used to generate the ventilating current. (B–D) Cross sections of types of decapod gills: (B) Dendrobranchiate. (C) Trichobranchiate. (D) Phyllobranchiate. (E,F) Paths of ventilating currents through the left branchial chambers of (E) a shrimp and (F) a brachyuran crab. (G) The branchial chamber (cross section) of a brachyuran crab, showing the position of a single phyllobranchiate podobranch. (H,I) A pleopod of the terrestrial isopod *Porcellio* (surface view and section). Note the pseudotracheae. (B–D after Meglitsch 1972.)

altogether, although it is replaced by a pumping vessel in the thoracicans. Large malacostracans tend to have well-developed vessel systems (Figure 21.27D,E). Studies using corrosion casting techniques and microCT scanning have shown how complex these vessel systems can be and have even called into question the paradigm of "open" vs. "closed" circulatory systems in invertebrates. Large or active crustaceans may also possess an anterior accessory pump called the **cor frontale**, which helps maintain blood pressure, and often a venous system for returning blood to the pericardial chamber.

Crustacean blood contains a variety of cell types, including phagocytic and granular amebocytes and special wandering explosive cells that release a clotting agent at sites of injury or autotomy. In nonmalacostracans, oxygen is either carried in solution or attached to dissolved hemoglobin. Most malacostracans possess hemocyanin in solution (although some contain hemoglobin within tissues). Hemoglobin uses iron as the oxygen-binding site, whereas hemocyanin uses copper. The latter can give a bluish color to the hemolymph; carotenoid pigments frequently give hemolymph a pale brown or orange color. Oxygen-binding pigments are never carried in corpuscles, as they are in the vertebrates.

We have mentioned the form and position of gas exchange organs (gills) for some groups of crustaceans in the taxonomic synopses. Some small forms (e.g., copepods, some ostracods) lack distinct gills and rely on cutaneous exchange, which is facilitated by their relatively thin cuticles and high surface-area-to-volume ratio. In the small forms of other groups, a thin, membranous inner lining of the carapace serves this purpose (e.g.,

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Cladocera, Cirripedia, Leptostraca, Cumacea, Mysida, Spinicaudata, and even some members of the Decapoda).

Most crustaceans, however, possess distinct gills of some sort (Figure 21.28). These structures are commonly derived from epipods (exites) on the thoracic legs that have been modified in various ways to provide a large surface area. The inner hollow chambers of these gills are confluent with the hemocoel or its vessels. Although the gills vary considerably in structure (recall the various decapod gills described earlier), they all operate on the basic principles of gas exchange organs addressed in Chapter 3 and throughout this text: the circulatory fluid is brought close to the oxygen source in an organ with a relatively high surface area. The gills provide a thin, moist, permeable surface between the internal and external environments. The gills of stomatopods and isopods (Figure 21.28H,I) are formed from the abdominal pleopods. In the first case they are branched processes off the bases of the pleopods, but in the isopods the flattened pleopods themselves are vascularized and provide the necessary surface area for exchange. Stomatopods also have epipodal gills on the thoracopods, but these are not large.

For gills to be efficient, a flow of water must be maintained across them. In stomatopods and aquatic isopods a current is generated by the beating of the pleopods. Similarly, the pereopodal gills of euphausiaceans are constantly flushed by water as the animals swim. In many crustaceans, however, the gills are concealed to various degrees and require special mechanisms in order to produce the ventilating currents. In most decapods, for example, the gills are contained in branchial chambers formed between the carapace and the body wall (Figure 21.28). Thus the delicate gills, while still technically outside the body, appear to be (and are protected as though they were) internal organs. While such an arrangement provides protection from damage to the fragile gill filaments, the openings to the chambers are generally small, restricting the passive flow of water. Not surprisingly, the solution to this dilemma comes once again from the evolutionary plasticity of crustacean appendages. Most decapods have elongate exopods on the maxillae, called gill bailers or **scaphognathites**, that vibrate to create ventilating currents through the branchial chambers (Figure 21.28A). These currents typically enter from the sides and rear through small openings around the coxae of the pereopods (called in crabs **Milne-Edwards openings**, after their discoverer), and they exit anteriorly from under the carapace in the vicinity of the mouth field (and antennal glands). They can be easily seen by observing a crab or lobster in quiet water. The flow rate of the currents can be altered, depending on environmental factors, and can also be reversed, thus allowing certain decapods to burrow in sand or mud with only their front ends exposed to the water.

The positioning of the gills in branchial chambers protects them from desiccation during exposure to air and thus enables many crustaceans to live in littoral habitats; diffusion of respiratory gases commonly continues even during low tides. Some decapods have even invaded land, especially certain crayfish and the anomuran and brachyuran crabs known as land crabs (e.g., certain Gecarcinidae, the hermit crab *Coenobita*, the coconut crab *Birgus*; Figure 21.1H). In these semiterrestrial species the gills are typically reduced in size. In *Birgus* the original gills are very small, and the vascularized cuticular surface of the gill chamber is used for gas exchange. Although young *Birgus* may carry shells (or coconuts) to protect the soft abdomen, adults do not and the abdomen is well sclerotized and hardened. Some land crabs in the genus *Gecarcinus*, which have been reported living at up to 3,000 m elevation (in Jamaica), have **nephritic pads** onto which the urine is deposited; microbes living on the pads cleanse the urine of its nitrogenous waste compounds before the fluid is reabsorbed by the crab. Interestingly, at least three species of *Drosophila* have adapted to this habitat, where they feed on the microbes and spend their entire lives in association with their crab hosts. Another striking decapod adaptation to life in air is displayed by the sand-bubbler crabs of the Indo-Pacific region (family Dotillidae: *Scopimera, Dotilla*). These crabs possess membranous discs on their legs or sternites that were once thought to be auditory organs but are now thought to function as gas exchange surfaces.

The most successful crustaceans on land are not the decapods, however, but the familiar sowbugs and pillbugs. The success of these oniscidean isopods (e.g., *Porcellio*) is due in part to the presence of aerial gas exchange organs called **pseudotrachea** (Figure 21.28H,I). These organs are inwardly directed, moderately branched, thin-walled, blind sacs located in some of the pleopodal exopods, connected to the outside via small pores (similar to the tracheae and spiracles of other terrestrial arthropods, such as some arachnids, myriapods, and hexapods). Air circulates through these sacs, and gases are exchanged with the blood in the pleopods. Thus, in these animals the original aquatic pleopodal gills have been refashioned for air breathing by moving the exchange surfaces inside, where they remain moist. The superficially similar tracheal systems of isopods, insects, myriapods, and arachnids evolved independently, by convergence, in association with other adaptations to life on land.

Excretion and Osmoregulation

Like other fundamentally aquatic invertebrates, crustaceans are ammonotelic, whether in fresh water or seawater or on land. They release ammonia both through nephridia and by way of the gills. As discussed in Chapter 20, most crustaceans possess nephridial excretory organs in the form of either antennal glands or maxillary glands (Figures 21.6A and 21.27). These are serially homologous structures, constructed similarly but differing in the position of their associated pores (at the base of the second antennae or the second maxillae,

respectively). The inner blind end is a coelomic remnant of the nephridium called the sacculus, which leads through a variably coiled duct to the pore. The duct may bear an enlarged bladder near the opening. Antennal glands are sometimes called "green glands."

Most crustaceans have only one pair of these nephridial organs, but lophogastridans and mysidans have both antennal and maxillary glands, and a few others (cephalocarids, and a few tanaidaceans and isopods) have well-developed maxillary and rudimentary antennal glands. Most nonmalacostracans have maxillary glands, as do stomatopods, cumaceans, and most tanaidaceans and isopods. Adult ostracods have maxillary glands, but antennal glands also occur in freshwater species. All of the other malacostracans have antennal glands.

Blood-filled channels of the hemocoel intermingle with branched extensions of the sacculus epithelium, creating a large surface area across which filtration occurs. The cells of the sacculus wall also actively take up and secrete material from the blood into the lumen of the excretory organ. These processes of filtration and secretion are to some degree selective, but most of the regulation of urine composition is accomplished by active exchange between the blood and the excretory tubule. These activities not only regulate the loss of metabolic wastes, but also are extremely important in water and ion balance, particularly in freshwater and terrestrial crustaceans.

The excretion and osmoregulation carried out by antennal and maxillary gland activity are supplemented by other mechanisms. The cuticle itself acts as a barrier to exchange between the internal and external environments and is especially important in preventing water loss on land or excessive uptake of water in fresh water. Moreover, thin areas of the cuticle (especially the gill surfaces) serve as sites of waste loss and ionic exchange. The epipods on the legs of Branchiopoda were long assumed to function in gas exchange (as "gills"), but they are now known to serve primarily as sites of osmoregulation (hence, the taxonomic name Branchiopoda, meaning "gill-footed," is a misnomer!). Phagocytic blood cells and certain regions of the midgut are also thought to accumulate wastes. In some terrestrial isopods, ammonia actually diffuses from the body in gaseous form.

Nervous System and Sense Organs

The central nervous system of crustaceans is constructed in concert with the segmented body structure, along the same lines as seen in other arthropods (Figure 21.29). In

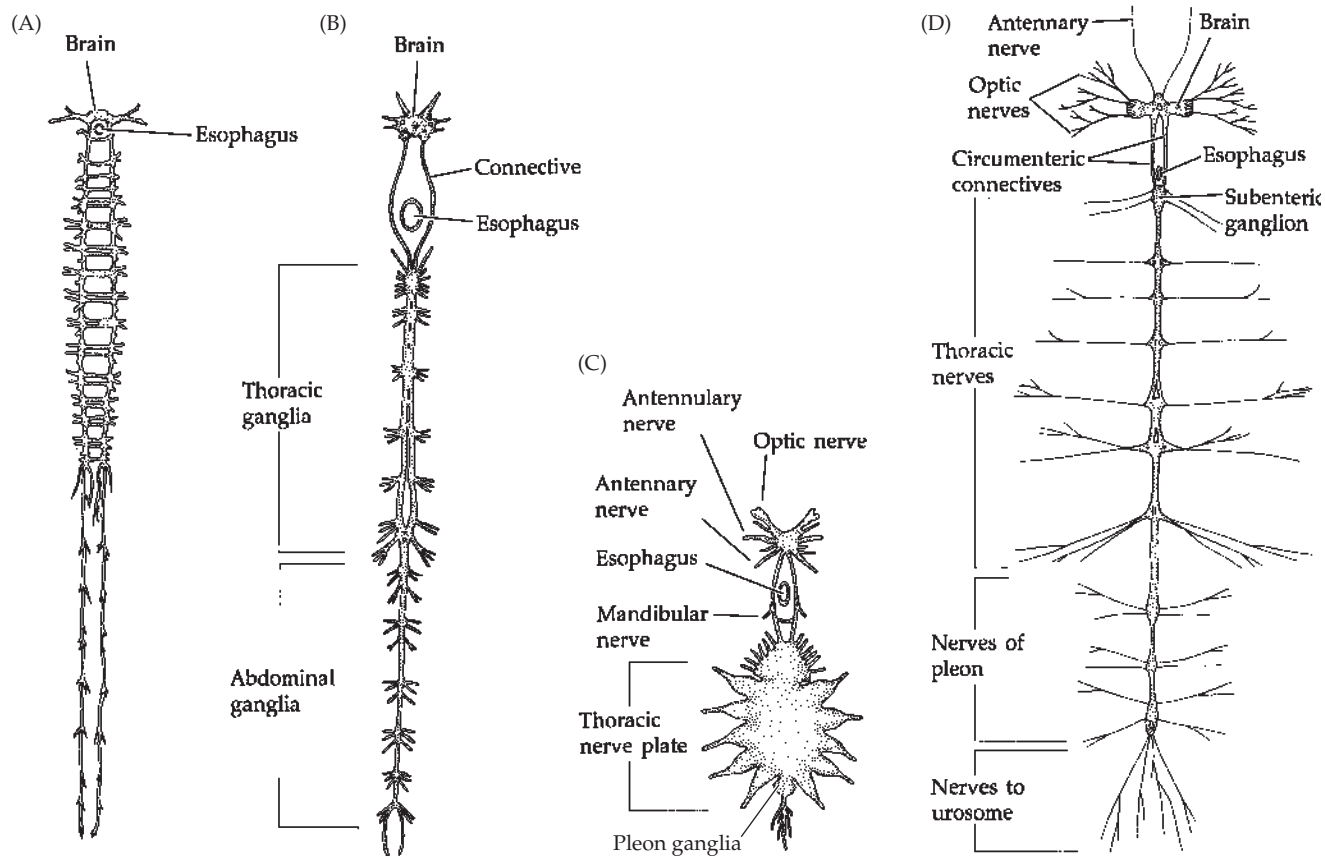

FIGURE 21.29 Central nervous systems of four crustaceans. (A) The ladderlike system of an anostracan. Note the absence of well-developed ganglia in the posterior, apodous, portion of the trunk. (B) Elongate metameric system of a crayfish. (C) Highly compacted system of a brachyuran crab, wherein all thoracic ganglia have fused and the abdominal ganglia are reduced. (D) Nervous system of a hyperiid amphipod. Note the loss of the urosomal ganglia typical of all amphipods. (D after G. J. Brusca. 1981. *J Crust Biol* 1: 358–375.)

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many groups the nervous system is ladderlike, the segmental ganglia being largely separate and linked by transverse commissures and longitudinal connectives (Figure 21.29A). The crustacean brain is composed of three fused ganglia, or neuromeres, the two anterior being the dorsal (supraesophageal) protocerebrum and deutocerebrum, which are thought to be preoral in origin. From the protocerebrum, optic nerves innervate the eyes. Mushroom bodies have been identified in many crustacean brains. From the deutocerebrum, antennulary nerves run to the antennules, while smaller nerves innervate the eyestalk musculature. The third ganglion of the brain is the tritocerebrum, which presumably represents the first postoral somite ganglion. The tritocerebrum forms a pair of circumenteric connectives that extend around the esophagus to a subesophageal or subenteric ganglion and link the brain with the ventral nerve cord bearing the segmental body ganglia. From the tritocerebrum also arise the antennary nerves as well as certain sensory nerves from the anterior region of the head. In tantulocarids, bizarre minute parasites on other crustaceans, the central nervous system has a dorsal brain and ventral nerve cord that runs through the thorax. The brain is formed of very small, tightly packed cells, and a neuropil is present (constituting almost half of the brain volume). The neuropil extends inside the ventral nerve cord.

The nature of the ventral nerve cord often clearly reflects the influence of body tagmosis. In crustaceans with relatively homonomous segmentation (e.g., remipedes, cephalocarids, and anostracan and notostracan branchiopods), the ganglia associated with each postantennary segment remain separate along the ventral nerve cord. In more heteronomous forms, however, a single large subenteric ganglionic mass is formed by the fusion of ganglia associated with the postoral cephalic segments (e.g., those of the mandibles, maxillules, maxillae, and, when present, maxillipeds). The ganglia of the thorax and abdomen may also be variably fused, depending on segment fusion and body compaction. For example, in most long-bodied decapods (lobsters and crayfish), the thoracic and abdominal ganglia are largely fused across the body midline but remain separate from one another longitudinally (Figure 21.29B). However, in short-bodied decapods (e.g., crabs), all of the thoracic segmental ganglia are fused to form a large ventral nerve plate, and the abdominal ganglia are much reduced (Figure 21.29C).

Most crustaceans have a variety of sensory receptors that transmit information to the central nervous system in spite of the imposition of the exoskeleton (as explained in Chapter 20) (Figure 21.30). Among the most obvious of these sensory structures are the many innervated setae or **sensilla** that cover various regions of the body and appendages (Figure 21.31). Studies of these structures suggest most function as both mechanoreceptors (sensing touch and currents) and chemoreceptors. Most crustaceans also possess special chemoreceptors in the form of clumps or rows of soft, tubular, cuticular processes called **aesthetascs** (Figure 21.30A) located on the antennules. In decapods, hundreds of neurons can innervate each aesthetasc. Thermoreceptors probably occur in many crustaceans (those living near hydrothermal vents in the deep sea would seem likely candidates) but are not yet documented. However, behaviors related to thermal avoidance and temperature preferences have been shown. A pair of unique sensory structures whose function is unknown, called **frontal processes**, occurs on the head of remipedes. Many crustaceans have dorsal organs, poorly understood glandular-sensory structures on the head, which actually constitute several different types of sensory structures that may or may not be homologous.

Like all arthropods, crustaceans contain well-developed proprioceptors that provide information about body and appendage position and movement during locomotion. A few taxa within the class Malacostraca possess statocysts, which either are fully closed and contain a secreted statolith (e.g., mysidans, some anthurid isopods) or are open to the outside through a small pore and contain a statolith formed of sand grains (e.g., many decapods and some asellote isopods) (Figure 21.30B,C). In the case of the decapods, the statocyst not only serves as a georeceptor, but also detects the angular and linear acceleration of the body relative to the surrounding water as well as the movement of water past the animal (i.e., the statolith is rheotactic). And in some shrimps the statocyst is apparently also engaged in hearing.

There are two types of rhabdomeric photoreceptors among crustaceans, median simple eyes and lateral compound eyes, and both are innervated by the protocerebrum. Many species possess both kinds of eyes, either simultaneously or at different stages of development. The compound eyes may be sessile or stalked. Stalked compound eyes occur in the Anostraca, many Malacostraca, and perhaps some Cumacea (and in anomalocaridids, and perhaps also some trilobites).

The median eye generally first appears during the nauplius larval stage, and for that reason it is often called a **naupliar eye**. Like the nauplius larva itself, the median eye is thought to be an ancestral (defining) feature of the Crustacea. Median eyes are in a sense "compound" in that they are composed of more than one photoreceptor unit (Figure 21.30D). There are typically three such units in the median eyes of nauplii and up to seven in the eyes of adults in which they persist. Except for their basic rhabdomeric nature, however, the structure of median eye units is unlike that of the ommatidia of true compound eyes. The former are inverse pigment cups, each with relatively few retinular (photoreceptor) cells. Cuticular lenses are present over the median eyes of most ostracods and some copepods. Simple crustacean eyes probably function only to detect light direction and intensity. Such information is of particular value as a means of orientation in planktonic forms without compound eyes, such as nauplius larvae, many copepods, etc. In some branchiopods, a space above the median eye is connected

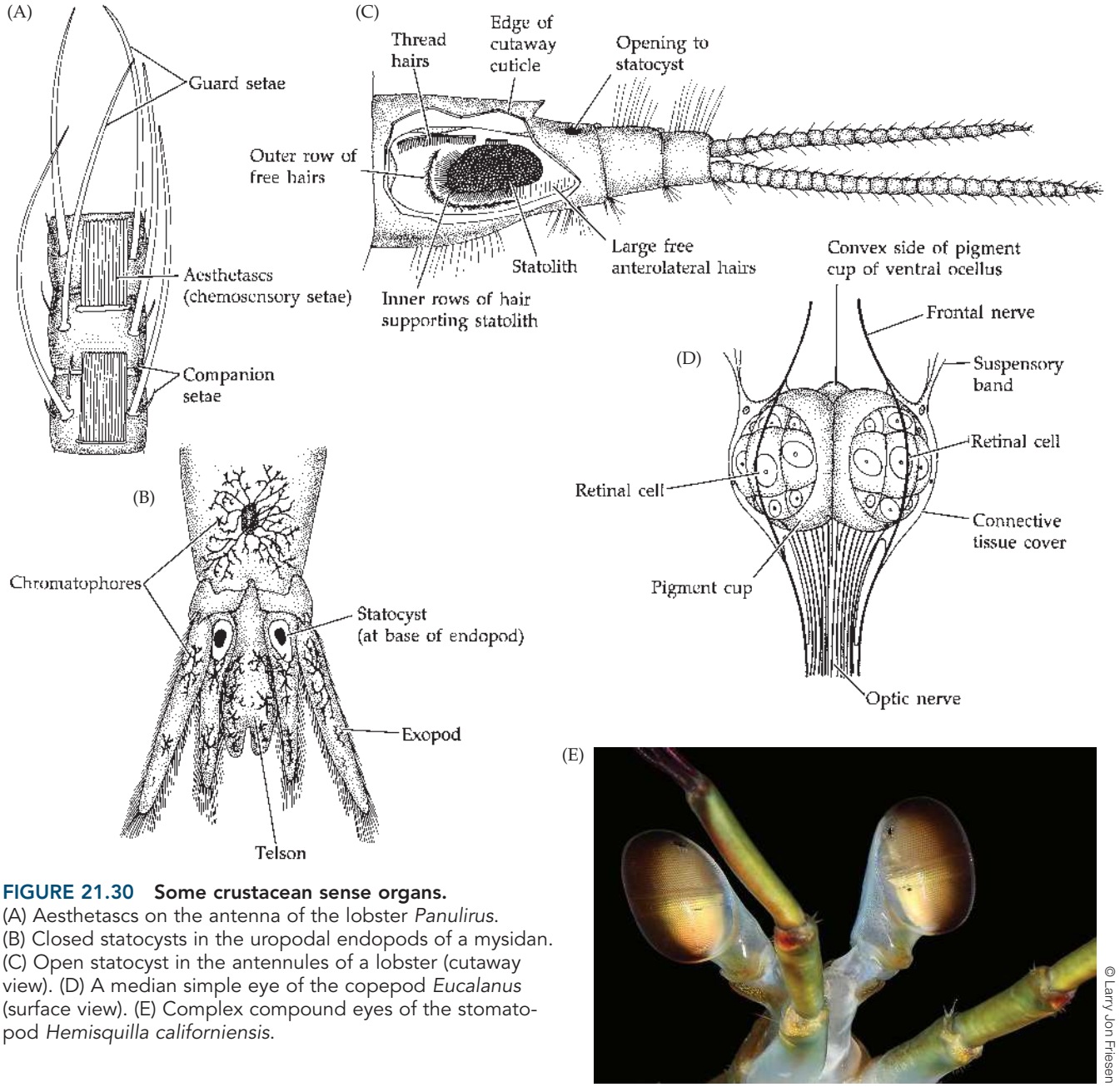

FIGURE 21.30 Some crustacean sense organs.
(A) Aesthetascs on the antenna of the lobster *Panulirus*. (B) Closed statocysts in the uropodal endopods of a mysidan. (C) Open statocyst in the antennules of a lobster (cutaway view). (D) A median simple eye of the copepod *Eucalanus* (surface view). (E) Complex compound eyes of the stomatopod *Hemisquilla californiensis*.

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to the external environment by a small pore, perhaps indicating an invagination of the eye at some point in the distant past, although the nature and function of the pore is not known.

The structure and function of compound eyes (ommatidia) were reviewed in Chapter 20. In terms of visual capacity, much more work has been done on the eyes of insects than on those of crustaceans, and we are left with a good deal of speculation in terms of what crustaceans actually see. Although most probably lack the visual acuity of many insects, it has been shown that many crustaceans can discern shapes, patterns, and movement; color vision has been demonstrated in some species (various species have been shown to respond to light wavelengths ranging from the blue-green region to the ultraviolet and far-red spectra, at least to 470–570 nm). Stomatopods, in particular, have been shown to have extremely complex and sensitive eyes with a wide range of capabilities. Running through the center of each stomatopod eye is a distinct band comprising six rows of ommatidia—which in most species contain four rows that make up a color vision system with 12 visual pigments—as well as two rows that analyze both linearly and circularly polarized light (Figure 21.30E). The ommatidia that deal with color have a three-tier structure: the top tier contains an ultraviolet-sensitive pigment, and below this are two tiers with different pigments sensitive to wavelengths in the human visible

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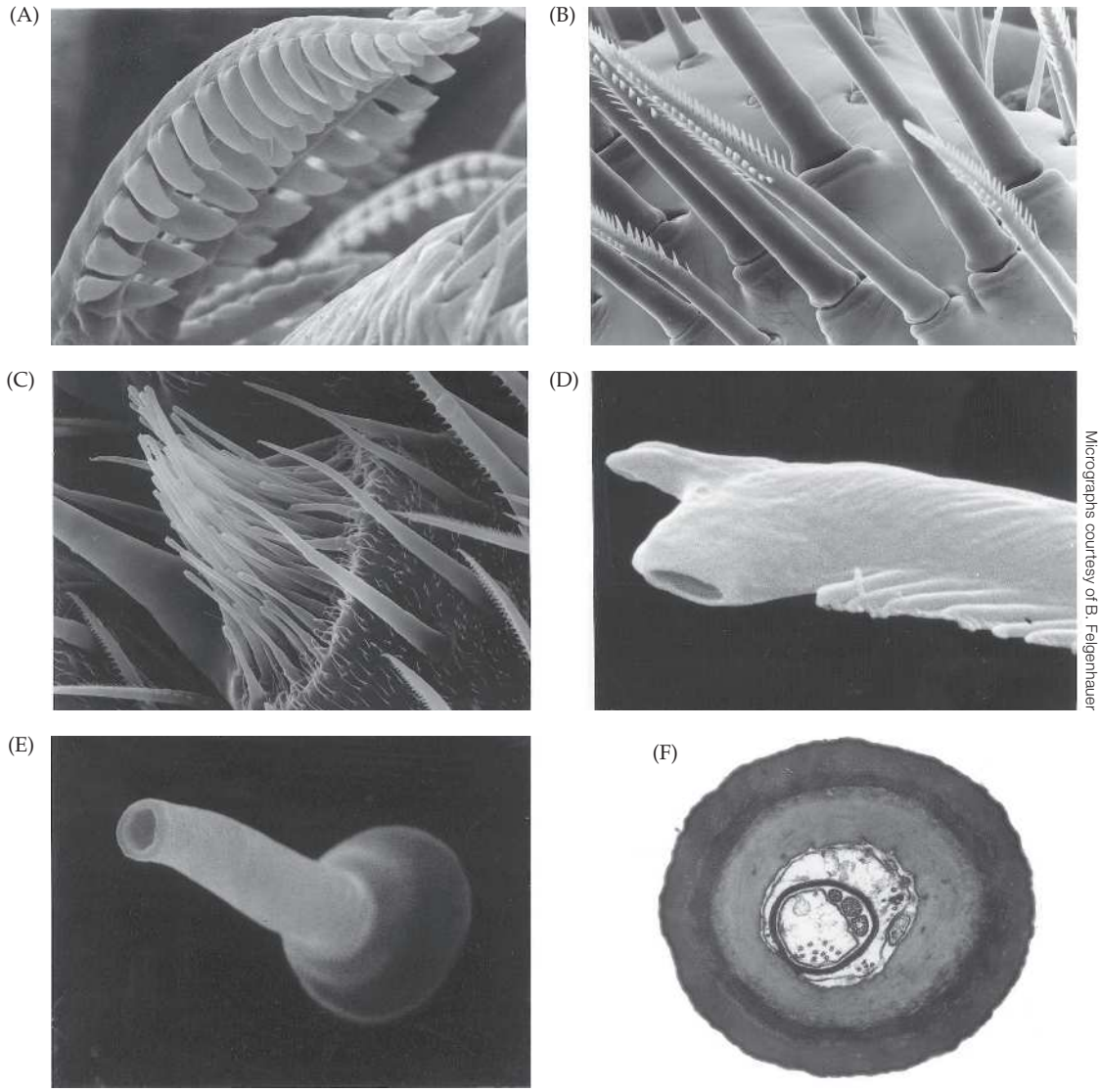
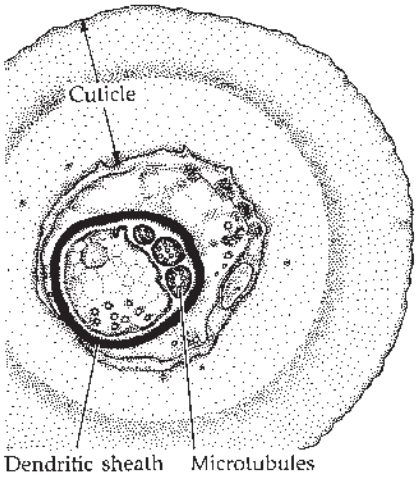


FIGURE 21.31 Sensilla of selected crustaceans. (A) Serrate seta (mechanoreceptor) of the second maxilliped of the anomuran *Petrolisthes armatus* (×428). (B) Sockets of serrate setae of the third maxilliped of the cleaning shrimp *Stenopus hispidus* (×228). (C) Current receptor from the anterior trunk limbs of the notostracan *Triops*. (D) Chemosensory seta from the first pereopod of the freshwater shrimp *Atya* (×5,700); note the characteristic apical pore. (E) A dual receptor (mechanoreceptor and chemoreceptor) seta from the maxilla of the remipede *Xibalbanus tulumensis* (×4,560). (F) Cross section of a dual receptor (micrograph and interpretive drawing). Note the microtubules within the dendrites and the dendritic sheath that attaches to the cuticle of the setal shaft (×17,100).



spectrum. The upper and lower halves of each eye also have overlapping visual fields, so each eye can act as a stereoscopic range finder. The 12 different photoreceptor types each sample a narrow set of wavelengths ranging from deep UV to far red (300 to 720 nm).

Although both insects and crustaceans have tetrapartite ommatidia, there are certain structural differences between the compound eyes of insects and those of crustaceans, probably as a result of adaptation to the requirements of aerial and aquatic vision. In water, light has a more restricted angular distribution, a lower intensity, and a narrower range of wavelengths than it does in air. Contrast is also somewhat reduced in water. All of these factors place a premium on enhancing the sensitivity and contrast perception of the eyes

of aquatic creatures. Mounting the eyes on stalks is one dramatic way in which many crustaceans increase the amount of information available to the eyes, by increasing the field of view and binocular range. Eyestalks are complex structural features with a dozen or so muscles controlling their movement.

Typical tetrapartite compound eyes are lacking in the small crustaceans formerly combined as "maxillopodans" (copepods, barnacles, etc.), but various forms of "compound eyes" do occur among the Branchiura, Ostracoda (Cypridinacea), and Cirripedia. Eyes in the first two taxa most closely resemble those of other crustaceans in general structure and may be homologous with them. In the Cirripedia, the median eye and two lateral eyes are all derived from a single tripartite ocellar eye of the nauplius larva, which splits into its three components, each forming an adult photoreceptor following metamorphosis of the nauplius into a cypris larva. All three of these eyes thus appear to be composed of simple ocelli, although the lateral eyes have three photoreceptor cells and for this reason are often called "compound eyes." Rhizocephalan nauplii also have a tripartite nauplius eye, which persists into the cypris larval stage.

Compound eyes are lacking altogether in many crustacean taxa (e.g., Copepoda, Mystacocarida, Cephalocarida, Tantulocarida, Pentastomida, Remipedia, and some Ostracoda). Members of some other groups possess compound eyes only in late larval stages and lose them at metamorphosis (e.g., some cirripedes). Reduction or loss of eyes is also common in many deep-sea species, burrowers, cave dwellers, and parasites.

Crustaceans have complex endocrine and neurosecretory systems, although our understanding of these systems is far from complete. In general, the phenomena of molting (see Chapter 20), chromatophore activity, and various aspects of reproduction are under hormonal and neurosecretory control. Interesting recent work indicates that juvenile hormone–like compounds, long thought to occur only in insects, may also occur in at least some crustaceans. (Juvenile hormones are a family of compounds that regulate adult metamorphosis and gametogenesis in insects.) Crustaceans are masters of autotomy, or the dropping of limbs at specific breakage planes to escape potentially lethal threats. The process occurs via an intrinsic neuromuscular mechanism (i.e., it is a nonreflexive process), and the break point is capable of rapid sealing. In most crustaceans, loss of a limb stimulates rapid regeneration, usually accompanied by an initial molt. In snapping shrimps (Alpheidae) and some others with unequal chelae, autotomy of a cheliped commonly results in claw reversal during the induced molt, transforming the larger claw into a small one, and vice versa—a remarkable process that involves changes in morphology, underlying muscle types, and external setae.

Bioluminescence also occurs in several crustacean groups—it is common among pelagic decapods, and it has also been reported in certain myodocopan ostracods, hyperiid amphipods, and copepod larvae. Some copepods (e.g., male *Sapphirina metallina*) display an iridescence, which is created by a multilayered-membrane structure in the epidermal cells of the dorsal integument (see discussion of bioluminescent ostracods below).

Reproduction and Development

Reproduction We have often mentioned the relationships between an animal's reproductive and developmental pattern and its lifestyle and overall survival strategy. With the exception of purely vegetative processes such as asexual budding, the crustaceans have managed to exploit virtually every life history scheme imaginable. The sexes are usually separate, although hermaphroditism is the rule in remipedes, cephalocarids, most cirripedes, and a few decapods. Sequential hermaphroditism is not uncommon and usually is expressed as protandry (individuals first mature as males, then later become females), although protogyny occurs in a few species (e.g., the marine isopod *Gnorimosphaeroma oregonense* [Sphaeromatidae]). In addition, parthenogenesis is known in some branchiopods and certain ostracods. In one species of clam shrimp (*Eulimnadia texana*) a rare type of mixed mating system exists, called **androgonochorism** (i.e., androdioecy in plants), in which males coexist with hermaphrodites, but there are no true females. Androgonochorism is rare, but it is also known in the nematode *Caenorhabditis elegans*, some thoracican barnacles (e.g., *Balanus galeatus*, *Scalpellum scalpellum*), and several other branchiopod crustaceans.

The reproductive systems of crustaceans are generally quite simple (Figure 21.27). The gonads are derived from coelomic remnants and lie as paired elongate structures in various regions of the trunk. In many cirripedes, however, the gonads lie in the cephalic region. In some cases the paired gonads are partially or wholly fused into a single mass. A pair of gonoducts extends from the gonads to genital pores located on one of the trunk segments, either on a sternite, on the arthrodial membrane between the sternite and leg protopods, or on the protopods themselves. In many crustaceans the paired penes are fused into a single median penis (e.g., in tantulocarids, cirripedes, and some isopods). The female system sometimes includes seminal receptacles. The position of the gonopores varies among the classes.

The curious phenomenon of **intersex**—having both male and female secondary sexual characteristics—is widespread among crustaceans. Intersexual development is often associated with the presence of endoparasites such as bacteria and microsporidians, and it has also been correlated with the presence of endocrine-disrupting environmental pollutants that seem to induce opposing secondary sexual characteristics.

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Most crustaceans copulate, and many have evolved courtship behaviors, the most elaborate and well known of which occur among the decapods. Although many crustaceans are gregarious (e.g., certain planktonic species, barnacles, many isopods and amphipods), most decapods live singly except during the mating season. More or less permanent, or at least seasonal, pairing is known among many crustaceans (e.g., stenopodid shrimps; certain parasitic and commensal isopods; pinnotherid "pea" crabs, which often live as pairs in the mantle cavities of bivalve molluscs or in burrows of axiid/lobster shrimps).

Even the parasitic pentastomids copulate (within the host's respiratory system) and have internal fertilization, relying on a transfer of sperm to the female's vagina by way of the male's cirri (penes). Pentastomid early embryos metamorphose into a so-called primary larva with two pairs of double-clawed legs and one or more piercing stylets (Figure 21.5E). The larvae may be autoinfective in the primary host, or they may migrate to the host's gut and pass out with the feces. In the latter case, an intermediate host is required, which may be almost any kind of vertebrate. The larvae bore through the gut wall of the intermediate host, where they undergo further development to the infective stage. Once the intermediate host is consumed by a definitive host (usually a predator), the parasite makes its way from the new host's stomach up the esophagus, or bores through the intestinal wall, eventually settling in the respiratory system.

Mating in nonpaired crustaceans requires mechanisms that facilitate location and recognition of partners. Among decapods, and perhaps many other crustaceans, scattered individuals apparently find one another either by distance chemoreception (pheromones) or through synchronized migrations associated with lunar periodicity, tidal movements, or some other environmental cue. Contact sex pheromones are also utilized. In one, unique lineage of myodocopan ostracods in the Caribbean, males produce complex bioluminescent displays similar to those of fireflies to attract females. Once prospective mates are near each other, recognition of conspecifics of the opposite sex may involve several mechanisms. Vision is known to be important in the stenopodid shrimps (most of which live in pairs), in certain anomurans (e.g., the family Porcellanidae), and in brachyurans (many grapsids and ocypodids).

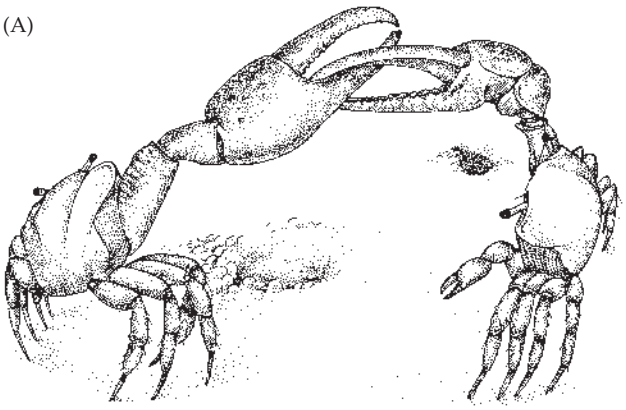
A good deal of work has been done on fiddler crabs (Ocypodidae: *Uca*), of which over 100 species have been described. In these species, males engage in dramatic cheliped waving (of their greatly enlarged chela, or **major claw**, which can account for more than 50% of the male's total mass—more than the largest rack of a male elk!) to attract females and repel competing males (Figure 21.32A–D). In addition, males produce sounds by stridulation and substratum thumping, which are thought to attract potential mates. Mating generally takes place once the male has enticed the female into his burrow. Males of some fiddler crab species build sand structures at the entrance of their burrow, which have been shown to attract females.

Among many crustaceans, the external sexual characteristics are associated with the actual mating process. For example, the antennae of male anostracans and some cladocerans, ostracods, and copepods are modified for grasping the female. Additionally, many males bear special sperm transfer structures, in the form of either modified appendages or special penes such as those of the thoracican barnacles (Figure 21.32E), anostracans, and ostracods. Examples of modified appendages include the last trunk limbs of copepods and the anterior pleopods of most male malacostracans (called gonopods in most malacostracans, or **petasma** in Dendrobranchiata) (Figure 21.32F). Sperm are transferred either loose in seminal fluid or (in copepods, and many malacostracans) packaged in spermatophores. Motile flagellated sperm occur only in a few groups; in most the sperm are nonmotile. Crustacean sperm are highly variable in shape, even bizarre in many instances, often being large round or stellate cells that move by pseudopods or are, seemingly, nonmotile.[9] Sperm are deposited directly into the oviduct or into a seminal receptacle in or near the female reproductive system. In some crustaceans females can store sperm for long periods (e.g., several years in the lobster *Homarus*), thus facilitating multiple broods from a single insemination.

The great majority of crustaceans brood their eggs until hatching occurs, and a variety of brooding strategies have evolved. Peracarids brood the developing embryos in a marsupium, a ventral brood pouch formed from inwardly directed plates of the leg coxae called **oostegites** (thermosbaenaceans are an exception among the Peracarida and use the carapace as a brood chamber). Other crustaceans attach the embryos to endites on the bases of the legs or to the pleopods (Figure 21.32H), usually using mucus secreted by specialized glands. In some cladocerans, brooding takes place in a dorsal brood chamber formed by the carapace. However, the syncarids, almost all dendrobranchiate shrimps, and most euphausiaceans shed the zygotes directly into the water. A few others deposit their fertilized eggs in the environment, usually attaching them to some object (e.g., branchiurans, some ostracods, many stomatopods). These deposited embryos may be abandoned or, as is the case in stomatopods, carefully tended by the female. Nonetheless, parental protection of the embryos until they hatch as larvae or juveniles is typical in crustaceans. Thus, crustaceans usually engage in mixed or direct life histories (Table 21.2).

[9] The sperm of freshwater ostracods are the longest in the animal kingdom, relative to body size (up to 10× body length). Even though their sperm are aflagellate, they are filiform and range from several hundred microns to millimeters in length.

(A)



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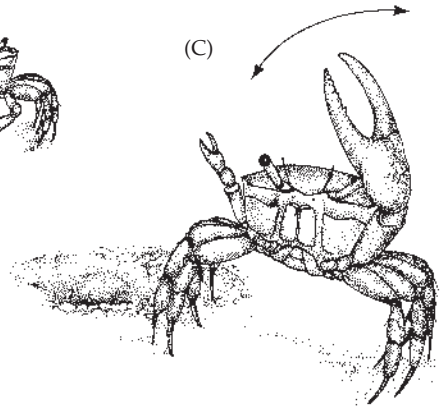

(D)

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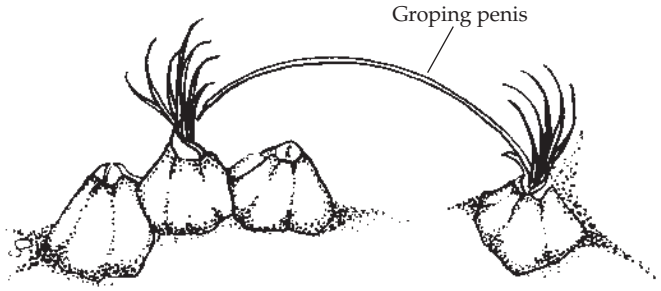

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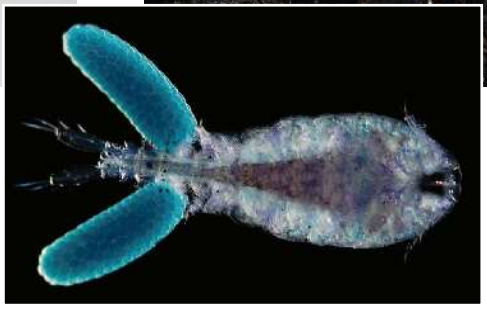

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◀ **FIGURE 21.32 Reproduction in Crustacea.** (A–D) Mating behaviors of the fiddler crab *Uca*. (A) Two males in ritualized combat for the favor of a female, while she watches (B). (C) A single male waving his enlarged cheliped to attract a female. (D) A male fiddler crab engaged in claw-waving behavior to attract a female. (E) A balanomorph barnacle, with cirri and groping penis extended, impregnating a neighbor. The advantage of a long penis in sessile animals is made obvious by this illustration. (F) Ventral views of a female and male brachyuran crab, *Metacarcinus magister*, showing the modified pleopods (setose appendages to retain eggs in female; modified as gonopod in male). (G) A copulating pair of *Hemigrapsus sexdentatus*. (H) Gravid female cancer crab, *Metacarcinus gracilis*, with clutch of developing eggs/embryos. (I) The planktonic copepod *Sapphirina*, with egg sacs. (E after G. Gerlach and C. Hinz. 2012. In C. Brönmark and L.-A. Hansson [Eds.], *Chemical Ecology in Aquatic Systems*. Oxford University Press, Oxford, UK.)

Development Although crustaceans are among the most widespread animals on Earth, we know surprisingly little about their embryogeny, which is extraordinarily diverse. The eggs are centrolecithal, with various amounts of yolk. The amount of yolk greatly influences the type of early cleavage and is often related to the time of hatching (see Chapter 4). As far as is known, the zygotes of most nonmalacostracans undergo some form of holoblastic cleavage, as do those of syncarids, euphausiaceans, penaeids, amphipods, and parasitic isopods. However, cleavage patterns are extremely variable, ranging from equal to unequal and from radial-like to unique. Early reports of modified spiral cleavage (see Figure 21.33A) in some crustaceans had once been viewed as evidence of close ties between the crustaceans and other spiralian groups such as the annelids. However, the generality of spiral-like cleavage among crustaceans has been called into question. Furthermore, evidence from molecular phylogenetics indicates arthropods belong to the Ecdysozoa clade of Protostomia, not the Spiralia (where annelids are nested). In fact, the cell lineages and germ layer origins in Crustacea are quite different from those of spirally cleaving embryos. For example, in barnacles the mesodermal germ layer arises from the 3A, 3B, and 3C cells, and the 4d cell contributes to ectoderm (Figure 21.33B)—whereas typical spiral cleavage involves a 4d origin of mesoderm. Euphausiaceans were long thought to have spiral cleavage, but recent work indicates they do not—only the oblique angle of the mitotic spindles during the transition from the two- to the four-cell stage superficially resembles spiral cleavage.

Meroblastic cleavage is the rule among many malacostracans. Here again, the exact pattern varies, but it generally involves intralecithal nuclear divisions followed by nuclear migration to the periphery of the embryo and subsequent partitioning of the nuclei into a cell layer around a central yolky mass (Figure 21.33C).

The form of the blastula and the method of gastrulation are dependent primarily on the preceding cleavage pattern and hence ultimately on the amount of yolk. Holoblastic cleavage may lead to a coeloblastula that undergoes invagination (as in syncarids) or ingression (as in many copepods and some cladocerans and anostracans). Other crustaceans form a stereoblastula followed by epibolic gastrulation (e.g., cirripedes). Most cases of meroblastic cleavage result in a periblastula and the subsequent formation of germinal centers.

As discussed above, crustaceans typically share a characteristic larval stage known as the nauplius larva, denoted by the appearance of the first three pairs of appendage-bearing somites (Figure 21.33D).[10] In those groups having little yolk in their eggs, the nauplius is generally free-living. In those species with yolky eggs, the nauplius stage is commonly passed through as part of a longer period of embryonic development (or a long brood period), and it is sometimes referred to as an **egg nauplius**. Free-living nauplii are usually planktotrophic, and their release corresponds to the depletion of stored yolk. However, in a few groups of crustaceans (e.g., euphausiaceans and dendrobranchiate shrimps), the nauplius exhibits lecithotrophy.

Crustacean development is either direct (the embryos hatch as juveniles that resemble miniature adults) or indirect (embryos hatch as a distinct larval stage) (Figure 21.32H). In direct development, the embryos are typically brooded. With indirect development, the embryos are typically released into the water (or in some cases deposited on the substratum). Some cases of indirect development can be viewed as "mixed development," in that embryos are brooded for a brief or prolonged period of time and early larval stages are passed within the brood. Larvae may pass through several phases, with each phase containing slightly different morphological steps called stages, before the adult condition is achieved. Direct development occurs in some cladocerans and branchiurans, and in all syncarids and peracarids. Ostracods also are typically viewed as having direct development. However, some ostracod species hatch with only the first three pairs of appendages present, a characteristic feature of nauplii, and thus some workers consider these to be naupliar larvae (even though they are in a bivalved carapace and add limbs gradually). The larval stages that have been recognized in the different crustacean groups have been assigned a plethora of names, and the homologies among these forms are not always understood. The more commonly encountered developmental forms are summarized below (also see Table 21.2 and Figure 21.33), but we do not attempt to describe them all.

[10] It was not until J. V. Thompson discovered the nauplius larvae of barnacles in the nineteenth century that this group was finally classified as Crustacea, a discovery that also marked the first use of larval features in understanding the phylogeny of marine invertebrates. An excellent atlas of crustacean larvae (Martin et al. 2014) includes historical notes on larval development in all major crustacean groups.

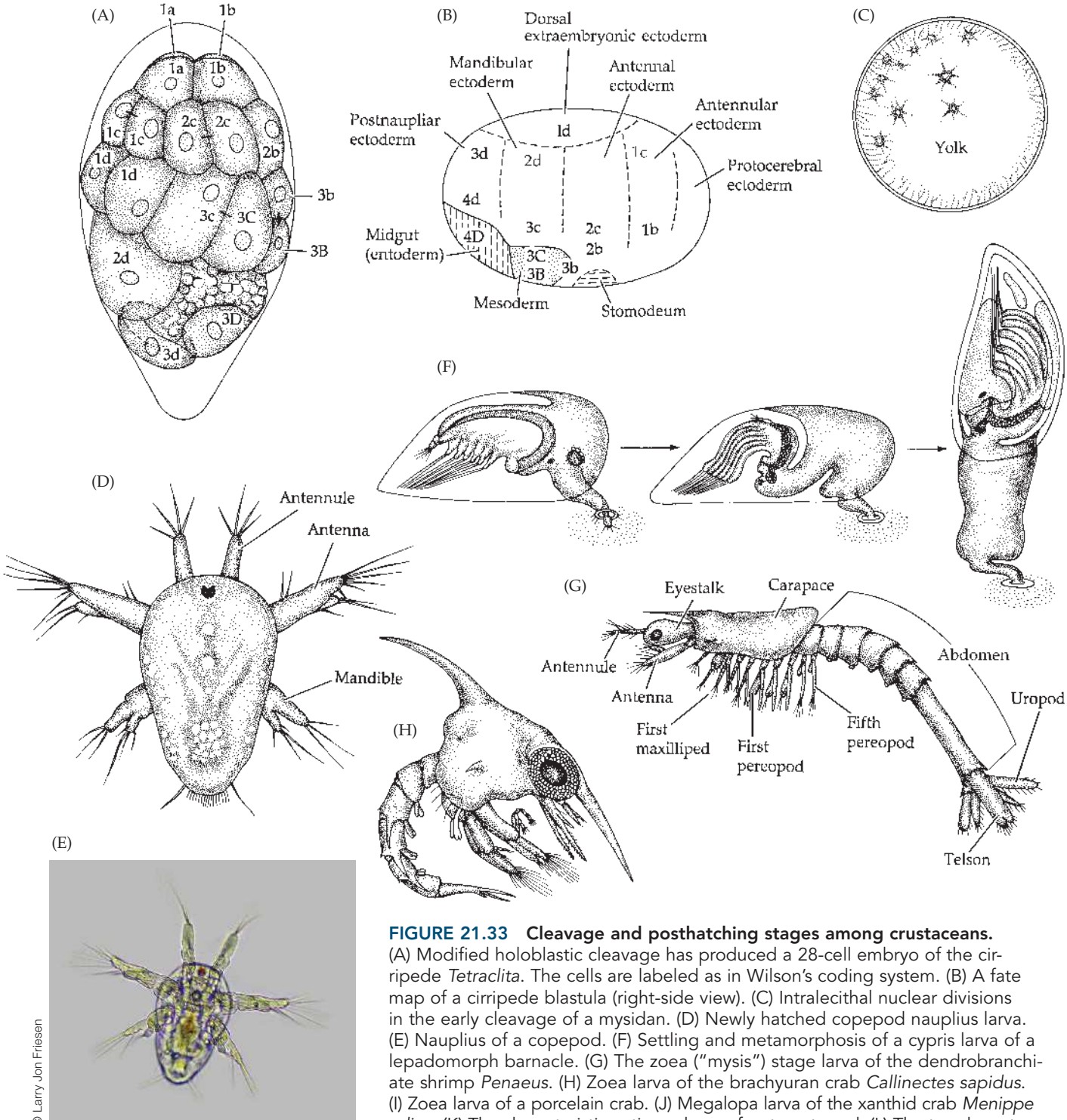

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FIGURE 21.33 Cleavage and posthatching stages among crustaceans. (A) Modified holoblastic cleavage has produced a 28-cell embryo of the cirripede *Tetraclita*. The cells are labeled as in Wilson's coding system. (B) A fate map of a cirripede blastula (right-side view). (C) Intralecithal nuclear divisions in the early cleavage of a mysidan. (D) Newly hatched copepod nauplius larva. (E) Nauplius of a copepod. (F) Settling and metamorphosis of a cypris larva of a lepadomorph barnacle. (G) The zoea ("mysis") stage larva of the dendrobranchiate shrimp *Penaeus*. (H) Zoea larva of the brachyuran crab *Callinectes sapidus*. (I) Zoea larva of a porcelain crab. (J) Megalopa larva of the xanthid crab *Menippe adina*. (K) The characteristic antizoea larva of a stomatopod. (L) The translucent, paper-thin phyllosoma larva of the lobster *Jasus*. (M) Cryptoniscus stage (not a true larva) of the epicaridean isopod *Probopyrus bithynis*. (N) Cyprid larva of a barnacle. (M after W. E. Dale and G. Anderson. 1982. *J Crust Biol* 2: 392–409.)

Crustacean development is sometimes described as being epimorphic, anamorphic, or metamorphic, a nomenclature more often used in myriapods (see Chapter 23). However, we caution readers that a clear evolutionary and functional understanding of crustacean developmental stages is still lacking, and thus the terms "indirect" and "direct" may be preferable, and less ambiguous, until we have a better understanding of these phenomena.

Anamorphic development is indirect, with larval stages, and the number of segments increases with each molt. **Epimorphic development** is direct, and in

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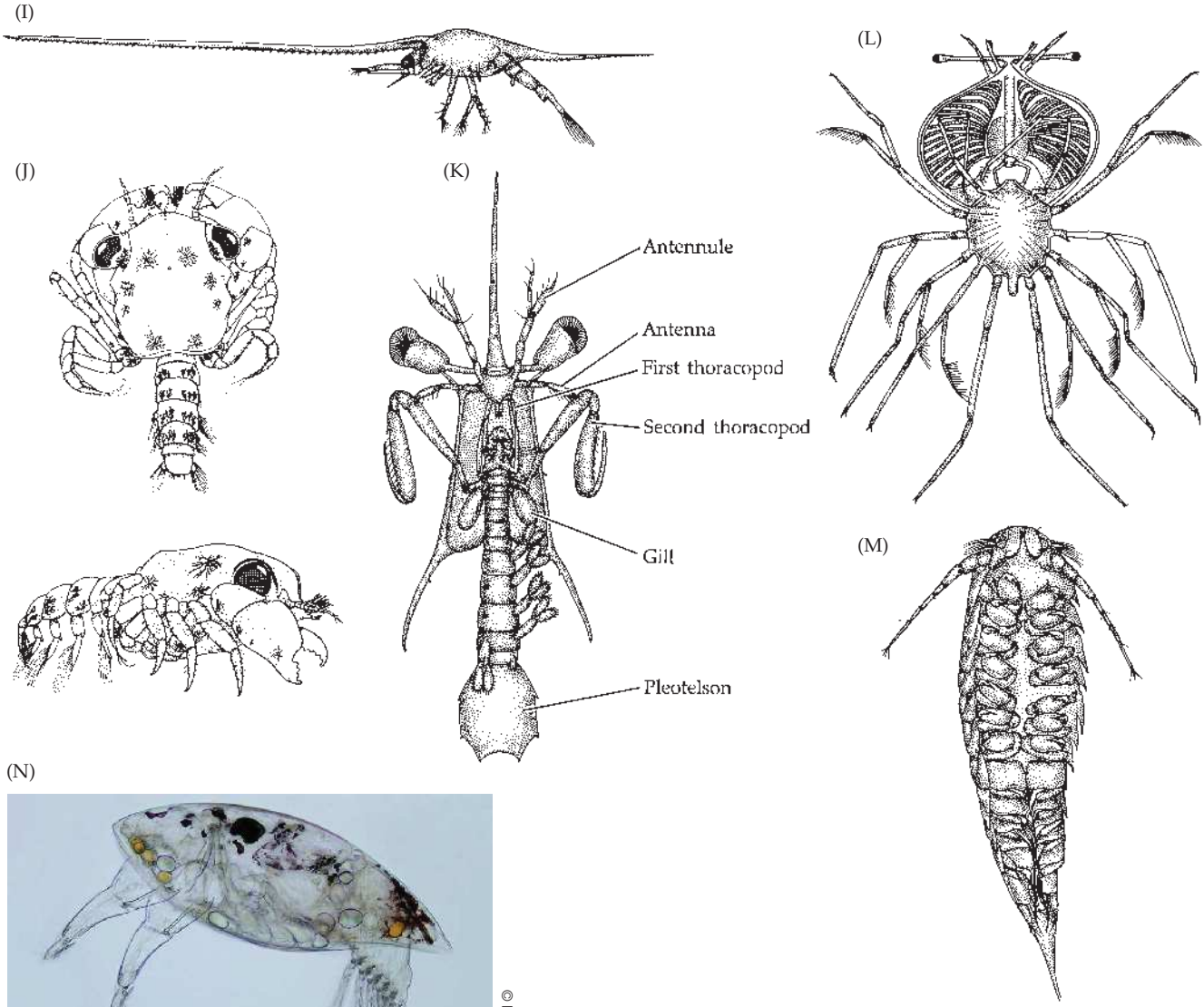

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crustaceans it is thought to result from a delay in the hatching of the embryo, which causes the nauplius (and any other possible larval stages) to be suppressed or absent. In epimorphic development the hatchlings have a full complement of segments and appendages. **Metamorphic development** is the type of extreme development seen among the Eucarida; it includes dramatic transitions in body form from one life history stage to another. In general, up to five distinct preadult, or larval, phases may be recognized among crustaceans: **nauplius**, **metanauplius**, **protozoea**, **zoea**, and "**postlarva**." The zoeal phase shows the greatest diversity in form among the various taxa, and especially in decapods it has been given different names in different groups (e.g., acanthosoma, antizoea, mysis, phyllosoma, pseudozoea). It is common for the zoeal phase to contain a large number of stages, each differing only slightly from the one preceding it.[11] Regardless of name, the zoea is characterized by the presence of natatory exopods on some or all of the thoracic appendages and by the pleopods being absent (or rudimentary). Use of the term "postlarva" is unfortunate, as these stages differ dramatically from the preceding larvae as well as from the adults; they represent unique transitional stages (both morphologically and ecologically). Examples in the Decapoda include the **megalopa** of true crabs and the **puerulus** larva of spiny lobsters. In this phase of development, the role of swimming has switched from the thoracopodal limbs to the appendages of the abdomen.

Anamorphic development is a less extreme type of indirect development in which the embryo hatches as a nauplius (or later) larva, but the adult form is achieved through a series of gradual changes in body morphology as new segments and appendages are added. It is similar in many ways to hemimetabolous development

[11] The zoea larvae of palinurid lobsters (phyllosoma larvae) are large, bizarre-appearing creatures (Figure 21.33L), which can occur in such large numbers as to be a favorite food of tuna.

in insects in that the postnaupliar stages gradually take on the adult form with succeeding molts; the classic example of anamorphic development is often said to be the Anostraca. But it differs from insect development in that insects are born with the full complement of segments and appendages. Cephalocarida, Remipedia, many Branchiopoda, and Mystacocarida are anamorphic—the nauplius larva grows by a series of molts that add new segments and appendages gradually as the adult morphology appears. In many groups hatching is somewhat delayed, and the emergent nauplius larva is termed a metanauplius. The basic nauplius possesses only three body somites, while the metanauplius has a few more; however, both possess only three pairs of similar-appearing appendages (which become the adult antennules, antennae, and mandibles). The end of the naupliar/metanaupliar stage is defined by the appearance of the fourth pair of functional limbs, the maxillules. In copepods a postnaupliar stage called a **copepodite** (simply a small juvenile) is often recognized.

The most extreme forms of metamorphic, or mixed, development occur in the malacostracan superorder Eucarida. The most complex developmental sequences are seen among the dendrobranchiate shrimps, which hatch as a typical nauplius larva that eventually undergoes a metamorphic molt to become a protozoea larva, with sessile compound eyes and a full complement of head appendages. The protozoea, after several molts, becomes a zoea larva, with stalked eyes and three pairs of thoracopods (as maxillipeds). The zoea eventually yields a juvenile stage (the "postlarva," a better term for which is "decapodid") that resembles a miniature adult but is not sexually mature. In some other eucarid groups (Caridea and Brachyura) the postlarva is called a **megalopa**, and in the Anomura it is often called a **glaucothoe**; in both cases there are setose natatory pleopods on some or all of the abdominal somites. In other eucarids, some (or all) of these stages are absent.

Various other terms have been coined for different (or similar) developmental stages. For example, the modified zoeal stages of some stomatopods are called **antizoea** and **pseudozoea** larvae, and the advanced zoeal stage of many other malacostracans is often called a **mysis larva**. In euphausiaceans, the nauplius is followed by two stages, the **calyptopis** and the **furcilia**, which roughly correspond to protozoea and zoea stages, before the juvenile morphology is attained.

We've only just skimmed the surface of postembryonic larval, or developmental stage names; some 140 different larval names have been used for decapods alone! But, from this wealth of terms and diversity of developmental sequences, we can draw two important generalizations concerning the biology and evolution of the crustaceans. First, different developmental strategies reflect adaptations to different lifestyles. In spite of many exceptions, we can cite the early release of dispersal larvae by groups with limited adult mobility, such as thoracican barnacles, and by groups whose resources may not permit production of huge quantities of yolk, such as the copepods. At the other end of this adaptive spectrum is the direct development of peracarids—a major factor allowing the invasion of land by certain isopod lineages. Between these extremes we see all degrees of mixed life histories, with larvae being released at various stages following brooding and care. Second, because developmental stages also evolve, an analysis of developmental sequences can sometimes provide information about the radiation of the principal crustacean lineages. For example, the evolution of oostegites and of direct development combine as a unique synapomorphy of the Peracarida. Similarly, the addition of a unique larval form, such as the **cypris larva** that follows the nauplius in the cirripedes, can be viewed as a unique specialization that demarcates that group (Cirripedia). The cyprid either hatches as the only free-living larva or is the final larval stage after a series of lecithotrophic or planktotrophic nauplius larval stages.

It should also be noted that the branchiopods and some freshwater ostracods have evolved specialized ways of coping with the harsh conditions of many freshwater environments. Parthenogenesis, for example, is common in freshwater ostracods. Other adaptations include production of special overwintering forms, usually eggs or zygotes that can survive extreme cold, lack of water, or anoxic conditions. Perhaps most remarkable in this respect are the large-bodied branchiopods (fairy shrimps, tadpole shrimps, and clam shrimps) whose encysted embryos are capable of an extreme state of anaerobic quiescence, or diapause. During these resistant stages, the metabolic rate of the embryos may drop to less than 10% of their normal rate. Interestingly, there is a large group of Ediacaran microfossils, called acritarchs, that look remarkably similar to branchiopod resting stages, although further research is needed to confirm the identity of these fossils.

Many crustaceans have **indeterminate growth**, that is, they continue to molt throughout their life. In contrast, other species have **determinate growth** and cease molting following puberty (this life history stage is sometimes referred to as the terminal molt, or terminal anecdysis). In some species, the terminal molt is sex specific; for example, in American blue crabs (*Callinectes sapidus*) only females have a terminal molt.

Crustacean Phylogeny

Countless phylogenetic studies have been published on the topic of crustacean evolution, but recent large-scale phylogenomic studies of the Pancrustacea have largely agreed on the higher-level structure of the group's phylogeny. Thus our tree (Figure 21.34A) depicts Pancrustacea comprising two large sister groups, Oligostraca and Altocrustacea. Oligostraca houses the Ostracoda, Mystacocarida, Branchiura, and Pentastomida (though

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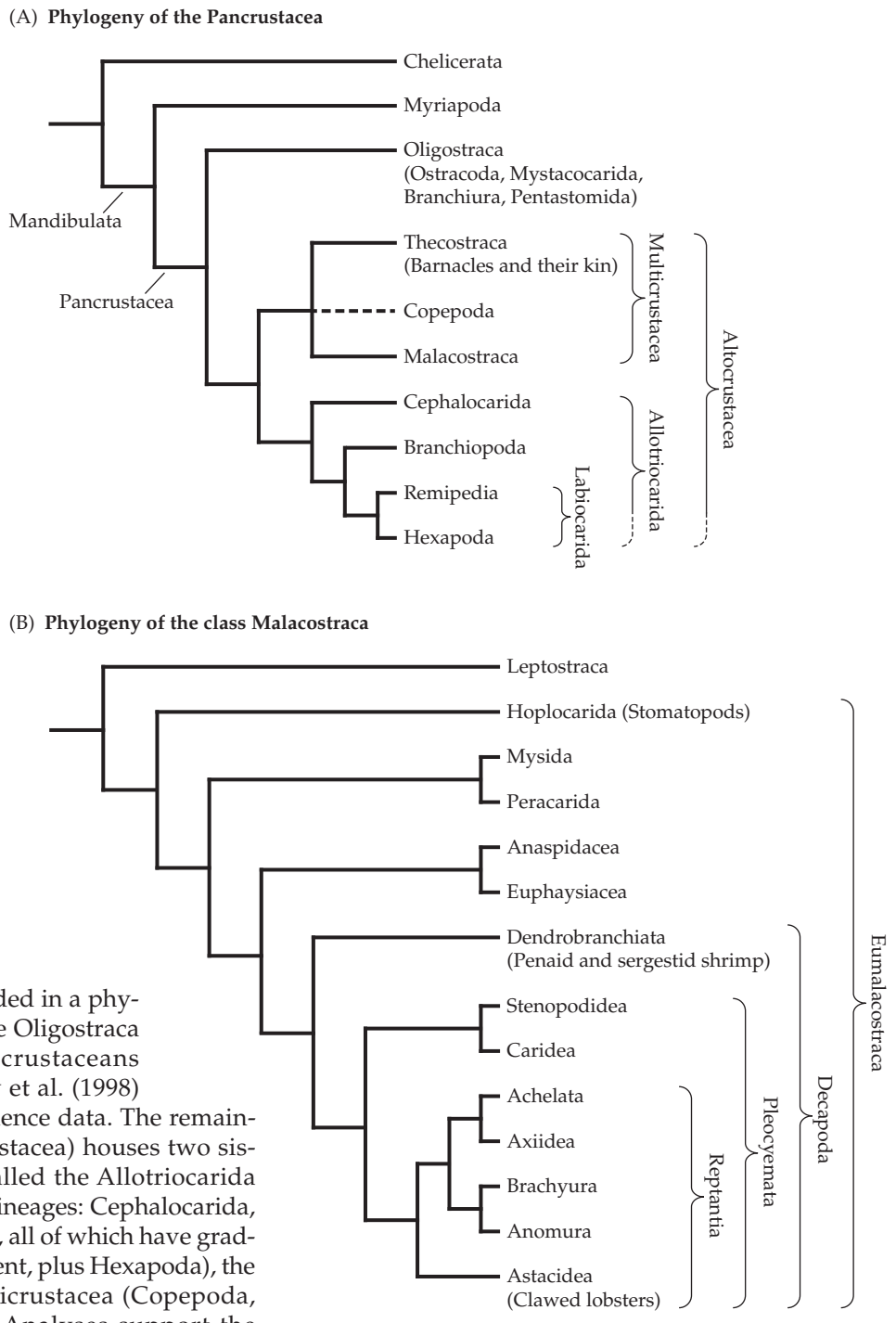


FIGURE 21.34
Crustacean phylogeny.
(A) A current view of relationships among the Pancrustacea. (B) A phylogeny of the class Malacostraca.

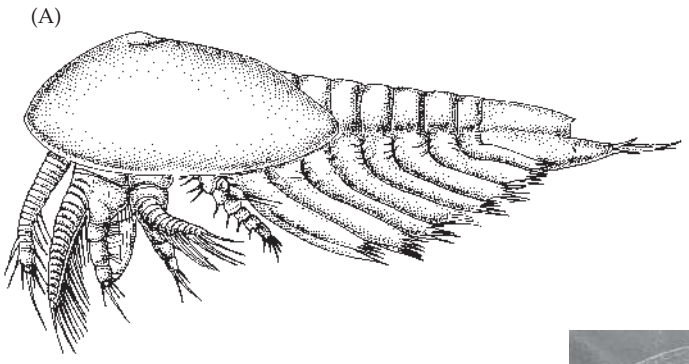
the last has not yet been included in a phylogenomic analysis). The clade Oligostraca is a group of short-bodied crustaceans initially suggested by Zrzavý et al. (1998) based primarily on gene sequence data. The remainder of the Crustacea (Altocrustacea) houses two sister groups, one sometimes called the Allotriocarida (the "leaf-footed" crustacean lineages: Cephalocarida, Branchiopoda, and Remipedia, all of which have gradual, or anamorphic, development, plus Hexapoda), the other sometimes called Multicrustacea (Copepoda, Thecostraca, Malacostraca). Analyses support the monophyly of most traditionally recognized taxa, such as Malacostraca, Peracarida, Dendrobranchiata, Decapoda, Pleocyemata, Reptantia, Thecostraca, Copepoda, Branchiopoda, Cephalocarida, Remipedia, and Hexapoda. Relationships within the Branchiopoda reflect current thinking based largely on morphology. Relationships among the major decapod clades are not yet fully resolved, and the precise position of Copepoda (within the Multicrustacea) is still uncertain. Hexapoda is likely a sister group to the Remipedia, the two taxa together called Labiocarida (based on the likely homology of the "lower lip" in remipedes and the "labium" in hexapods). The former groups known as "Maxillopoda" and "Entomostraca" are not supported by molecular analyses.

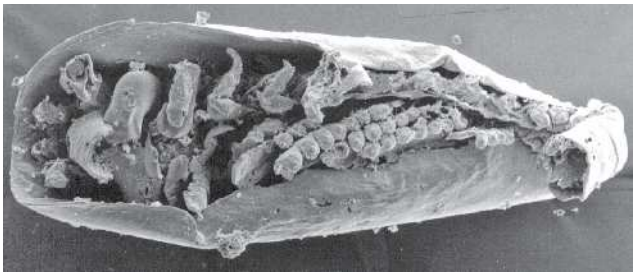
Within the class Malacostraca there are two clades: Leptostraca, which have phyllopodous limbs and seven abdominal somites, and Eumalacostraca, which lack phyllopodous limbs, have six abdominal segments, and have the sixth abdominal appendages modified as uropods (which can work in conjunction with the telson as a tail fan). Relationships among the main eumalacostracan lines are shown in Figure 21.34B.

The class Branchiopoda is monophyletic in molecular analyses, but it is difficult to define on the basis of unique synapomorphies because it shows such great morphological variation. The extreme reduction of adult maxillae, as well as certain naupliar characters (e.g., reduced and tubular antennules, uniramous mandibles) strongly support monophyly, as do almost all studies employing molecular data. Apparently some branchiopods have secondarily lost the carapace, and others have secondarily lost most or all of the abdominal appendages.

That a group of crustaceans gave rise to the megadiverse group of arthropods called the Hexapoda (insects and their kin) is now almost universally agreed upon, based on a wide array of evidence that includes molecular sequence data, neuroanatomy, and other information. This realization renders the group called "Crustacea" paraphyletic. The monophyletic clade containing both crustaceans and insects is referred to as the Pancrustacea, or Tetraconata (a name that recognizes the unique presence and anatomy of four crystalline cone cells, known as Semper cells, in the ommatidia). Like the arthropods in general, crustaceans exhibit high levels of evolutionary parallelism and convergence and many apparent reversals of character states. This genetic flexibility is no doubt due in part to the nature of the segmented body, the serially homologous appendages, and the flexibility of developmental genes, which, as we have stressed, provide enormous opportunity for evolutionary experimentation. Any conceivable cladogram of crustacean phylogeny will require the acceptance of considerable homoplasy.

Fossil data (including the Cambrian Orsten fauna, Figure 21.35) seem to favor phyllopodous limbs as the primitive condition. However, developmental studies following the expression of *Distal-less* and other





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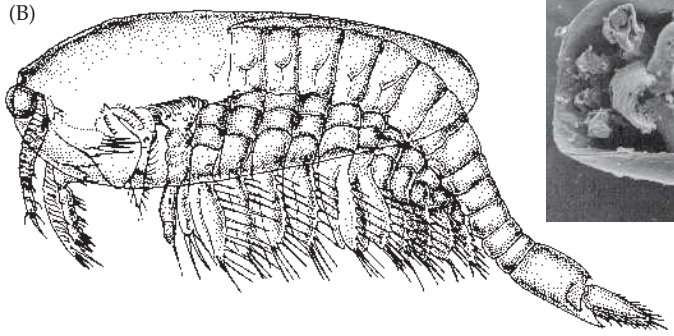

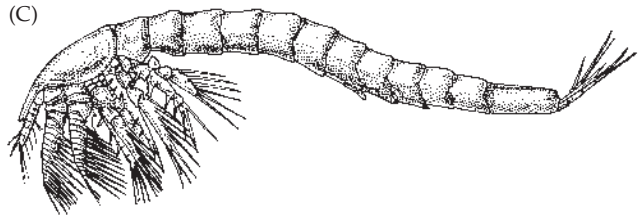

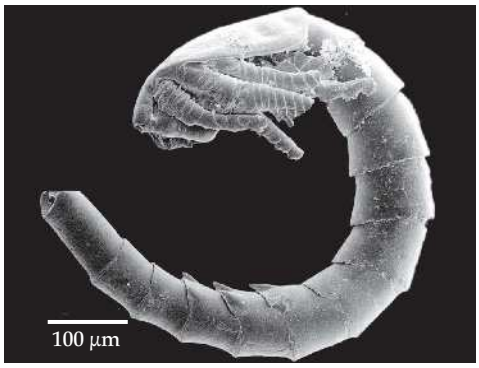

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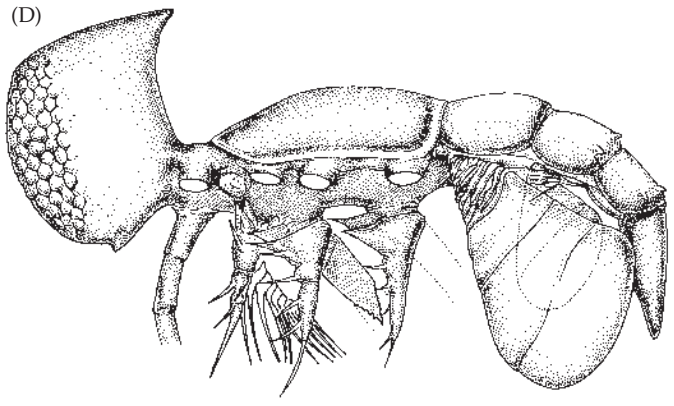

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developmental genes suggest that the early embryogeny of limbs is very similar among crustaceans. For example, trunk limbs always emerge as ventral, subdivided limb buds. In phyllopodous limbs, the subdivisions of these limb buds grow to become the endites and the endopod of the natatory/filtratory adult limbs. In stenopodous limbs, the same limb bud subdivisions end up developing into the actual segments of the adult limb. Hence, the endites of phyllopodous limbs appear to be homologous to the segments of the stenopodous limbs. This discovery supports an emerging view of developmental plasticity in arthropod limbs, and it suggests that relatively simple genetic "switches" can account for major differences in adult morphologies. Thus, it is quite plausible that stenopodous limbs have evolved multiple times from phyllopodous ancestors, and this is the scenario depicted in the tree in Figure 21.34B.

Work by Klaus Müller and Dieter Waloszek on three-dimensionally preserved microscopic arthropods from the middle Cambrian Orsten (about 510 Ma) deposits of Sweden has documented a diverse fauna of minute crustaceans and their larvae. Among them, for example, is *Skara* (Figure 21.35C), a cephalocarid- or mystacocarid-like crustacean for which both naupliar larvae and adults have been recovered (the nauplius larvae are only a couple hundred microns long; adults are about 1 mm in length). *Skara* and many other Orsten crustaceans were probably meiofaunal animals not unlike modern marine meiofaunal forms (e.g., the mystacocarids). Dozens of Orsten microcrustaceans have so far been described (Figure 21.35). In 2001, a beautifully preserved fossil, *Ercaia minuscula*, was described from the middle Cambrian (520 Ma; Series 2) of South China. It has an untagmatized, 13-segmented trunk with serially repeated biramous appendages and a head with stalked eyes and five pairs of head appendages, including two pairs of antennae. *Ercaia minuscula* is only 2–4 mm long (hence the species name) and bears resemblances to both cephalocarids and "maxillopodans" (Figure 21.35F).

Studies on Cambrian fossils from the Swedish Orsten fauna (510 Ma), Burgess Shale–like deposits from around the world (520 Ma), and the Chengjiang fossils from China (530 Ma) have shown that Cambrian

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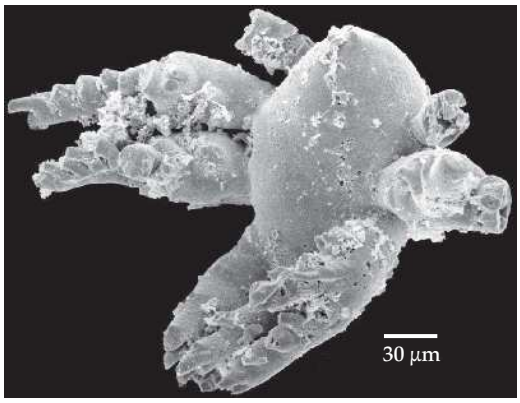

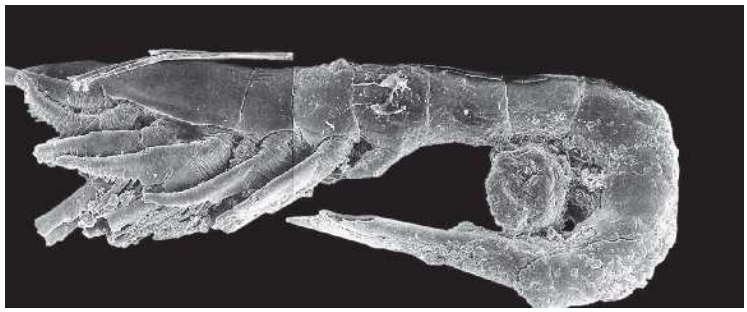

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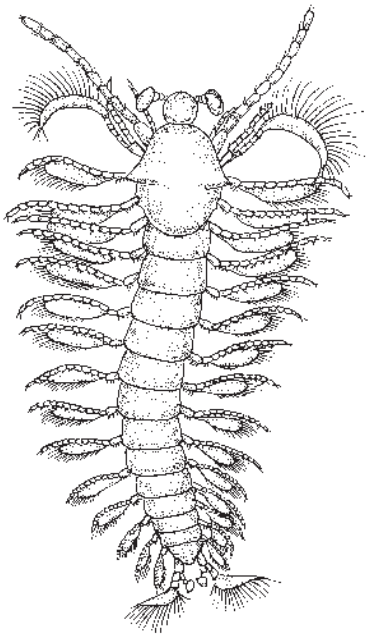

FIGURE 21.35 (A–E) Examples of upper Cambrian (~510 Ma), probably meiofaunal crustacean fossils from the spectacular Swedish Orsten deposits. This ancient crustacean fauna possessed the key attributes of modern Crustacea, including compound eyes, head shields/carapaces, naupliar larvae (with locomotory first antennae), and biramous appendages on the second and third head segments (the second antennae and mandibles). (A) *Bredocaris*. (B) *Rehbachiella*, an early branchiopod, lateral (drawing) and ventral (SEM) views. (C) *Skara*, drawing and SEM. (D) *Cambropachycope clarksoni*, a bizarre species with an expanded head and two pairs of enlarged thoracopods, drawing and SEM. (E) *Martinssonia elongata*, SEMs of first larva and postlarval stage. (F) *Ercaia minuscula*, an early Cambrian (520 Ma) crustacean from South China.

crustaceans had all the attributes of modern ones, such as compound eyes, an ocular segment, distinct head and trunk tagmata, at least four head appendages, a carapace (or head shield), naupliar (or "head") larvae (with locomotory first antennae), and biramous appendages on the second and third head somites (the second antennae and mandibles). We thus know that the crustaceans are an ancient group. Their fossil record dates back to the early Cambrian (the Fortunian stage), or likely the Ediacaran period if some arthropod fossils from those strata are viewed as Crustacea. The earliest undisputed crustacean larval stage is a fossil of a slightly advanced nauplius (called a metanauplius) from the Terreneuvian (525 Ma) of China that in many ways resembles the naupliar larva of modern cirripedes. This is remarkable, as it confirms not only the great age of the Crustacea as a whole but also the age of groups within the Crustacea, such as the cirripedes, that were already becoming distinct.

Chapter Summary

The subphylum Crustacea is a paraphyletic group, because it excludes the Hexapoda (insects and their kin), which evolved from within Crustacea close to 500 million years ago. The sister group of Hexapoda may be Remipedia. Phylogenetically, Crustacea and Hexapoda comprise the clade Pancrustacea (sometimes called Tetraconata). As with the insects on land, crustaceans have been hugely successful in the aquatic world. Close to 60,000 living crustacean species have been described, but five or ten times that number probably await discovery. As with insects, the morphological disparity within Crustacea is staggering, with body sizes ranging from less than 100 μm in length to over 4 meters in width. Given that most of Earth is covered with water, and the great depths of world's seas, crustaceans are the most widespread animals on the planet! Crustaceans are well understood, in part, because of their economic importance, especially as seafood. A number of groups, notably isopods and amphipods, have successfully invaded the terrestrial world. The crustacean body is divided into a head (bearing 5 pairs of appendages) and trunk, the latter being subdivided into a thorax and abdomen in all but the class Remipedia. The head, and often some of the thoracic segments, are commonly covered by a dorsal shield called the carapace. Paralleling their morphological diversity, crustaceans exhibit a wide range of locomotory strategies that include swimming, walking, and hopping. They also have numerous modes of feeding, including suspension feeding, deposit feeding, active predation, and parasitism. The body is a hemocoel, but a dorsal ostiate (pumping) heart is usually present, as are small vessels that distribute the hemocoel. Excretion relies on various nephridially-derived structures and diffusion across the gills. The central nervous system follows the general arthropod plan, with a brain composed of three fused pairs of ganglia (protocerebrum, deutocerebrum, tritocerebrum), the tritocerebrum forming a pair of circumenteric connectives around the esophagus to a subenteric ganglion that links to the ventral nerve cord formed of paired segmental ganglia. Most crustaceans are gonochoristic, although hermaphroditism is not uncommon (usually expressed as protandry or protogyny). Parthenogenesis is known in some groups. Cleavage patterns in embryos are highly diverse and largely dependent on the amount of yolk present, ranging from equal to unequal. Crustacea have a characteristic first larval stage called the nauplius larva (suppressed or bypassed in some groups), denoted by three pairs of appendage-bearing somites. In some groups, various other postnaupliar larvae occur (e.g., metanauplius, protozoea, zoea, megalopa). A rich record of Cambrian fossil Crustacea has been described from Sweden, China, and elsewhere. We now know that Pancrustacea likely comprises three great clades: Oligostraca (Ostracoda, Mystacocarida, Branchiura, Pentastomida), Multicrustacea (Thecostraca, Copepoda, Malacostraca), and Allotriocarida (Cephalocarida, Branchiopoda, Remipedia, Hexapoda).

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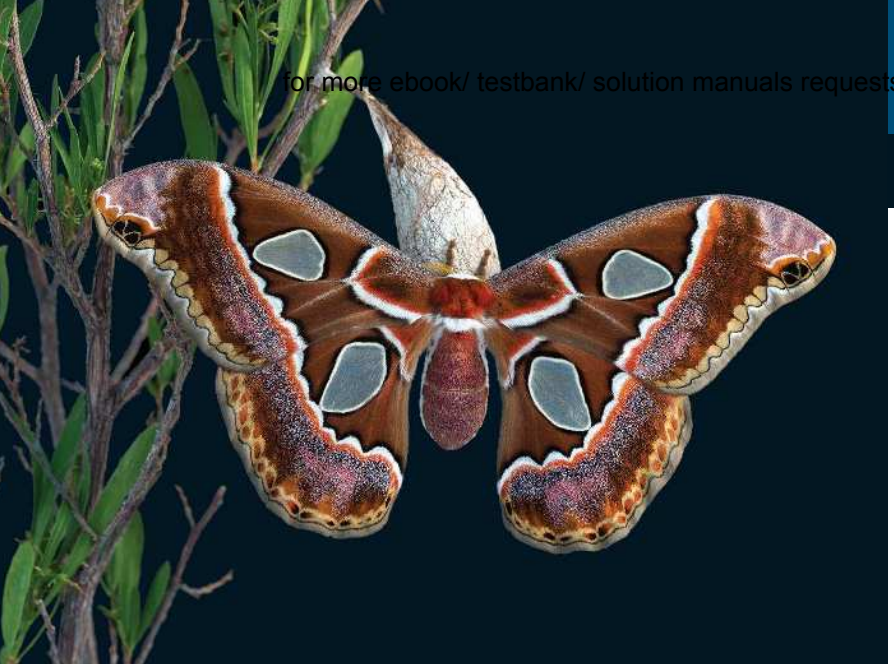

Courtesy of Bruce D. Taubert

CHAPTER 22

Phylum Arthropoda

Subphylum Hexapoda: Insects and Their Kin

Arthropods stand out among all other invertebrates for being far and away the most diverse phylum of animals on Earth. This is due, entirely, to the hexapod class Insecta—their diversity and abundance nearly defy imagination. Insects are the only invertebrates that fly, and the only terrestrial invertebrate group whose members undergo either indirect development or complete metamorphosis.

The arthropod subphylum Hexapoda comprises the class Insecta and three other small, wingless, insectlike groups: Collembola, Protura, and Diplura. All hexapods have a distinct body plan consisting of a head, a 3-segmented thorax, and an abdomen of 11 segments (or fewer in groups that have a secondarily reduced abdomen). The thorax bears three pairs of legs and, in the Pterygota, two pairs of wings. The head bears a single pair of antennae (vestigial in Protura) and three sets of mouthparts (mandibles, maxillae, and labium). They have an aerial gas exchange system, composed of tracheae and spiracles, and Malpighian tubules formed as proctodeal (ectodermal) evaginations (Box 22A). The presence of a thorax fixed at three segments, each with a pair of walking legs, is an apomorphy of Hexapoda. Other apomorphies include the presence of a large fat body (mainly concentrated in the abdomen) and fusion of the second maxillae to form a lower lip (the labium).

Hexapods evolved on land; groups inhabiting aquatic environments today have secondarily invaded those habitats through physiological adaptations and modifications of their aerial gas exchange systems. The earliest undisputed fossils of hexapods are Early Devonian (412 Ma). However, there are Silurian trace fossils that are very hexapod-like, and molecular clock data suggest an Early Ordovician origin for Hexapods at about 480 million

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

BOX 22A Characteristics of the Subphylum Hexapoda

1. Body composed of 20 segments organized as a head (6 somites), thorax (3 somites), and abdomen (11 somites; or fewer in groups with a reduced abdomen); due to fusion of somites, body segments are not always externally obvious
2. Head bears the following structures (from anterior to posterior): compound eyes and ocelli, antennae, clypeolabrum, mandibles, maxillae, labium (fused second maxillae); ocelli (and compound eyes) secondarily lost in some groups
3. Legs uniramous, present on the three thoracic segments of adults. Legs composed of six articles: coxa, trochanter, femur, tibia, tarsus, and pretarsus; tarsus often subdivided, pretarsus typically clawed.
4. Gas exchange by spiracles and tracheae
5. Gut with gastric (digestive) ceca
6. Large fat body is mainly concentrated in abdomen
7. Fused exoskeleton of head forms a unique internal tentorium
8. Ectodermally derived Malpighian tubules (proctodeal evaginations)
9. Gonopores open on the last abdominal segment, or on abdominal segment 7, 8, or 9
10. Gonochoristic; development direct or indirect

years ago and an early Silurian origin about 440 million years ago for Insecta.

The most spectacular evolutionary radiation among the Hexapoda (in fact among all eukaryotic life) has, of course, been within the insects, which inhabit nearly every conceivable terrestrial and freshwater habitat and, less commonly, even the sea surface and the marine littoral region. Insects are also found in such unlikely places as oil swamps and seeps, sulfur springs, glaciers and glacial streams, and brine ponds. They often live where only few other animals or plants can exist. It is no exaggeration to say that insects rule the land.

We do not know how many species of Hexapoda there are on the planet, or even precisely how many have already been described. Published estimates of the number of described (living) species range from 890,000 to well over a million; we estimate there are nearly 996,000 described species of hexapods. An average of about 3,500 new species have been described annually since the publication of Linnaeus's *Systema Naturae* in 1758, although in recent years the average has climbed to around 7,000 new species annually. Estimates of the number of insect species remaining to be described range from 3 million to 100 million. The Coleoptera (beetles), with an estimated 387,000 described species, is far and away the largest insect order (more than a quarter of all described animal species are beetles). The beetle family Curculionidae (the weevils) contains about 65,000 described species (nearly 5% of all described animal species). The rich diversity of insects seems to have come about through a combination of advantageous features, including the evolutionary exploitation of developmental genes working on segmented and compartmentalized bodies, coevolution with plants (particularly the flowering plants), miniaturization, and their ability to fly.

Insects are not only diverse, but also incredibly abundant. For every human alive, there are an estimated 200 million insects. Howard Ensign Evans estimated that an acre of ordinary English pasture supports an astonishing 248,375,000 springtails and 17,825,000 beetles. In tropical rainforests, insects can constitute 40% of the total animal biomass (dry weight), and the biomass of the ants can be far greater than that of the combined mammal fauna (up to 15% of the total animal biomass). A single colony of the African driver ant *Anomma wilverthi* may contain as many as 22 million workers. Based on his research in the tropics, biodiversity sleuth Terry Erwin calculated that there are about 3.2×10^8 individual arthropods per hectare, representing more than 60,000 species, in the western Amazon. In Maryland, a single population of the mound-building ant *Formica exsectoides* comprised 73 nests covering an area of 10 acres and containing approximately 12 million workers. Termites have colonies of similar magnitudes. E. O. Wilson calculated that, at any given time, 10^{15} (a million billion) ants are alive on Earth! And in one 4 ha patch of cloud forest in Costa Rica an astounding 4,332 species of Diptera were found; this amounts to more than half the number of named species of flies for all of Central America!

In most parts of the world, insects are among the principal predators of other invertebrates. Insects are also key prey in the diets of many terrestrial vertebrates and other arthropods, especially arachnids and myriapods, and they play a major role as reducer-level organisms (detritivores and decomposers) in food webs. Due to their diversity and abundance, they constitute much of the fabric of terrestrial food webs. Their biomass and energy consumption exceed those of vertebrates in most terrestrial habitats. In deserts and in the tropics, ants replace earthworms as the most abundant earth movers (ants are nearly as important as earthworms even in temperate regions). Termites are among the chief decomposers of dead wood and leaf litter around the world, and without dung beetles African savannas would be buried under the excrement of the tens of thousands of large grazing mammals.

Without insects, life as we know it would cease to exist. In fact, E. O. Wilson stated, "So important are insects and other land-dwelling arthropods that if all were to disappear, humanity probably could not last more than a few months." Some 80% of the world's crop species, including food, medicine, and fiber crops, rely

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on animal pollinators, nearly all of which are insects. Insects also play key roles in pollinating wild, native plants, and there is evidence (in mid-Cretaceous Burmese amber fossils) of specialized beetle-angiosperm pollination as early as 99 million years ago. Beekeeping began long ago, at least by 600 BCE in the Nile Valley and probably well before that. The first migratory beekeepers were Egyptians who floated hives up and down the Nile to provide pollination services to floodplain farmers while simultaneously producing a honey crop. Domestic honeybees (*Apis mellifera*), introduced to North America from Europe in the mid-1600s, are now the dominant pollinators of most food crops grown around the world, and they play some role in pollinating 80% of the crop varieties grown in the United States.[1]

Interactions between insects and flowering plants have been going on for a very long time, beginning over 100 million years ago with the origin of the angiosperms and accelerating with the ascendancy of these flowering plants during the early Cenozoic. Millions of years of plant-insect coevolution have resulted in flowers with anatomy and scents that are finely tuned to their insect partners. In exchange for pollination services, flowers provide insects with food (nectar, pollen), shelter, and chemicals used by the insects to produce such things as pheromones. In general, insect pollination is accomplished coincidentally, as the pollinators visit flowers for other reasons. But in a few cases, such as that of the yucca moths of the American Southwest (*Tegiticula* spp.), the insects actually gather up pollen and force it into the receptive stigma of the flower, initiating pollination. The moth's goal is to assure a supply of yucca seed for its larvae, which develop within the yucca's fruits. Some insects also play important roles as seed dispersers, especially ants. More than 3,000 plant species (in 60 families) are known to rely on ants for the dispersal of their seeds.

Like all other animals on Earth, insects are facing enormous threats of extinction. Certainly many thousands of species have become extinct over the past century as a result of rampant land use change and deforestation. With accelerating biodiversity losses worldwide, estimates of the number of insect species that have already gone extinct range into the millions. Further, widespread and often inappropriate use of pesticides (e.g., neonicotinoids) has created a "pollination crisis" in many parts of the world, as pollinating insects are locally extirpated and native plant and domestic crop pollination plummets.

As valuable as insects are to human life, some species seem to conspire to give the whole group a bad name. Some insect species are pests that consume about a third of our potential annual harvest, and some other species transmit devastating human diseases. Every year we spend billions of dollars on insect control. Malaria, transmitted by mosquitoes, kills 1 to 3 million people annually (mostly children), and each year nearly 500 million people contract the disease. It is the leading cause of death from infectious disease, and it has plagued humans for at least 3,000 years (Egyptian mummies have been found with malaria antigens in their blood). One of the most widespread and fastest-spreading human viral diseases, dengue, is transmitted by mosquitoes of the genus *Aedes*. Dengue is essentially an urban disease, almost entirely associated with anthropogenic environments because its main vectors, *A. albopictus* and *A. aegypti*, breed primarily in artificial containers (e.g., flower vases, discarded tires, water tanks). In recent years, these species have spread throughout the tropics, often following the international trade in used tires. Although these mosquitoes have not penetrated very far into the temperate zones, they have become established in the southern United States. Another variety of mosquitoes transmits the filarial nematode *Wuchereria bancrofti*, the causative agent of lymphatic filariasis ("elephantiasis") throughout the world's tropics. Chagas' disease (American trypanosomiasis) is transmitted by certain hemipteran bugs in the subfamily Triatominae (family Reduviidae) and causes chronic degenerative disease of the heart and intestine. The species of triatomine bugs that occur in the southwestern United States tend not to defecate when they feed, greatly reducing the possibility of humans contracting Chagas' disease in that area. However, global warming is now increasing the spread of *Aedes*, *Culex*, triatomines, and other tropical disease vectors.

Natural history writer David Quammen, speaking of the blood-sucking varieties of mosquitoes, notes that the average blood meal of a female (the only sex that feeds on blood) amounts to 2.5 times the original weight of the insect—the equivalent, Quammen notes, "of Audrey Hepburn sitting down to dinner and getting up from the table weighting 380 pounds, then, for that matter, flying away." But as Quammen also points out, mosquitoes have made tropical rainforests (the most diverse ecosystems on Earth) largely uninhabitable to humans, thus helping to preserve them!

The enormous diversification of Hexapoda is often attributed to the evolution of three key innovations: the ability to fly, the ability to fold back their wings, and hemimetabolous and holometabolous development. The persistence of the main lineages of insects since the Devonian and their ecological and morphological

[1] The study of bees is called "melittophily." The study of honeybees (*Apis* spp.) and their management is called "apiculture." The management of bumblebees (*Bombus* spp.) is "bombiculture." The ritualized keeping of stingless bees is "meliponiculture." The Asian honeybee, *Apis dorsata*, is a giant, reaching an inch in length. Its droppings are quite noticeable, and the mass defecations of these bees at sunset create a "golden shower" that provides significant nutrient enrichment to tropical soils. Their droppings were once confused with the dreaded "yellow rain," a deadly form of biochemical warfare that poisoned thousands of villagers during the Vietnam War.

versatility have undoubtedly contributed to making Hexapoda the dominant group in extant terrestrial ecosystems, with respect to species diversity, functional diversity, and overall biomass. Obviously, the subject of insect biology, or entomology, is a discipline in its own right, and a multitude of books and college courses on the subject exists. If we apportioned pages to animal groups on the basis of numbers of species, overall abundance, or economic importance, insect chapters could easily fill 85% of this textbook. The Selected References at the end of this book provide entry into some of the current literature on insects.

There are as many orders of Hexapoda as there are phyla of animals (31). Because hexapods comprise such a large and diverse assemblage of arthropods, we first present a brief classification of the recognized orders, followed by more detailed synopses, brief diagnoses, and comments on each order. These two sections serve as a preface to the body plan discussion that follows and also provide a reference that the reader can refer to as needed.

Classification of the Subphylum Hexapoda

Our classification scheme recognizes 31 orders of living hexapods. Three entognathous, or noninsect, hexapod orders (formerly classified as Entognatha) are basal to the monophyletic class Insecta. The Insecta comprise two monophyletic sister groups, the order Archaeognatha (with monocondylic mandibles) and all the others (with dicondylic mandibles). The subclass Pterygota, or flying insects, comprise two groups: the Palaeoptera (Ephemeroptera, Odonata), which may be a paraphyletic group, and the monophyletic infraclass Neoptera. We recognize three superorders within the modern winged insects, or Neoptera: the Polyneoptera (Blattodea, Dermaptera, Embioptera, Grylloblattodea, Mantodea, Mantophasmatodea, Orthoptera, Phasmida, Plecoptera, and Zoraptera), the Acercaria (Hemiptera, Psocodea, Thysanoptera), and the Holometabola (all the remaining orders). Within the Holometabola we recognize four well-supported, but unranked clades: Coleopetrida (Coleoptera, Strepsiptera), Neuropterida (Megaloptera, Neuroptera, Raphidioptera), Antliophora (Diptera, Mecoptera, Siphonaptera), and Amphiesmenoptera (Lepidoptera, Trichoptera). With nearly a million named species of Hexapoda, we have opted to include representative families of only the most diverse and common orders in the taxonomic synopses.

SUBPHYLUM HEXAPODA

(Note: Entognatha is a paraphyletic group; Diplura is the sister group of Insecta. Palaeoptera is likely a paraphyletic group.)

ENTOGNATHA

ORDER COLLEMBOLA Springtails

ORDER PROTURA Proturans

ORDER DIPLURA Diplurans

CLASS INSECTA (= ECTOGNATHA)

ORDER ARCHAEOGNATHA Jumping bristletails

DICONDYLIA

ORDER ZYGENTOMA Silverfish

SUBCLASS PTERYGOTA Winged insects

INFRACLASS PALAEOPTERA Ancient winged insects

ORDER EPHEMEROPTERA Mayflies

ORDER ODONATA Dragonflies and damselflies

INFRACLASS NEOPTERA Modern, wing-folding insects

SUPERORDER POLYNEOPTERA

ORDER PLECOPTERA Stoneflies

ORDER BLATTODEA Cockroaches and termites

ORDER MANTODEA Mantises

ORDER PHASMIDA (= PHASMATODEA) Stick and leaf insects

ORDER GRYLLOBLATTODEA Rock crawlers

ORDER DERMAPTERA Earwigs

ORDER ORTHOPTERA Locusts, katydids, crickets, grasshoppers

ORDER MANTOPHASMATODEA Heel-walkers or gladiators

ORDER EMBIOPTERA (= EMBIIDINA) Web-spinners

ORDER ZORAPTERA Zorapterans

SUPERORDER ACERCARIA (= PARANEOPTERA)

ORDER THYSANOPTERA Thrips

ORDER HEMIPTERA True bugs

ORDER PSOCODEA Book lice, bark lice, true lice

SUPERORDER HOLOMETABOLA

ORDER HYMENOPTERA Ants, bees, wasps

COLEOPTERIDA

ORDER COLEOPTERA Beetles, weevils, ladybugs, etc.

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ORDER STREPSIPTERA Twisted-wing parasites

NEUROPTERIDA

ORDER MEGALOPTERA Alderflies, dobsonflies, fishflies

ORDER RAPHIDIOPTERA Snakeflies

ORDER NEUROPTERA Lacewings, ant lions, mantisflies, owlflies

ANTLIOPHORA

ORDER MECOPTERA Scorpionflies, hangingflies, snow scorpionflies (possibly paraphyletic within Siphonaptera)

ORDER SIPHONAPTERA Fleas

ORDER DIPTERA True flies, mosquitoes, gnats, hoverflies

AMPHIESMENOPTERA

ORDER TRICHOPTERA Caddisflies

ORDER LEPIDOPTERA Butterflies, moths

Synopses of Hexapod Groups

Subphylum Hexapoda

Body differentiated into head (of six segments), thorax (3 segments), and abdomen (11 or fewer segments); head with 1 pair of lateral compound eyes and often with a triad or pair of medial ocelli; with 1 pair of uniramous multiarticulate antennae, mandibles, and maxillae; second pair of maxillae fused to form a complex labium; each thoracic segment with 1 pair of uniramous legs; wings often present on second and third thoracic segments (in pterygote insects); abdomen without fully developed legs, but "prolegs" (presumably homologous with the ancestral arthropod abdominal appendages) occur in at least 7 orders (in adults of some Diplura, Zygentoma, and Archaeognatha; in larvae of some Diptera, Trichoptera, Lepidoptera, and Hymenoptera); abdomen with a large fat body; gonopores open on the last abdominal segment or on the seventh, eighth, or ninth abdominal segment; paired cerci often present; males commonly with intromittent and clasping structures; development direct, involving relatively slight changes in body form (ametabolous or hemimetabolous), or indirect with striking changes (holometabolous). About 996,000 described, extant species.

Entognatha

Mouthparts with bases hidden within the head capsule ("ento-gnathous"); mandibles with single articulation; most or all antennal articles with intrinsic musculature; wingless; without, or with poorly developed, Malpighian tubules; legs with 1 (undivided) tarsus. The 3 orders of entognathous hexapods do not form a monophyletic group. Recent data from paleontology, comparative anatomy, and molecular phylogenetics suggest that Diplura is the sister group of Insecta and therefore more closely related to the Insecta than to the other entognathous orders.

Order Collembola Approximately 6,000 described species (Figure 22.1A,B). Small (most less than 6 mm); biting-chewing mouthparts; with or without small compound eyes; ocelli vestigial; antennae with 4 articles, first 3 with intrinsic muscles; tarsus of legs indistinct (perhaps fused with tibia); pretarsus of legs with single claw; abdomen with a reduced number of segments (6, or fewer in Symphypleona); first abdominal segment with ventral tube (collophore) of unknown function; third abdominal segment with small process (retinaculum); a forked tail-like appendage on fourth or fifth abdominal segment (furcula); without cerci; with gonopores on last abdominal segment; without Malpighian tubules; often without spiracles or tracheae.

The earliest known hexapods in the fossil record are collembolans. *Rhyniella praecursor* and other species from the Lower Devonian closely resemble some modern collembolan families. Unlike most other hexapods, which breathe using internal tubes called tracheae, springtails breathe air directly through their cuticle and epidermis. Their cuticle repels water, allowing them to live in moist environments without suffocating. They also have a remarkable system for escaping predators. While they are at rest, the furcula is retracted under the abdomen and held in place by the retinaculum. When the furcula and retinaculum disassociate, the furcula swings downwards with such force that it hits the substrate and quickly propels the collembolan high into the air. Many workers believe that springtails evolved via neoteny.

Order Protura Approximately 200 described species (Figure 22.1D). Minute (smaller than 2 mm); whitish; without eyes, abdominal spiracles, hypopharynx, or cerci; Malpighian tubules are small papillae; sucking mouthparts; styletlike mandibles; vestigial antennae; first pair of legs carried in an elevated position and used as surrogate "antennae"; pretarsus of legs with single claw; 11-segmented abdomen, with a telson (perhaps reminiscent of their crustacean ancestors); the segmental nature of this telson or twelfth "segment" has not been confirmed; first 3 abdominal segments with small appendages; without external genitalia, but male gonopores on protrusible phallic complex; gonopores on last abdominal segment; with or without tracheae; simple development.

Proturans are the only hexapods with anamorphic development, a type of development in which a new abdominal segment is added with each instar (or molt).

FIGURE 22.1 Representatives of the three orders of entognathous (noninsect) hexapods. (A) *Anurida granaria*, a springtail (order Collembola, suborder Poduromorpha). (B) *Ptenothrix* sp., a springtail (order Collembola, suborder Symphypleona). (C) A campodeid dipluran from New Zealand (order Diplura). (D) A proturan from British Columbia (order Protura).

All other insects have epimorphic development, in which segmentation is complete before hatching. Proturans are rare, and live in leaf litter, moist soils, and rotting vegetation.

Order Diplura Approximately 800 described species (Figure 22.1C); fossils date to the Carboniferous. Small (usually 0.3 to 1.0 cm in length, although the largest species reaches 5 cm); whitish; without eyes, ocelli, external genitalia, or Malpighian tubules; chewing mouthparts; 11-segmented abdomen, but embryonic segments 10 and 11 fuse before hatching; gonopores on ninth abdominal segment; 7 pairs of lateral abdominal leglets; 2 caudal cerci, enlarged and forming a pair of pincers in japygids; with tracheae and up to 7 pairs of abdominal spiracles; antennae multiarticulate, each article with intrinsic musculature; simple development. Most species live in mesic habitats beneath rocks, rotting logs, leaf litter, humus, and soil.

Class Insecta

Mouth appendages ectognathous (exposed and projecting from the head capsule); mandibles with 2 points of articulation (except Archaeognatha); intrinsic musculature of antennal articles greatly reduced; antennal pedicel with a mechanoreceptor that perceives the movement of the flagellum, called the Johnston's organ; head with a tentorial bridge connecting the posterior tentorial arms; tarsi subdivided into tarsomeres; with well-developed Malpighian tubules; ovipositor formed from modifications of the appendages of abdominal segments 8 and 9. The Insecta comprise 2 clades, the order Archaeognatha (with monocondylic mandibles) and all other insects (the clade Dicondylia, with dicondylic mandibles). Dicondylia also comprise two clades, the order Zygentoma and the subclass Pterygota (winged insects).

Order Archaeognatha Approximately 390 described species (Figure 22.2A,B). Small (to 15 mm), wingless (perhaps secondarily), resembling silverfish but body more cylindrical; ocelli present; compound eyes large and contiguous; body usually covered with scales; mandibles biting-chewing; with a single condyle (articulation point); maxillary palp large and leglike; 3-articulate tarsi; middle and hind coxae usually with exites ("styli"); 11-segmented abdomen, with 3 to 8 pairs of lateral leglets ("styli") and 3 caudal filaments; simple development. Jumping bristletails are usually found in grassy or wooded areas under leaves, bark, or stones.

Dicondylia

Includes Thysaura and the Pterygota (the winged insects). These two large insect clades are characterized by mandibles with two condyles (articulation points).

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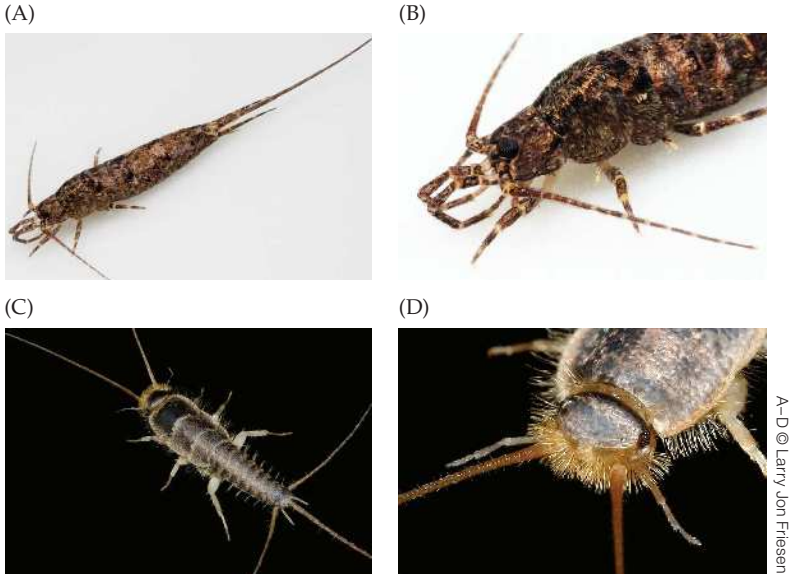

FIGURE 22.2 Representatives of the two orders of wingless Insecta. (A) Jumping bristletail (order Archaeognatha) and (B) close-up of jumping bristletail head (note the eyes are contiguous). (C) A silverfish (order Zygentoma). (D) Close-up of silverfish head. Note that eyes are not contiguous, but set wide apart, and that the bodies of both of these groups are covered with scales.

Order Zygentoma Approximately 450 described species (Figure 22.2C,D). Small, wingless, resembling Archaeognatha but with flattened body; with or without ocelli; compound eyes reduced, not contiguous; body usually covered with scales; mandibles biting-chewing; antennae multiarticulate, but only basal article with musculature; 3- to 5-articulate tarsi; 11-segmented abdomen, with lateral leglets (often called styli) on segments 2–9, 7–9, or 8–9; 3 caudal cerci; female gonopores on eighth abdominal segment, male gonopores on tenth; without copulatory organs; with tracheae; simple development. Silverfish occur in leaf litter or under bark or stones, or in buildings, where they may feed on wallpaper paste, bookbindings, and the starch sizing of some fabrics.

Subclass Pterygota

The winged insects, with a pair of wings on the second and third thoracic segments, the forewings (front wings) and hindwings; wings may be secondarily lost in one or both sexes, or modified for functions other than flight; adults without abdominal leglets except on genital segments; female gonopores on eighth abdominal segment, male on tenth; female often with ovipositor; molting ceases at maturity.

Palaeoptera

Wings cannot be folded, and when the individual is at rest, wings are held either straight out to the side or vertically above the abdomen (with dorsal surfaces pressed together); wings always membranous, with many longitudinal and cross veins; wings tend to be fluted, or accordion-like; antennae highly reduced or vestigial in adults; hemimetabolous development, but with aquatic young/immatures (naiads) that differ markedly from adults; larvae aquatic. Two extant orders; many extinct groups.

Order Ephemeroptera Approximately 2,500 described species (Figure 22.3A). Adults with vestigial mouthparts, minute antennae, and soft bodies; wings held vertically over body when at rest; forewings present; hindwings absent or present but much smaller than forewings; long, articulated cerci, usually with medial

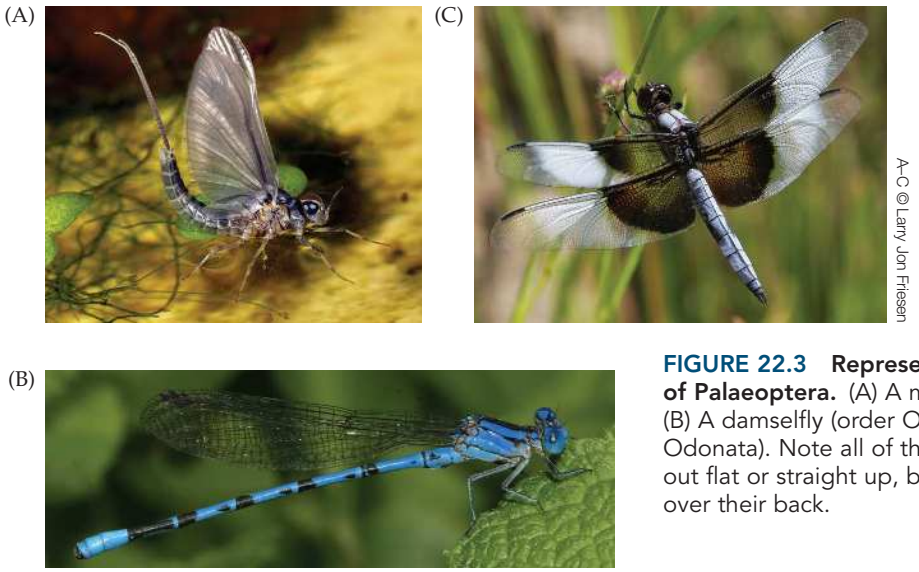

FIGURE 22.3 Representatives of the two orders of Palaeoptera. (A) A mayfly (order Ephemeroptera). (B) A damselfly (order Odonata). (C) A dragonfly (order Odonata). Note all of these insects hold their wings either out flat or straight up, but they cannot fold their wings over their back.

caudal filament; male with first pair of legs elongated for clasping female in flight; second and third legs of male, and all legs of female, may be vestigial or absent (Polymitarcyidae); 10-segmented abdomen; immature aquatic naiads with paired articulated lateral gills, caudal filaments, and well-developed mouthparts; adults preceded by winged subimago stage. The mayfly subimago (subadult) is the only winged insect known to undergo an additional molt. It is the one exception to the rule that an insect with wings is a mature adult insect and will never undergo another molt.

Mayflies are primitive winged insects in which the aquatic naiad stage dominates the life cycle. Larvae hatch in fresh water and become long-lived nymphs, passing through many instars. Mayfly nymphs are important food for many stream and lake fishes. Adults eclose in synchrony and live only a few hours or days (hence the name "ephemeral winged"), do not feed, and copulate in the air, sometimes in large nuptial swarms.

Order Odonata Approximately 6,000 described species (Figure 22.3B,C). Adults with small filiform antennae, large compound eyes, and chewing mouthparts with massive mandibles; larval labium modified into prehensile organ; adult with 2 pairs of large wings, held outstretched (dragonflies) or straight up over body (damselflies) when at rest; 10-segmented abdomen slender and elongate; male with accessory genitalia on second and third abdominal sternites; eggs and larvae aquatic, with caudal or rectal gills.

Dragonflies and damselflies are spectacular insects with broad public appeal, not only for their beauty but because they are fast, strong flyers and consume large numbers of insect pests, including mosquitoes. Naiads and adults are both highly active predators, with larvae consuming various invertebrates or small vertebrates, and adults capturing other flying insects. Many species are 7–8 cm long, while some extinct forms had a wingspan of over 70 cm.

Infraclass Neoptera

The modern, wing-folding insects. Modifications of the sclerites and an associated muscle at the base of the wings allow neopterans to rotate their wing joint and fold back their wings when they are not flying. This is one of the most important evolutionary innovations in hexapods. Wing folding allows insects to protect their fragile wings, especially from abrasion, thereby allowing them to live in tight spaces such as crevices under bark, under rocks, and in burrows, nests, and tunnels.

Superorder Polyneoptera

Polyneopterans are a morphologically diverse group of insects with biting-chewing mouthparts and hemimetabolous development (although Plecoptera have aquatic young called naiads). The phylogenetic relationships among the orders within Polyneoptera and the monophyly of the group itself have long been controversial. However, recent phylogenomic work based upon 1,478 single-copy nuclear genes recovered strong support that the 10 polyneopteran orders form a monophyletic group (Misof et al. 2014).

Order Plecoptera Approximately 1,700 described species (Figure 22.4A). Adults with reduced mouthparts, elongate antennae, (usually) long articulated cerci, soft bodies, and a 10-segmented abdomen; without ovipositor; wings membranous, pleated, folded over and around abdomen when at rest; wings with primitive venation; nymphs aquatic (naiads), with gills.

Stonefly naiads live in well-oxygenated lakes and streams where they are either herbivores, feeding on submerged leaves and benthic algae, or predators of other aquatic arthropods. They are an important food resource for fish. Plecopteran nymphs are intolerant of water pollution, and their presence is often used as a bioindicator of high water quality. Adults of most species are short-lived and die soon after mating.

Order Blattodea Approximately 7,000 described species (Figure 22.4B,C). Two major body forms: cockroaches and termites, the latter previously classified as Isoptera. Cockroaches have a dorsoventrally flattened body; large pronotum, with expanded margins extending over the head; forewings (when present) leathery; hindwings expansive and fanlike; ovipositor reduced; cerci multiarticulate; legs adapted for running; eggs laid in cases (ootheca). Termites are small, soft-bodied, eusocial species characterized by wings that are equal in size, elongate, membranous, and dehiscent (shed by breaking at basal line of weakness); antennae short, filamentous, with 11–33 articles; cerci small to minute; ovipositor reduced or absent; many with rudimentary or no external genitalia; marked polymorphism.

Of the 4,000 described species of cockroaches, fewer than 40 are domestic (household inhabitants). Some species are omnivores, while others are restricted in diet. Most species are tropical, but some live in temperate habitats, caves, deserts, and ant and bird nests. Some live in and feed on wood and have intestinal flora that aid in cellulose digestion (*Cryptocercus*). These wood-feeding cockroaches share a most recent common ancestor with the termites (infraorder Isoptera), a strictly social group of insects, usually with three distinct types of individuals, or castes, in a species: workers, soldiers, and alates (reproductive individuals). Workers are generally sterile, blind individuals with normal mandibles; they are responsible for foraging, nest construction, and caring for members of the other castes. Soldiers are blind, usually sterile, wingless forms with powerful enlarged mandibles used to defend the colony. Alates have wings and

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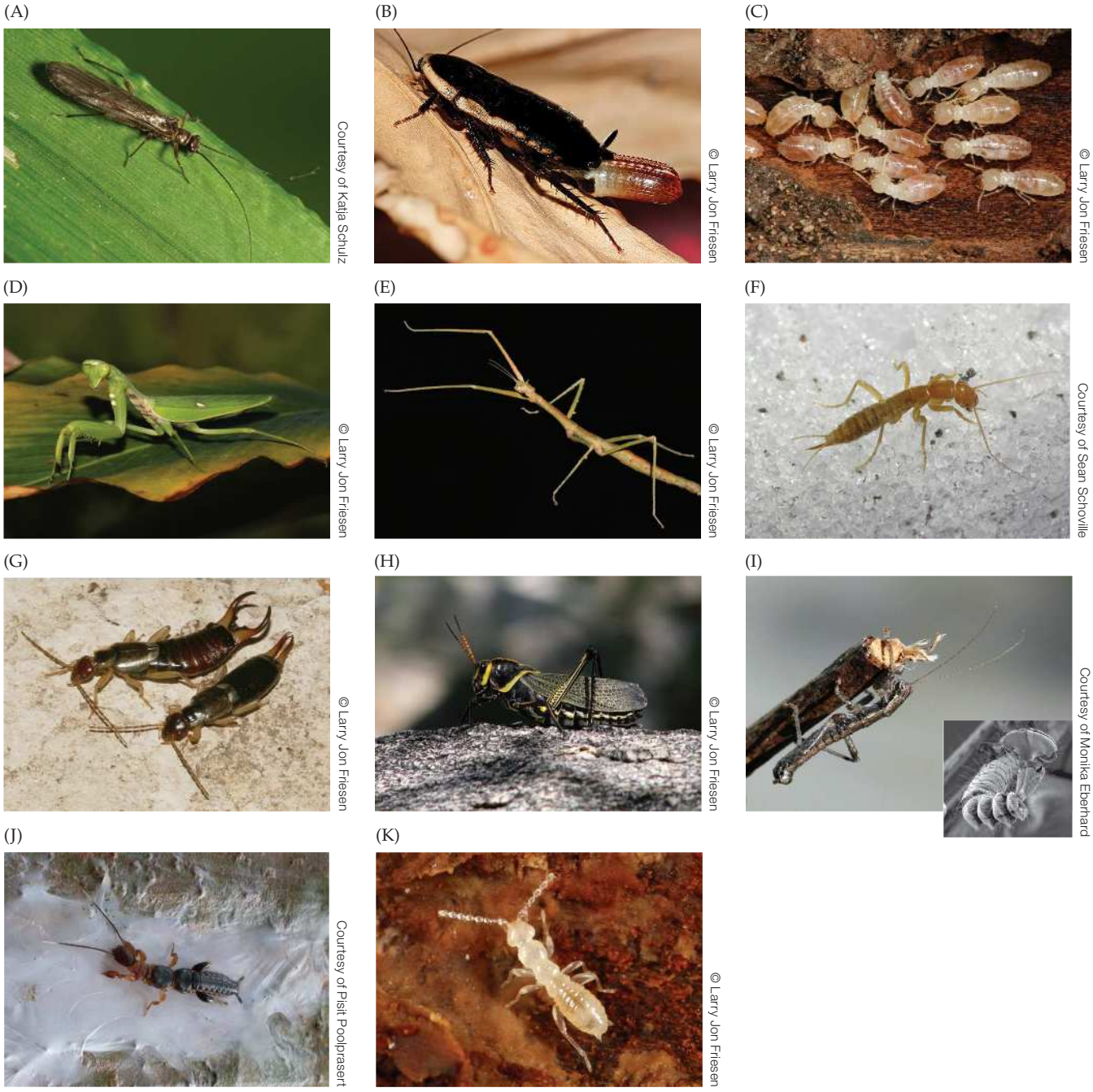

FIGURE 22.4 Representatives of the ten orders of Polyneoptera. (A) A stonefly (order Plecoptera). (B) A cockroach (order Blattodea) laying an egg case. (C) Termites (order Blattodea, infraorder Isoptera). (D) A mantid (order Mantodea). (E) A stick insect (order Phasmida). (F) A rock crawler (order Grylloblattodea). (G) Earwigs (order Dermaptera). (H) A horse lubber grasshopper (order Orthoptera). (I) A heel-walker (order Mantophasmatodea), inset SEM of the tarsus of a heel-walker showing enlarged arolium. (J) A webspinner (order Embioptera). (K) A zorapteran (order Zoraptera).

fully formed compound eyes. They are produced in large numbers at certain times of the year, whereupon they emerge from the colony in swarms. Mating occurs at this time, and individual pairs start new colonies. Wings are shed after copulation. Colonies form nests (termitaria) in wood that is in or on the ground. Workers harbor a variety of symbiotic cellulose-digesting flagellate protists in special chambers in the hindgut. Some families contain symbiotic bacteria that serve the same purpose. Termites often occur in enormous numbers; one spectacular estimate suggests that there are about three-quarters of a ton of termites for every person on Earth!

There is strong morphological and molecular evidence that order Blattodea is the sister group of the order Mantodea. Together these two groups are referred to as the Dictyoptera.

Order Mantodea Approximately 2,400 described species (Figure 22.4D). First pair of legs large and raptorial; prothorax elongate; head highly mobile due to cervical sclerites that lend structural and musculature support, with very large compound eyes, not covered by the pronotum; forewings thickened, hindwings membranous; 11-segmented abdomen, 10 visible segments and the fragmented epiproct (which is made up of a median and 2 lateral components); reduced ovipositor made up of 3 valvular structures; male genitalia made up of 3 phallomeric lobes; 1 pair of multiarticulate cerci; styli sometimes present in males.

Mantises are obligate predators, mostly on insects and spiders. While many species are highly cryptic in both color and structural morphology, some species feature brightly colored patches on the anteroventral surface of their forecoxae to use in threat displays or courtship displays. They have very good eyesight, which they use to locate and track prey before striking with their raptorial forelegs, using either an ambush or cursorial hunting strategy. Females lay many eggs together in an ootheca, a protective matrix of hardened foam, which is characteristic of this order. Mantises are distributed around the world, with their greatest diversity in the Indo-Malaysian, tropical African, and Neotropical regions.

Order Phasmida Approximately 3,000 described species (Figure 22.4E). Body cylindrical or markedly flattened dorsoventrally, usually elongate; biting-chewing mouthparts; prothorax short, with specialized glands for the excretion of noxious chemicals when disturbed; meso- and metathorax greatly elongate; forewings absent, or forming small to moderately elongate, leathery tegmina; hindwings absent, reduced to leathery tegmina, or fanlike; tarsomeres with ventral adhesive pads (euplantulae); short, unsegmented cerci; male with vomer—a specialized sclerite on venter of abdominal segment 10; ovipositor of female weak.

Stick and leaf insects ("walking sticks") and other phasmids are large, tropical, predominantly nocturnal herbivores and are some of the most spectacular and oddest of all the insects. Although resembling orthopterans in basic form, they are clearly a distinct radiation. Their ability to mimic plant parts is legendary, and many have evolved as perfect mimics of twigs, leaves, bark, broken branches, moss, or lichens. Stick and leaf insects are the only hexapods that can regenerate lost limbs while still immature (e.g., due to predation), as their crustacean ancestors could; regeneration occurs during molts, with the new legs markedly smaller than original limbs but increasing in relative size with each successive molt (as in Crustacea). Phasmids are the only insect order with species-specific egg morphology across the entire order. The eggs of some species even mimic angiosperm seeds and are spread via ant-mediated dispersal. The order includes the longest insects still extant, including the world's longest at just over 56 cm, though some are less than 4 cm. Sexual dimorphism is so striking that males and females have often mistakenly been given different species names. Phasmids are facultatively parthenogenetic; in the absence of males, females can produce viable eggs that are genetic clones of their mother, and this is why some species now thrive in the pet industry.

Order Grylloblattodea Approximately 33 species (Figure 22.4F). Slender, elongate, cylindrical, wingless insects, usually 15–30 mm long. Body usually pale or golden and finely pubescent; compound eyes small or absent; no ocelli; mouthparts mandibulate; antennae long and filiform, of 23–45 antennomeres, cerci long, 8-segmented; terminal sword-shaped ovipositor of similar length as cerci.

Rock crawlers were not discovered until 1914, and today 33 species are known, roughly half of which are from North America. They inhabit cold, rocky habitats, including snow fields below glaciers and ice caves. Most species cannot tolerate warm temperatures but thrive at below freezing temperatures. Due to the cold temperature at which they live, growth and development are very slow. Rock crawlers may require up to 7 years to complete a single generation. They are nocturnal scavengers on dead insects and other organic matter.

Order Dermaptera Approximately 1,800 described species (Figure 22.4G). Cerci usually form heavily sclerotized posterior forceps; forewings (when present) form short, leathery tegmina, without veins and serving as covers for the semicircular, membranous hindwings (when present); ovipositor reduced or absent.

Earwigs are common in urban environments. Most appear to be nocturnal scavenging omnivores. The forceps are used in predation, for defense, to hold a mate during courtship, for grooming the body, and for folding the hindwings under leathery forewings. Some species eject a foul-smelling liquid from abdominal glands when disturbed. Most species are tropical, although many also inhabit temperate regions.

Order Orthoptera Approximately 23,000 described species (Figure 22.4H). Pronotum unusually large, extending posteriorly over mesonotum; forewings with thickened and leathery region (tegmina), occasionally modified for stridulation or camouflage; hindwings membranous, fanlike; hindlegs often large, adapted for jumping; auditory tympana present on forelegs and abdomen; tarsomeres with ventral adhesive pads (euplantulae); ovipositor large; male genitalia complex; cerci distinct, short, and jointed.

Grasshoppers, crickets, and their kin are common and abundant insects at all but the coldest latitudes. This order includes some of the largest living insects.

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Most are herbivores, but many are omnivorous, and some are predatory. Stridulation, which is common among males, is usually accomplished by rubbing the specially modified forewings (tegmina) together or by rubbing a ridge on the inside of the hind femur against a special vein of the tegmen. No orthopterans stridulate by rubbing the hindlegs together, as is often thought. Common families include Acrididae (short-horned grasshoppers), Gryllotalpidae (mole crickets), Tetrigidae (pygmy grasshoppers), Gryllidae (crickets), Tettigoniidae (long-horned grasshoppers, katydids).

Order Mantophasmatodea Approximately 21 species (Figure 22.4I). Head hypognathous, with generalized mouthparts; antennae long, filiform; ocelli absent; wings entirely lacking; coxae elongate; tarsi with 5 tarsomeres, pretarsus of all legs with an unusually large arolium; cerci short, with 1 segment.

The Mantophasmatodea is the most recently described order of insects (2002) and the only new insect order described since 1914. The order includes several living species (from Namibia, South Africa, Tanzania, and Malawi) and six fossil species (five from Baltic amber and one fossil from China). They resemble a mix between praying mantises and phasmids, but molecular evidence indicates that they are most closely related to the Grylloblattodea.

Mantophasmatodeans have several distinct characteristics, including a hypognathous head, and most strikingly, when walking, all species keep the fifth tarsomere and pretarsus (a greatly enlarged arolium plus two tarsal claws) of each leg turned upwards and off the substrate, giving them the appearance of "walking on their heels." Both sexes are wingless. They are highly flexible along their longitudinal body axis, enabling them to clean their external genitalia with their mouthparts. During the day they hide in bushes, rock crevices, or clumps of grass and prey on spiders and insects at night. Males and females produce percussive signals by tapping their abdomens on the substrate to locate mates.

Order Embioptera (Embiidina) Approximately 430 described species (Figure 22.4J). Males somewhat flattened; females and young cylindrical. Most about 10 mm long; however, Southeast Asian species in the genus *Ptilocerembia* are approximately 20 mm long. Antennae filiform; ocelli lacking; chewing mouthparts; head prognathous; legs short and stout; 3-articulate tarsi; hind femora greatly enlarged. The basal article of the front tarsus is enlarged and contains glands that produce silk, which is spun from a dense field of hollow hairlike structures on the ventral surface. Males of most species are winged, but some are wingless; females and nymphs are always wingless. Abdomen has 10 segments, with rudiments of the eleventh segment, and a pair of short cerci.

Webspinners are small, slender, chiefly tropical insects. They live gregariously in silken galleries that they construct in leaf litter, under or on stones, in soil cracks, in bark crevices, and in epiphytic plants. Wings are made rigid for flight and flexible in galleries by regulation of the hemocoelic fluid pressure in the radial blood sinuses in both pairs of wings. They feed mostly on dead plant material and also graze on the outer bark of trees and on mosses and lichens.

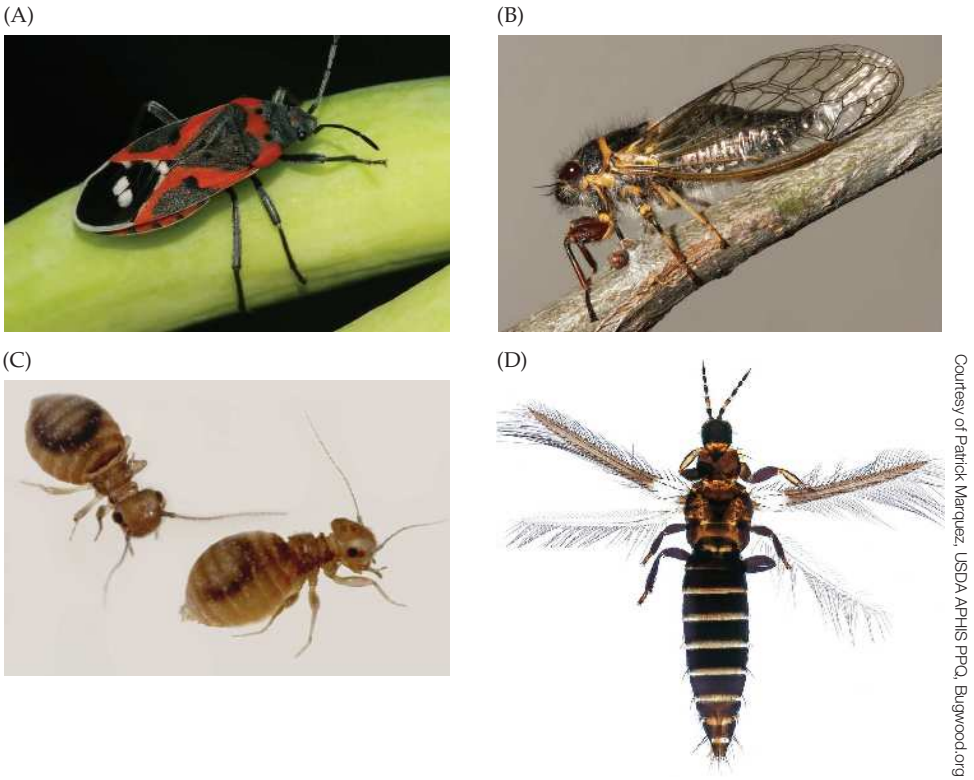
Order Zoraptera Approximately 40 species (Figure 22.4K). Minute (to 3 mm); similar to termites; colonial; wingless or with wings; wings eventually shed; 9-articulate antennae moniliform; 10-segmented abdomen short, oval; chewing mouthparts; simple hemimetabolous development. These uncommon insects are usually found in gregarious colonies in dead wood, but they do not have a division of labor or polymorphism (as in termites and ants). They feed chiefly on mites and other small arthropods. All extant species are classified in the single genus *Zorotypus*. The sister-group relationship of this order remains controversial and elusive.

Superorder Acercaria

The superorder Acercaria is sometimes referred to as the Paraneoptera or the "hemipteroids." These insects are characterized by (usually) short antennae, enlarged cibarial (feeding) muscles, visible externally as an enlarged portion of the head; lacinia slender and elongate; sucking mouthparts, tarsi with 3 or fewer tarsomeres, absence of abdominal cerci, lack of true male gonopods, wings (when present) with reduced venation, and hemimetabolous development (although life cycles in several groups includes 1 or 2 inactive pupalike stages).

Order Thysanoptera Approximately 5,000 described species (Figure 22.5D). Slender, minute (0.5–1.5 mm) insects with long, narrow wings (when present) bearing long marginal setal fringes; mouthparts form a conical, asymmetrical sucking beak; left mandible a stylet, right mandible vestigial; with compound eyes; antennae with 4–10 flagellomeres; 10-segmented abdomen; without cerci; tarsi with 1–2 segments, with a pretarsal eversible adhesive sac, or arolium. Thrips are mostly herbivores or predators, and many pollinate flowers. They are known to transmit plant viruses and fungal spores. "Thrips" is both singular and plural.

Order Hemiptera Approximately 85,000 species (Figure 22.5A,B). Piercing-sucking mouthparts form an articulated beak, styletlike mandibles and first maxillae lying in dorsally grooved labium; forewings either completely membranous or hardened basally and membranous only distally; hindwings membranous; pronotum large.



A–C © Larry Jon Friesen

Courtesy of Patrick Marquez, USDA APHIS PPQ, Bugwood.org

FIGURE 22.5 Representatives of the three orders of Acercaria. (A) A true bug (order Hemiptera). (B) A cicada (order Hemiptera). (C) Two bark lice (order Psocodea). (D) A thrips (order Thysanoptera). Note that "thrips" is both singular and plural.

Hemipterans occur worldwide and in virtually all habitats. Hemipterans are liquid feeders. Most feed on the xylem or phloem of plants, although many feed on the hemolymph of arthropods or blood of vertebrates, and some are specialized ectoparasites. They are of considerable economic importance because many are serious crop pests. Members of one subfamily of Reduviidae (Triatominae, the assassin or kissing bugs) transmit Chagas' disease. Others have more positive economic importance to humans, such as the cochineal bugs (Dactylopiidae), from which a safe red dye (cochineal) is extracted for use in the food industry. Shellac is made from lac, a chemical produced by members of the family Kerriidae (lac insects). Two of the most famous hemipterans are the periodical 13-year and 17-year cicadas of eastern North America (genus *Magicicada*), which have a very long life cycle and synchronized development and can reach plaguelike levels of abundance (to 3.7 million individuals per hectare). Common predacious hemipteran families include Nepidae (water scorpions), Belostomatidae (giant water bugs or "toe biters"), Corixidae (water boatmen), Notonectidae (backswimmers), Gerridae (water striders), Saldidae (shore bugs), Cimicidae (bedbugs), and Reduviidae (assassin bugs).

Many others are plant feeders (hence the common name "plant bugs"). Heavy infestations of these insects on plants may cause wilting, stunting, or even death, and some are vectors of important plant diseases. Common herbivorous families include the Cicadidae (cicadas), Cicadellidae (leafhoppers), Fulgoridae (planthoppers), Membracidae (treehoppers), Cercopidae (spittle bugs and froghoppers), Aleyrodidae (whiteflies), and Aphididae (aphids), as well as members of the large superfamily Coccoidea (coccoids, scale insects, mealybugs, and many others).

Order Psocodea Approximately 8,500 described species (Figure 22.5C). Until recently, species in this order were classified in 2 separate orders: the Psocoptera (the book and bark lice) and the Phthiraptera (the true lice). Psocopterans are small (1–10 mm long), with long, filiform, multiarticulate antennae; short prothorax; meso- and metathorax often fused; chewing mouthparts; 9-segmented abdomen; without cerci. Phthirapterans are even smaller (less than 5 mm), wingless, blood-sucking, obligate ectoparasites of birds and mammals; thoracic segments completely fused; cuticle largely membranous and expandable to permit engorgement; compound eyes absent or of 1–2 ommatidia; ocelli absent; piercing-sucking mouthparts retractable into a buccal pouch; antennae short (5 or fewer flagellomeres), exposed or concealed in grooves beneath the head; with 1 pair dorsal thoracic spiracles and 6 or fewer abdominal spiracles; without cerci; females lack ovipositor.

Psocids—the book and bark lice—generally feed on algae and fungi and occur in suitably moist areas (e.g., under bark, in leaf litter, under stones, in human habitations where humid climates prevail). They are often pests that get into various stored food products or consume insect and plant collections; some species live in books and eat the bindings. Commonly called sucking

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lice ("Anoplura") and biting lice ("Mallophaga"), phthirapterans spend their entire life on one host. A number of phthirapteran species are specialized to feed on the feathers and skin of birds (feather-feeding insects of uncertain taxonomic affinity have been described in association with dinosaur feathers from mid-Cretaceous Burmese amber). Eggs (nits) are usually attached to the hair or feathers of the host, although the human body louse (a "sucking louse") may attach eggs to clothing. No biting lice are known to infest humans. Posthatching development comprises three "nymphal" instars. Some species that infest domestic birds and mammals are of economic significance.

Superorder Holometabola

Holometabola is a monophyletic group strongly supported by both morphological and molecular data. One of its key apomorphies is holometabolous development, with distinct egg, larval, pupal, and adult states. During the pupal stage, most tissues undergo a complete reorganization (e.g., larval eyes [stemmata] disintegrate, and adult compound eyes and ocelli form de novo). Another key apomorphy is the presence of internal wing buds (imaginal discs) in the larval stage; these clusters of early embryonic cells arise from localized invaginations of the ectoderm in the early embryo and form adult structures during pupation. Holometabola contains the 4 most diverse orders of insects (Hymenoptera, Coleoptera, Diptera, and Lepidoptera), and thus this type of development is considered by many as a key innovation in insect evolution, perhaps even more important than the origin of flight.

Order Hymenoptera Approximately 115,000 described species (Figure 22.6A). Mouthparts often elongate and modified for ingesting floral nectar, although mandibles usually remain functional; labium often (bees) distally expanded as paired lobelike structures called glossae and paraglossae; 3 ocelli; usually with 2 pairs of membranous wings; hindwings small, coupled to forewings by hooks (hamuli); wing venation highly reduced; antennae well developed, of various forms and with 3–70 flagellomeres, reduced metathorax usually fused to first abdominal segment; males with complex genitalia; females with ovipositor (in most), modified for sawing, piercing, or stinging.

The earliest fossil Hymenoptera date from the Upper Triassic (220–207 Ma). Ants, bees, wasps, sawflies, and their relatives are all active insects with a tendency to form polymorphic social communities. Two suborders are generally recognized. Suborder Symphyta contains the primitive, wasplike, "thick-waisted" hymenopterans (sawflies, horntails, and their kin). They rarely show conspicuous sexual dimorphism and are always fully winged. The first and second abdominal segments are broadly joined. Larvae are mostly caterpillar-like, with a well-developed head capsule, true legs, and often also with abdominal prolegs. The suborder Apocrita contains the "narrow-waisted" hymenopterans (true wasps, bees, and ants), in which the first and second abdominal segments are joined by a distinct and often elongate constriction. Adults tend to be strongly social and display marked polymorphism. Social communities often include distinct castes of queens, haploid males, parthenogenetic females, and individuals with other sex-related specializations, as well as nonreproducing worker and soldier forms. Common families of Hymenoptera include the Apidae (bumblebees and honeybees), Formicidae (ants), Vespidae (yellow jackets, hornets, paper wasps, and potter wasps), Halictidae (sweat bees), Sphecidae (sand wasps, digger wasps, and mud daubers), and three large groups of parasitic wasps (Ichneumonidae, Braconidae, Chalcidoidea). One of the major trends in the evolution of parasitoid wasps is miniaturization, which has produced the smallest known insects, species of *Megaphragma* (family Trichogrammatidae), some of which are smaller than some unicellular organisms with an adult body length of just 170 µm.

Coleopterida

The Coleopterida includes 2 orders: the Coleoptera (beetles) and the Strepsiptera (twisted-wing parasites). This clade includes the most diverse order of insects (Coleoptera) and an order with the most highly modified and morphologically and developmentally aberrant groups of parasites (Strepsiptera). Largely due to their bizarre combination of morphological characters and the high rate of molecular evolution in many strepsipteran genes, the sister-group relationship of the Strepsiptera eluded researchers until very recently. In the past, Strepsiptera were considered at various times to be close relatives of either Hymenoptera, Diptera, or Coleoptera. Recent genome-wide analyses and new morphological evidence strongly suggest that they are in fact the sister group to the Coleoptera.

Order Coleoptera Approximately 387,100 described species (Figure 22.6B). Body usually heavily sclerotized; forewings sclerotized and modified as rigid covers (elytra) over hindwings and body; membranous hindwings fold both transversely and longitudinally and are often reduced or absent; biting-chewing mouthparts; antennae usually with 8–11 flagellomeres; prothorax large and mobile; mesothorax reduced; abdomen typically of 5 (or up to 8) segments; without ovipositor; male genitalia retractable.

Coleoptera is the largest order of insects. Many hypotheses have been proposed to explain the extraordinary diversity of beetles: (1) The oldest fossils date to the early Permian, but they most probably arose in the late Carboniferous (300 Ma). (2) Their

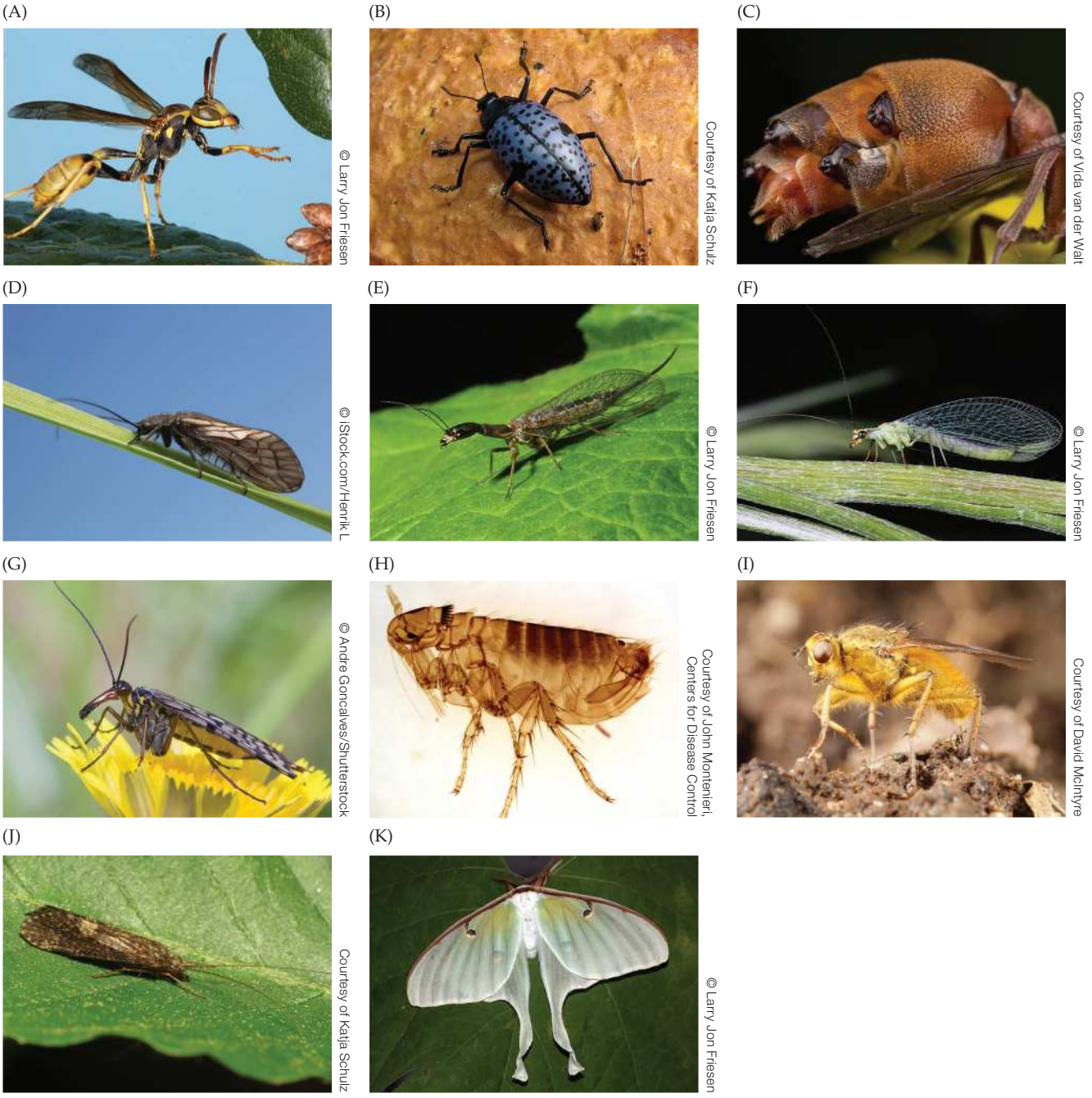

FIGURE 22.6 Representatives of the 11 orders of Holometabola. (A) A paper wasp (order Hymenoptera). (B) A pleasing fungus beetle, *Gibbifer californicus* (order Coleoptera). (C) Female twisted-wing parasites (order Strepsiptera) visible between the abdominal sclerites of a wasp (order Hymenoptera). (D) An alderfly (order Megaloptera). (E) A snakefly (order Raphidioptera). (F) A green lacewing (order Neuroptera). (G) A scorpionfly (order Mecoptera). (H) A adult male *Oropsylla montana* flea (order Siphonaptera). (I) A golden dung fly (*Scathophaga stercoraria)* (order Diptera). (J) A caddisfly (order Trichoptera). (K) A luna moth (order Lepidoptera).

heavily sclerotized bodies, including their protective elytra, and general lack of exposed membranous surfaces facilitated their adaptation to a wide variety of tight narrow spaces and reduced their risk of predation and desiccation. (3) They co-evolved with the great angiosperm radiation in the Cretaceous Period. Today, beetles range from minute (0.30 mm, *Nanosella fungi*) to very large (20 cm, *Titanus giganteus*) and occur in all the world's environments (except the open sea). Some of the world's strongest animals are beetles: rhinoceros beetles can carry up to 100 times their own weight for short distances, and 30 times their weight indefinitely (equivalent to a 150-pound man walking with a Cadillac on his head—without tiring). Humans have had a long fascination with beetles, and beetle worship can be traced back to at

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least 2500 BCE. (The venerated scarab of early Egyptians was actually a dung beetle.)

Some common coleopteran families include Carabidae (ground beetles), Dytiscidae (predaceous diving beetles), Gyrinidae (whirligig beetles), Hydrophilidae (water scavenger beetles), Staphylinidae (rove beetles), Cantharidae (soldier beetles), Lampyridae (fireflies and lightning bugs), Phengodidae (glowworm beetles), Elateridae (click beetles), Buprestidae (metallic wood-boring beetles), Coccinellidae (ladybugs or ladybird beetles), Meloidae (blister beetles), Tenebrionidae (darkling beetles), Scarabaeidae (scarab beetles, dung beetles, June "bugs"), Cerambycidae (long-horned beetles), Chrysomelidae (leaf beetles), Curculionidae (weevils), Brentidae (primitive weevils), and Ptiliidae (feather-winged beetles, the smallest of all free-living insects, some with body lengths of just 300 µm).

Order Strepsiptera Approximately 600 described species (Figure 22.6C). Extreme sexual dimorphism; males free-living and winged; females wingless, usually parasitic. Females of free-living species with distinct head, simple antennae, chewing mouthparts, and compound eyes. Females of parasitic species neotenous, larviform, usually without eyes, antennae, and legs; with indistinct body segmentation. Male antennae often with elongate processes on flagellomeres; forewings reduced to clublike structures resembling halteres of Diptera; hindwings large and membranous, with reduced venation; raspberry-like eyes.

Most of these minute insects are parasitic on other insects. Adult females of parasitic species are larviform and most commonly live between the abdominal sclerites of flying insects that pollinate flowers, such as bees and wasps. The winged male finds the female on the bee or wasp abdomen and mates with her there. The fertilized eggs hatch into first-instar larvae inside their mother's body. These larvae, called triungulins, have well-developed eyes and legs, and they actively crawl out of their mother to invade the soil and vegetation. The triungulins eventually locate a new host insect and enter it, wherein they molt into a legless wormlike larval stage that feeds in the host's body cavity. Pupation also takes place within the host's body, where the females remain for the rest of their lives; the free-living males emerge as fully formed flying adults.

Neuropterida

The three orders of Neuropterida have always been considered close relatives. Some workers subsume the Megaloptera and Raphidioptera within the Neuroptera, but all 3 groups are monophyletic, making such a taxonomic decision arbitrary. These 3 orders have 2 pairs of membranous wings with many cross veins, 5-segmented tarsi, adults with mandibles, and decticous pupae (with articulated mandibles).

Order Megaloptera Approximately 300 described species (Figure 22.6D). Ocelli present or absent; larvae aquatic, with lateral abdominal gills. Megalopterans (alderflies, dobsonflies, fishflies) strongly resemble neuropterans (and are often regarded as a suborder), but their hindwings are broader at the base than the forewings, and the longitudinal veins do not have branches near the wing margin. Larvae of some megalopterans (hellgrammites) are commonly used as fish bait.

Order Raphidioptera Approximately 260 described species (Figure 22.6E). Snakeflies strongly resemble neuropterans (and are often regarded as a suborder) but are unique in having the prothorax elongate (as in the mantises), but the forelegs are similar to the other legs. The head can be raised above the rest of the body, as in a snake preparing to strike. Adults and larvae are predators on small insects.

Order Neuroptera Approximately 6,000 described species (Figure 22.6F). Adults soft-bodied; with 2 pairs of similar, highly veined wings held tentlike over the abdomen when at rest; with biting-chewing mouthparts; 10-segmented abdomen; without cerci; larvae with mandibles and maxillae co-adapted to create a sucking tube; mouth closed off by modified labrum and labium; well-developed legs; larval midgut is closed off posteriorly (larval waste accumulates until the adult emerges); Malpighian tubules secrete silk, via the anus, to construct the pupal cocoon.

The lacewings, ant lions, mantisflies, spongillaflies, and owlflies form a complex group, the adults of which are often important predators of insect pests (e.g., aphids). The larvae of many species have piercing-sucking mouthparts, and those of other species are predaceous and have biting mouthparts. The pupae are often unusual in possessing free appendages and functional mandibles used for defense; they may actively walk about prior to the adult molt, but they do not feed. Common families include Chrysopidae (green lacewings), Myrmeleontidae (ant lions), Ascalaphidae (owlflies), and Mantispidae (mantidflies).

Antliophora

The Antliophora include 3 orders: the Mecoptera, Siphonaptera, and Diptera. There is strong molecular and morphological support for the monophyly of this group. The males of all members of Antliophora have a sperm pump, a structure that aids in sperm transfer during copulation. Many other characters also define this grouping, most of which have to do with relatively subtle aspects of the adult mouthparts.

Order Mecoptera Approximately 600 described species (Figure 22.6G). Two pairs of similar, narrow,

membranous wings, held horizontally from sides of body when at rest; antennae long, slender, and of many flagellomeres (about half the body length); head with ventral rostrum and reduced biting mouthparts; long, slender legs; mesothorax, metathorax, and first abdominal tergum fused; 11-segmented abdomen; female with 2 cerci; male genitalia prominent and complex, at apex of attenuate abdomen and often resembling a scorpion's stinger. The larvae of some species are remarkable in having compound eyes, a condition unknown among larvae of other insects having complete metamorphosis.

Mecopterans are usually found in moist places, often in forests, where most are diurnal flyers. They are best represented in the Holarctic region. Some feed on nectar; others prey on insects or are scavengers. There are several families, including Panorpidae (scorpionflies), Bittacidae (hangingflies), Boreidae (snow scorpionflies), and the enigmatic Nannochoristidae.

Order Siphonaptera Approximately 2,700 described species (Figure 22.6H). Small (less than 3 mm long); wingless; body laterally compressed and heavily sclerotized; short antennae lie in deep grooves on sides of head; piercing-sucking mouthparts; compound eyes often absent; legs modified for clinging and (especially hindlegs) jumping; 11-segmented abdomen; abdominal segment 10 with distinct dorsal pincushion-like sensillum, containing a number of sensory organs; without ovipositor; pupal stage passed in a cocoon.

Adult fleas are ectoparasites on mammals and birds, from which they take blood meals. They occur wherever suitable hosts are found, including the Arctic and Antarctic. Larvae usually feed on organic debris in the nest or dwelling place of the host. Host specificity is often weak, particularly among the parasites of mammals, and fleas regularly commute from one host species to another. Fleas act as intermediate hosts and vectors for organisms such as plague bacteria, dog and cat tapeworms, and various nematodes. Commonly encountered species include *Ctenocephalides felis* (cat flea), *C. canis* (dog flea), *Pulex irritans* (domestic flea), and *Oropsylla montanus* (western squirrel flea).

Siphonaptera has long been considered closely related to Mecoptera, and while the monophyly of Siphonaptera is not questioned, there is controversy about whether or not Siphonaptera arose from *within* Mecoptera, which would render Mecoptera paraphyletic. A recent study based on transcriptomic data concludes this is the case and that Siphonaptera is the sister group of the mecopteran family Nannochoristidae (Tihelka et al. 2020), while similar studies find less clear evidence for this relationship, depending upon whether the data are analyzed at the nucleotide or amino acid levels (Meusemann et al. 2020). Given the lack of conclusive evidence, we keep Siphonaptera as an order in this text, but note the potential for it to be subsumed under Mecoptera sometime in the future.

Order Diptera Approximately 159,295 described species (Figure 22.6I). Adults with one pair of membranous mesothoracic forewings and a metathoracic pair of clublike halteres (organs of balance); head large and mobile; compound eyes, large sometimes stalked; antennae primitively filiform, with 7–16 flagellomeres and often secondarily annulated (reduced to only a few articles in some groups); mouthparts adapted for sponging, sucking, or lapping; mandibles of blood-sucking females developed as piercing stylets; hypopharynx, laciniae, galeae, and mandibles variously modified as stylets in parasitic and predatory groups; labium forms a proboscis ("tongue"), consisting of distinct basal and distal portions, the latter in higher families forming a spongelike pad (labellum) with absorptive canals; mesothorax greatly enlarged; abdomen primitively 11-segmented, but reduced or fused in many higher forms; male genitalia complex; females without true ovipositor, but many with secondary ovipositor composed of telescoping posterior abdominal segments; larvae lack true legs, although ambulatory structures (prolegs and "pseudopods") occur in many.

The true flies (which include mosquitoes and gnats) are a large and ecologically diverse group, notable for their excellent vision and aeronautic capabilities. The mouthparts and digestive system are modified for a fluid diet, and several groups feed on blood or plant juice. Dipterans are vastly important carriers of human diseases, such as sleeping sickness, yellow fever, African river blindness, and various enteric diseases. It has been said that mosquitoes (and the diseases they carry) prevented Genghis Khan from conquering Russia, killed Alexander the Great, and played pivotal roles in both world wars. Myiasis—the infestation of living tissue by dipteran larvae—is often a problem for livestock and occasionally for humans. Many dipterans are also beneficial to humans as parasites or predators of other insects and as pollinators of flowering plants. Dipterans occur worldwide and in virtually every major environment (except the open sea). Some breed in extreme environments, such as hot springs, saline desert lakes, oil seeps, tundra pools, and even shallow benthic marine habitats.

Some common dipteran families include Asilidae (robber flies), Bombyliidae (bee flies), Calliphoridae (blowflies, bluebottles, greenbottles, screwworm flies, etc.), Chironomidae (midges), Culicidae (mosquitoes: *Culex*, *Anopheles*, etc.), Drosophilidae (pomace or vinegar flies; often also called "fruit flies"), Ephydridae (shore flies and brine flies), Glossinidae (tsetse flies), Muscidae (houseflies, stable flies, etc.), Sarcophagidae (flesh flies), Simuliidae (blackflies and buffalo gnats), Syrphidae (hover flies and flower flies), Tabanidae (horseflies,

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deerflies, and clegs), Tachinidae (tachinid flies), Tephritidae (fruit flies), and Tipulidae (crane flies).

Amphiesmenoptera

The Amphiesmenoptera contains the orders Trichoptera and Lepidoptera. Some characteristics that unite these 2 groups include the presence of hairy wings (with the hairs modified into scales in Lepidoptera), the females as the heterogametic sex, and the larval labium and hypopharynx being fused into a composite lobe with the opening of an associated silk gland at its apex.

Order Trichoptera Approximately 12,000 described species (Figure 22.6J). Adults resemble small moths, but with body and wings covered with short hairs; 2 pairs of wings, tented in oblique vertical plane (rooflike) over abdomen when at rest; compound eyes present; mandibles minute or absent; antennae usually as long or longer than body, setaceous; legs long and slender; larvae and pupae mainly in fresh water, adults terrestrial; larvae with abdominal prolegs on terminal segment.

The freshwater larvae of caddisflies construct fixed or portable "houses" (cases) made of sand grains, wood fragments, or other material bound together by silk emitted through the labium. Larvae are primarily herbivorous scavengers; some use silk to produce food-filtering devices. Most larvae inhabit benthic habitats in temperate streams, ponds, and lakes. Adults are strictly terrestrial and have liquid diets.

Order Lepidoptera Approximately 157,402 described species (Figure 22.6K). Minute to large; sucking mouthparts; mandibles usually vestigial; maxillae coupled, forming a tubular sucking proboscis, coiled between labial palps when not in use; head, body, wings, and legs usually densely scaled; compound eyes well developed; usually with 2 pairs of large and colorfully scaled wings, coupled to one another by various mechanisms; protibia with epiphysis used for cleaning antennae; male genitalia complex; females with ovipositor.

Butterflies and moths are among the best known and most colorful of all the insects. The adults are primarily nectar feeders, and many are important pollinators, some of the best known being the large hawk, or sphinx, moths (Sphingidae). A few tropical species are known to feed on animal blood, and some even drink the tears of mammals. The larvae (caterpillars) feed on green plants, but a few are carnivorous. Caterpillars have three pairs of thoracic legs and a pair of soft prolegs on each of abdominal segments 3–6; the anal segment bears a pair of prolegs or claspers. Butterflies can be distinguished from moths by two features: their antennae are always long and slender, ending in a knob (moth antennae are never knobbed), and their wings are typically held together above the body at rest (moths never hold their wings in this position). Over 80% of the described Lepidoptera are moths.

Other common families include Psychidae (bag worms), Cossidae (carpenter worms), Pyralidae (snout moths), Saturniidae (silk moths), Hesperiidae (skippers), Geometridae (inch worms), Arctiidae (tiger moths), Noctuidae (owlet moths), Papilionidae (swallowtails), Nymphalidae (brush-footed butterflies), Pieridae (whites and sulphurs), Lycaenidae (gossamer-winged butterflies), and Riodinidae (metalmarks).[2]

The Hexapod Body Plan

General Morphology

In Chapter 20 we briefly discussed the various advantages and constraints imposed by the phenomenon of arthropodization, including those associated with the establishment of a terrestrial lifestyle. Departure from the ancestral aquatic environment necessitated the evolution of stronger and more efficient support and locomotory appendages, special adaptations to withstand osmotic and ionic stress, and aerial gas exchange structures. The basic arthropod body plan included many preadaptations to life in a "dry" world. As we have seen, the arthropod exoskeleton inherently provides physical support and protection from predators, and by incorporating waxes into the epicuticle, the insects, like the arachnids, acquired an effective barrier to water loss. Similarly, within the Hexapoda, the highly adaptable, serially arranged arthropod limbs evolved into a variety of specialized locomotory and food-capturing appendages. Reproductive behavior became increasingly complex, and in many cases highly evolved social systems developed. Within the class Insecta, many taxa underwent intimate coevolution with land plants, particularly angiosperms. The adaptive potential of insects is evident in the many species that have evolved striking camouflage, warning coloration, and chemical defense (Figure 22.7).

Non-insect hexapods (proturans, collembolans, and diplurans—the entognathous hexapods) differ from insects in several important ways. The mouthparts are not fully exposed (i.e., they are **entognathous**), the

[2]One of the best-known butterfly taxonomists was the great Russian novelist Vladimir Nabokov (*Lolita*, *Pale Fire*, *The Gift*), who left Saint Petersburg in 1917 to travel around Europe and eventually settled in the United States (first working at the American Museum of Natural History in New York, then at Cornell and Harvard Universities). Nabokov was a specialist on the blue butterflies (Polyommatini) of the New World and a pioneer anatomist, coining such alliterative anatomical terms as "alula" and "bullula." Butterflies, real and imaginary, flit through 60 years of Nabokov's fiction, and many lepidopterists have named butterflies after characters in his life and writings (e.g., species epithets include *lolita*, *humbert*, *ada*, *zembla*, and *vokoban*—a reversal of Nabokov). Nabokov's descriptions of Lolita were patterned after his species descriptions of butterflies (e.g., "her fine downy limbs").

FIGURE 22.7 Defense, warning coloration, and camouflage in insects. (A) A leaf-mimicking katydid (Orthoptera: Tettigoniidae) from Ecuador is perfectly camouflaged. (B) The bright coloration of the silkmoth caterpillar (Lepidoptera: Saturniidae: *Hyalophora euryalus*) warns potential predators of the defensive hairs on its back. (C) A bombardier beetle (Coleoptera: Carabidae: *Brachinus*) sprays noxious benzoquinones in defense while being "attacked" by forceps. (D) Close-up of an "eye spot" on a luna moth (see Figure 22.6K) (Lepidoptera: Saturniidae). Eyespots attract predators away from the moth's head and body and encourage focus on the moth's wings. Since butterflies and moths can fly even with slight wing damage, eyespots are a commonly used defense mechanism. (E) A spittlebug (Hemiptera: Cercopoidea) produces a cover of frothed-up plant sap resembling saliva, which hides the nymph from the view of predators and parasites.

mandibles have a single point of articulation, development is always simple (ametabolous), the abdomen may have a reduced number of segments, and they never developed flight.

Insects are primitively composed of 20 somites (as in the eumalacostracan Crustacea; Chapter 21), although these are not always obvious. The consolidation and specialization of these body segments (i.e., tagmosis) has played a key role in hexapod evolution and has opened the way for further adaptive radiation. The body is always organized into a head, thorax, and abdomen (Figures 22.8 and 22.9), comprising 6, 3, and 11 (or fewer) segments, respectively. In contrast to marine arthropods, a true carapace never develops in hexapods. In the head, all body sclerites are more or less fused as a solid head capsule. In the thorax and abdomen, the adult sclerites usually develop embryologically such that they overlap the primary segment articulations, forming secondary segments, and these are the "segments" we typically see when we examine an insect externally (e.g., the tergum and sternum of each adult abdominal secondary segment actually overlap its adjacent anterior primary segment) (Figure 22.10). The primitive (primary) body segmentation can be seen in unsclerotized larvae by the insertions of the segmental muscles and transverse grooves on the body surface.

Most insects are small, between 0.5 and 3.0 cm in length. The smallest are the thrips, feather-winged beetles, and certain parasitic wasps, which are all nearly microscopic. The largest are certain beetles, orthopterans, and stick insects, the last attaining lengths greater than 56 cm. However, certain Paleozoic species grew to twice that size. To familiarize you with the hexapod body plan and its terminology, we briefly discuss each of the main body regions (tagmata) here.

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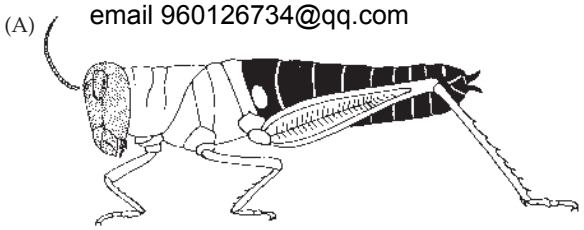
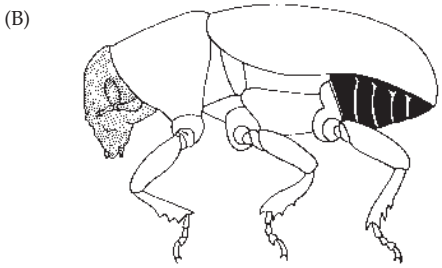




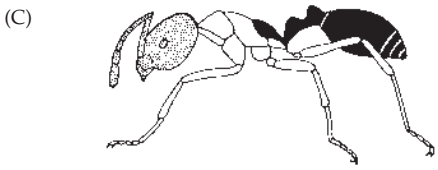
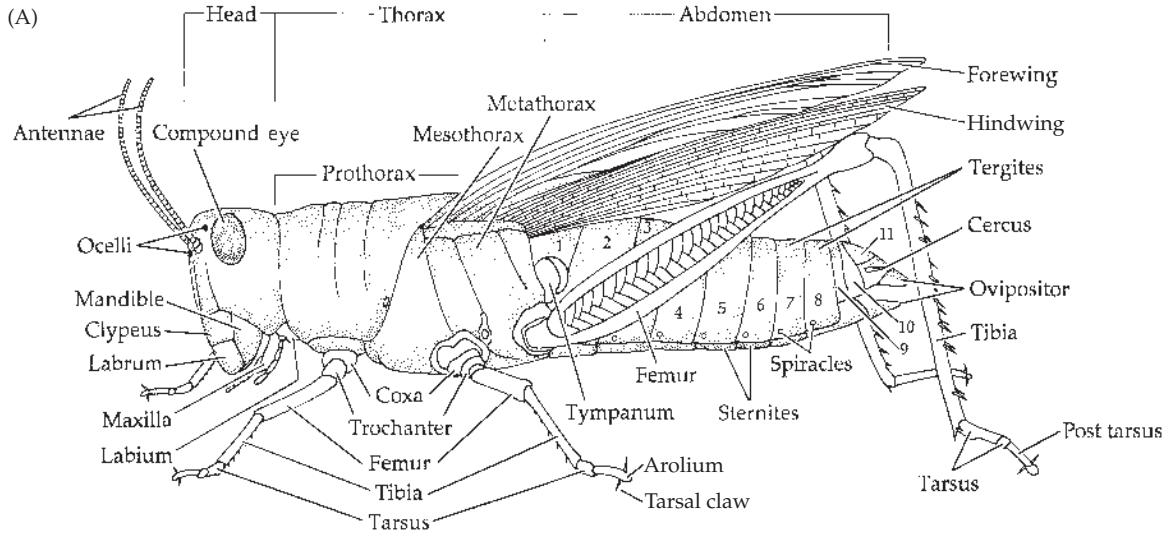
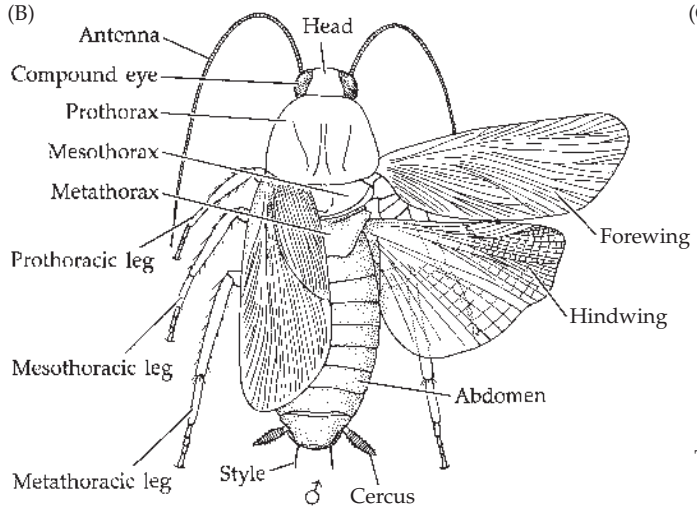


FIGURE 22.8 The principal body regions of hexapods, illustrated by three kinds of insects. (A) A grasshopper (wings removed). (B) A beetle. (C) An ant. In each case, the stippled region is the head; the white region is the thorax; the black region is the abdomen.

The hexapod head The hexapod head comprises six segments, bearing (from anterior to posterior) the eyes, antennae, clypeolabrum, and three pairs of mouth appendages (mandibles, maxillae, labium) (Figure 22.11). Compound eyes, as well as three **simple eyes** (**ocelli**), are typically present in adult hexapods. The median (anterior) ocellus is thought to have arisen through the fusion of two separate ocelli. The internal manifestation of the fused exoskeleton of the head forms a variety of apodemes, braces, and struts collectively called the **tentorium**. Externally, the head may also bear lines that may demarcate its original segmental divisions, and others that represent the dorsal (and





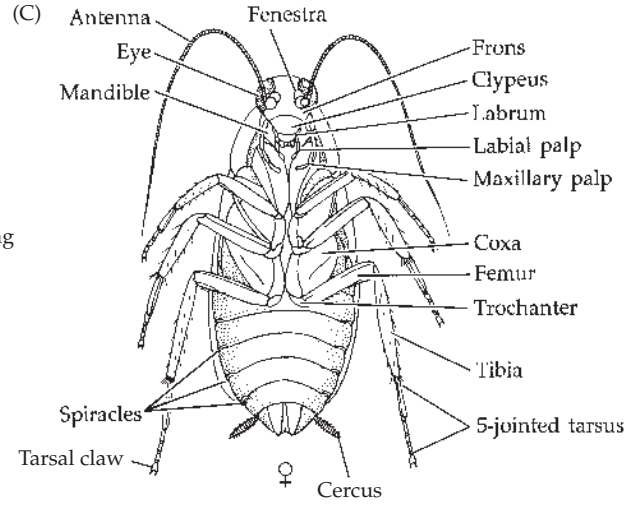


FIGURE 22.9 General body anatomy of insects. (A) A grasshopper (order Orthoptera). (B,C) Dorsal and ventral views of a cockroach (order Blattodea).

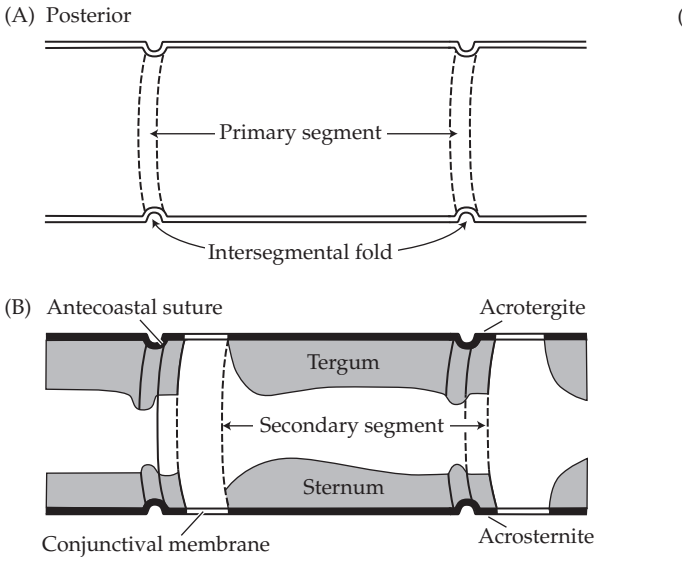


FIGURE 22.10 The ontogenesis of insect body segments. (A) Primary segmentation. (B) Simple secondary segmentation. (C) More advanced secondary segmentation.

ventral) ecdysial lines, where the head capsule splits in immature insects and which persist as unpigmented lines in some adults. Still other lines represent inflections of the surface associated with internal apodemes.

The antennae (Figure 22.12) are composed of three regions: the scape, pedicel, and multijointed sensory flagellum. The **scape** and **pedicel** constitute the **protopod**; the **flagellum** represents the telopod. Among the entognathous insects, muscles intrinsic to the scape, pedicel, and flagellum are retained. But in the class Insecta, the intrinsic muscles of the antennae have been lost except for those in the scape. In addition, in many insects the joints, or **flagellomeres**, of the flagellum may have been secondarily subdivided (or annulated), producing additional unmuscled joints and increasing the length and flexibility of the antenna.

The mouth is bordered anteriorly by the clypeolabrum, posteriorly by the labium, and on the sides by the mandibles and maxillae. In the entognathans, the mouthparts are sunk within the head capsule and largely hidden from view. In contrast, the mouthparts of insects are exposed (**ectognathous**) and ventrally

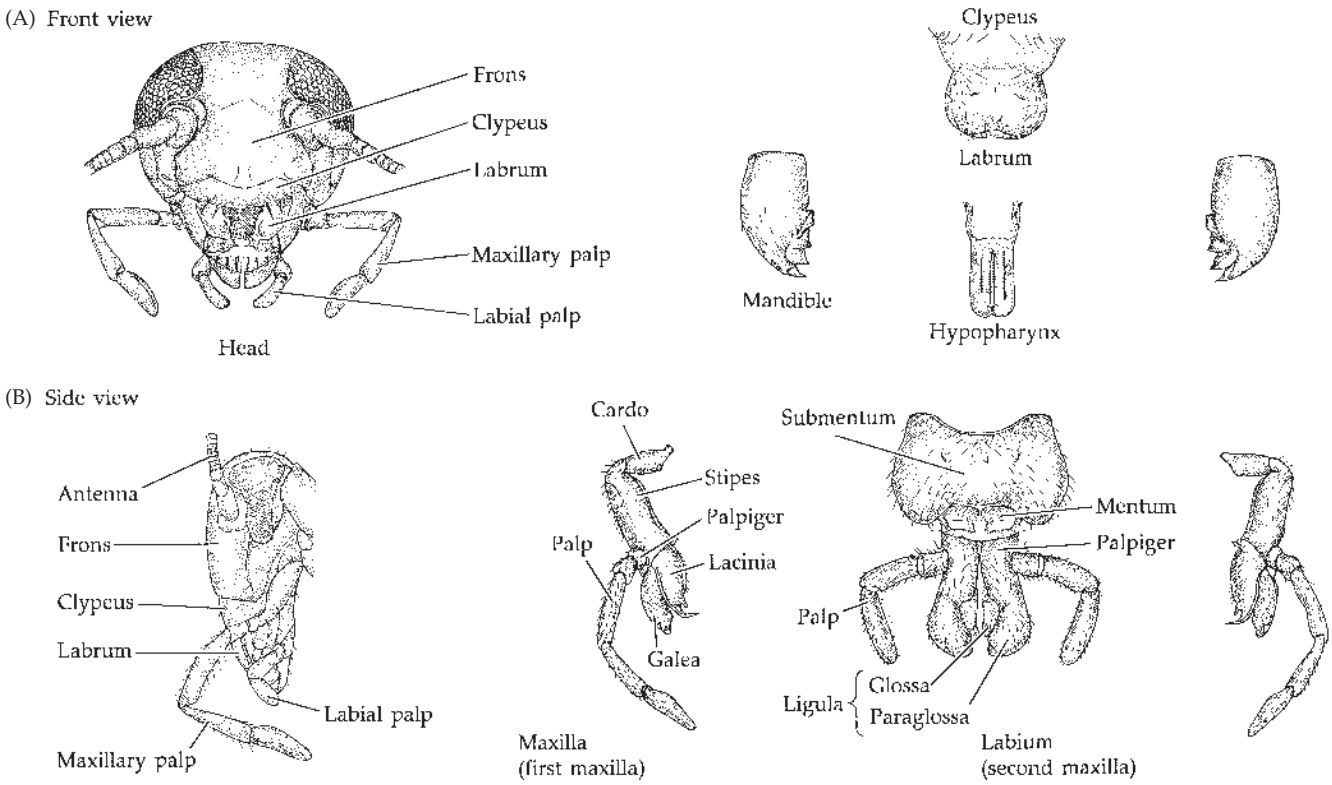


FIGURE 22.11 The mouth appendages of a typical biting-chewing insect: a grasshopper (order Orthoptera). (A) Front view. (B) Side view.

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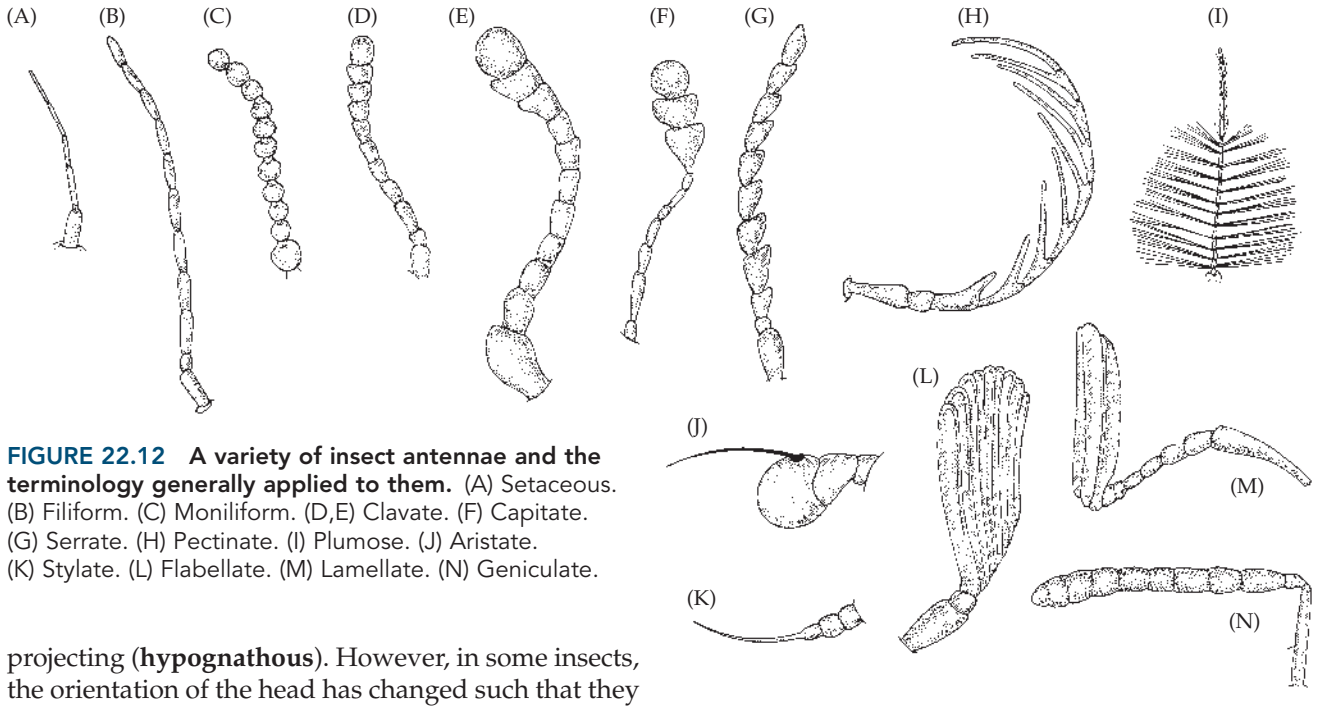

FIGURE 22.12 A variety of insect antennae and the terminology generally applied to them. (A) Setaceous. (B) Filiform. (C) Moniliform. (D,E) Clavate. (F) Capitate. (G) Serrate. (H) Pectinate. (I) Plumose. (J) Aristate. (K) Stylate. (L) Flabellate. (M) Lamellate. (N) Geniculate.

projecting (**hypognathous**). However, in some insects, the orientation of the head has changed such that they are **prognathous** (projecting anteriorly) or **opisthognathous** (projecting posteriorly) (Figure 22.13).

The labrum is a movable plate attached to the margin of the clypeus (a projecting frontal head piece), and together they form the **clypeolabrum**. Some workers regard the clypeolabrum to be an independently derived structure of the exoskeleton; others believe it could be derived from fused head appendages. The mandibles (Figure 22.14) are strongly sclerotized, usually toothed, and they lack a palp. In most insects the mandible is of one article, but in some primitive groups (and fossil taxa) it is composed of several articles. However, the gene *Distal-less* (*Dll*) is apparently never expressed in the embryogeny of hexapodan mandibles, suggesting that they are fully gnathobasic (i.e., protopodal). The maxillae are generally multiarticulate and bear a palp of one to seven articles. The labium comprises the fused second maxillae and typically bears two palps. In addition to these appendages, there is a median, unpaired, tonguelike organ called the hypopharynx that projects forward from the back of the preoral cavity. The salivary glands open through the hypopharynx.[3]

[3]Study of the *Dll* gene reveals that it was probably primitively expressed in the distal parts of all arthropod appendages. It is also expressed in the endites, or inner lobes, of arthropod limbs (e.g., in the phyllopodous limbs of Branchiopoda and in the maxillae of Malacostraca). In crustaceans and myriapods there is an initial *Dll* expression in the mandibular limb buds that is displaced laterally and continues in the mandibular palp in crustaceans. In insects, no *Dll* expression at all is seen in the mandibles—it has apparently been completely lost. Thus, the mandibles of all three groups are gnathobasic. The palp of the crustacean mandible represents the distal portion of the mandibular limb, altogether lost in hexapods and myriapods. The only real "whole-limb jaws" among the panarthropods are those of onychophorans. *Dll* is also expressed in the coxal endites of chelicerates and the pedipalp endites of arachnids. The complete loss of *Dll* expression in hexapod mandibles may be a synapomorphy for the group.

In the past, variations in feeding appendages were often used to define the major insect clades, and more recent molecular phylogenetic work has largely corroborated those ideas, although a number of cases of convergent evolution in mouthparts have also been revealed. In sucking insects both mandibles and maxillae may be transformed into spearlike structures (stylets), or the mandibles may be absent altogether (Figure 22.15 and 22.24). In most Lepidoptera, the maxillae form an elongate coiled sucking tube, the proboscis. In some insects (e.g., Hemiptera), the labium is drawn out into an elongate trough to hold the other mouthparts, and its palps may be absent; in others (e.g., Diptera), the labium is modified distally into a pair of fleshy porous lobes called labellae (sing. labellum).

The hexapod thorax The three segments of the thorax are the **prothorax**, **mesothorax**, and **metathorax** (Figure 22.9). Their tergites carry the same prefixes: **pronotum**, **mesonotum**, **metanotum**. In the winged insects (Pterygota), the mesothorax and metathorax are enlarged and closely united to form a rigid **pterothorax**. Wings, when present, are borne on these two segments and articulate with processes on the tergite (notum) and pleura of the somites. The prothorax is sometimes greatly reduced, but in some insects it is greatly enlarged (e.g., beetles) or even expanded into a large shield (e.g., cockroaches). The lateral, pleural sclerites are complex and thought to be derived, at least in part, from subcoxal (protopodal) elements of the ancestral legs that became incorporated into the lateral body wall. The sternites may be simple, or may be divided into multiple sclerites on each segment.

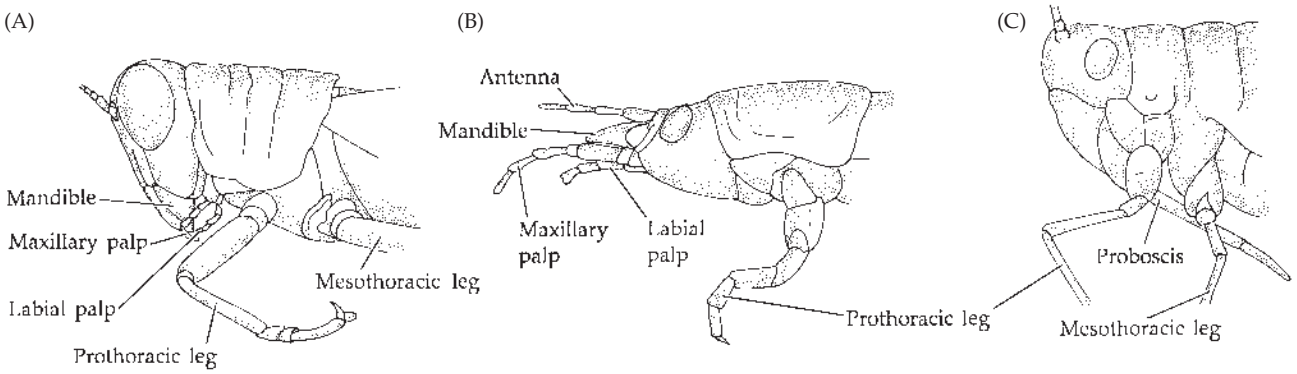

FIGURE 22.13 Different positions of head and mouthparts relative to the rest of the body. (A) Hypognathous condition (grasshopper). (B) Prognathous condition (beetle larva). (C) Opisthorhynchous condition (aphid). (After S. J. Simpson. 2012. In R. F. Chapman [Ed.] *The Insects*, 5th Ed., pp. 1–13. Cambridge University Press, Cambridge.)

Each of the three thoracic somites bears a pair of legs (Figure 22.9), composed of two parts, a proximal protopod and a distal telopod. The protopod (sometimes called a "coxopodite" by entomologists) is composed of two articles (**coxa**, **trochanter**), and the telopod is composed of four articles (**femur, tibia, tarsus, pretarsus**) (Figure 22.16). The tarsus is often subdivided into additional pseudoarticles called tarsomeres. The basal hexapods have a single tarsus (Protura and Diplura) or an indistinct tarsus (Collembola; probably fused with the tibia). In the Archaeognatha the tarsus is usually composed of three tarsomeres, and in the Pterygota it is composed of one, three, or five tarsomeres.[4] Whatever the number of tarsal articles, no intrinsic musculature occurs in them, and they are thus viewed as subdivisions of a single original article. The whole length of the tarsus is crossed by the tendon of the flexor muscle of the pretarsus, whose fibers usually arise on the tibia (Figure 22.17). The pretarsus is a minute article that usually bears a pair of lateral claws. In most adult hexapods, the pretarsus also bears a median **arolium** (which functions as an adhesive pad on smooth surfaces) or a median **unguitractor plate** or a median claw.

In insects, many adult organs derive from clusters of early embryonic cells called **imaginal discs**, which arise from localized invaginations of the ectoderm in the early embryo. The embryonic thorax contains three pairs of leg discs, and as development proceeds, these discs develop a series of concentric rings, which are the presumptive leg articles. The center of the disc corresponds to the distal-most articles (tarsus and pretarsus) of the future leg, while the peripheral rings correspond to its proximal region (coxa, trochanter). During embryogenesis, the leg telescopes out as it subdivides into the component articles. The gene *Distal-less* (*Dll*) is expressed in the presumptive distal region of the limb, while the gene *Extradenticle* (*Exd*) is necessary for the development of the proximal portion of the limb. Thus the protopod of the leg is under its own genetic control, as is the telopod, and this is why the mandible is considered gnathobasic, as it does not express *Dll* (see above).

Within the Pterygota, most species also have a pair of wings on the second and third thoracic segments. Wing morphology has been more extensively used in insect classification than the morphology of any other single structure. Wings are often the only remains of insects preserved as fossils. The wings of modern insects develop as evaginations of the integument, with thin cuticular membranes forming the upper and lower surfaces of each wing. Wing **veins**, which contain circulating hemolymph, anastomose and eventually

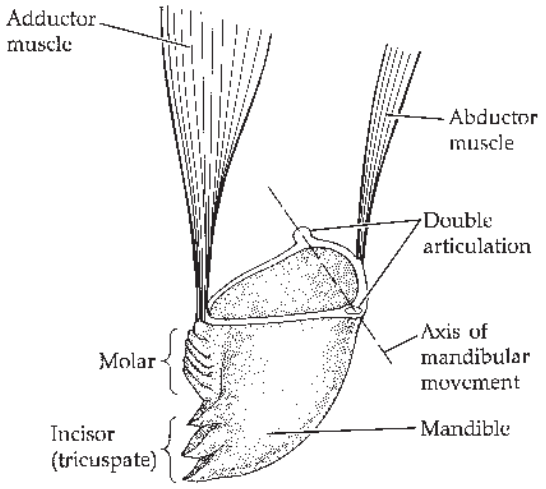

FIGURE 22.14 The musculature of an insect mandible.

[4]It is unclear whether having one or several tarsomeres is the primitive condition for the Hexapoda. Homologization of the leg articles among the various arthropod groups is a popular and often rancorous pastime. The issue is further confused when the number of articles differs from the norm (e.g., some insects have two trochanters, the number of tarsi varies from one to five, etc.). The protopods of myriapods, chelicerates, and trilobites all seem to consist of a single basal article (usually called the coxa). In the latter case, Kukalová-Peck hypothesizes that three "missing" protopodal articles were lost by fusion among themselves and with the pleural region. See Chapter 20 for a discussion of ancestral arthropod legs.

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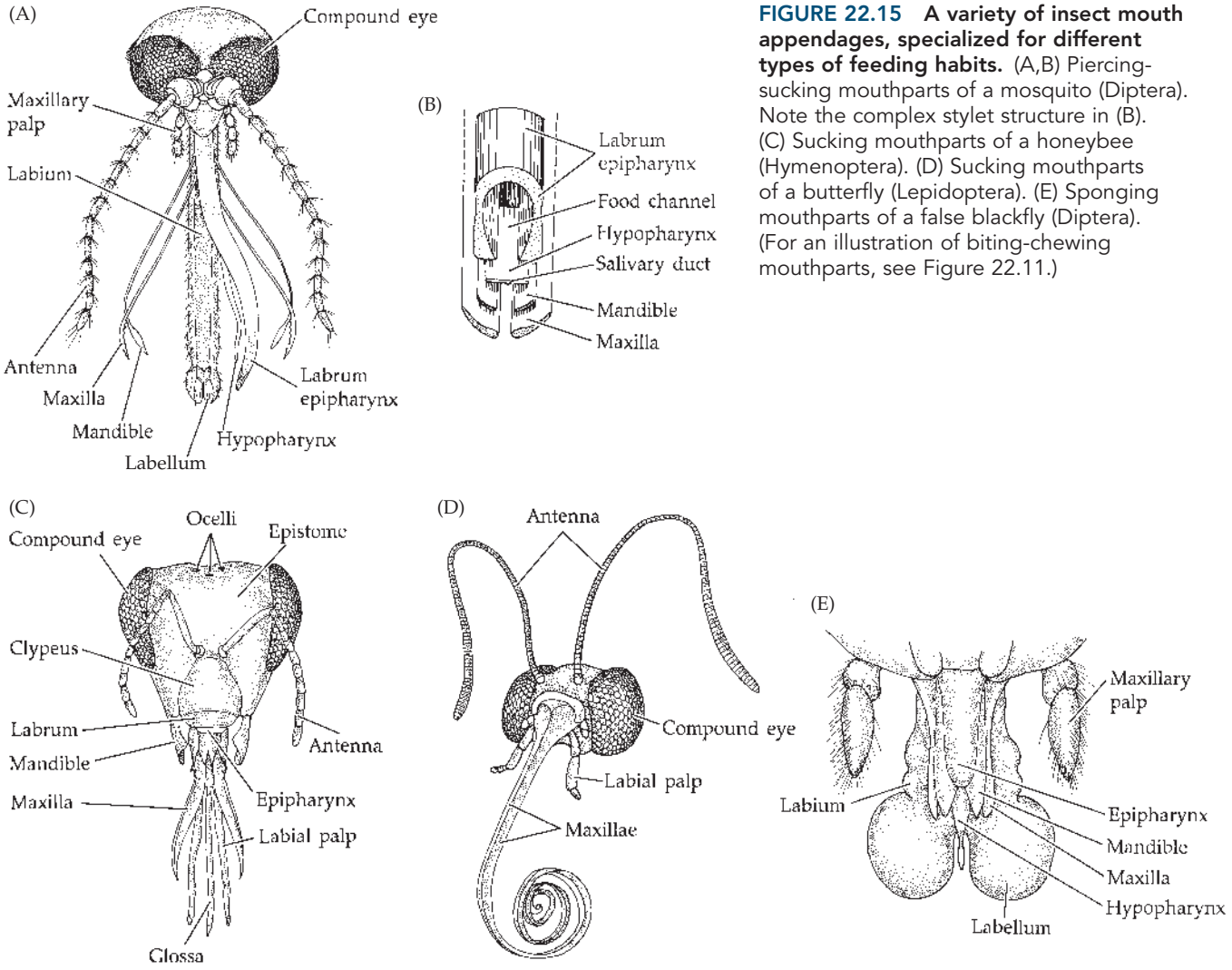

FIGURE 22.15 A variety of insect mouth appendages, specialized for different types of feeding habits. (A,B) Piercing-sucking mouthparts of a mosquito (Diptera). Note the complex stylet structure in (B). (C) Sucking mouthparts of a honeybee (Hymenoptera). (D) Sucking mouthparts of a butterfly (Lepidoptera). (E) Sponging mouthparts of a false blackfly (Diptera). (For an illustration of biting-chewing mouthparts, see Figure 22.11.)

open into the body. The arrangement of veins in insect wings provides important diagnostic characters at all taxonomic levels. The origin and homologies of wing venation have been heavily debated over the decades. Most workers use a consistent naming system that recognizes six major veins: costa (C), subcosta (SC), radius (R), media (M), cubitus (CU), and anal (A) (Figure 22.18). Areas in the wings that are enclosed by longitudinal and cross veins are called **cells**, and these too have a somewhat complex nomenclature. In some groups (e.g., Orthoptera, Dermaptera) the forewings develop heavily sclerotized regions called **tegmina** (sing. tegmin), used for protection, stridulation, or other purposes. In many sedentary, cryptic, parasitic, and insular lineages the wings have become shortened (brachypterous) or lost (apterous). Insects often couple their wings together for flight by means of hooklike devices along the margin between the posterior border of the forewing and the anterior margin of the hindwing (e.g., **hamuli** in Hymenoptera; **frenula** in many Lepidoptera). In these insects the coupled wings function together as a single unit.

The hexapod abdomen The abdomen primitively comprises 11 segments, although the first is often reduced or even incorporated into the thorax, and the last segment may be vestigial. Abdominal pleura are greatly reduced or absent. The occurrence of true (though minute) abdominal leglets (sometimes called "prolegs" or "styli") on the pregenital segments is commonplace among the apterygotes and also occurs in the larvae of many pterygotes (e.g., the legs of caterpillars). In addition, transitory limb buds or rudiments appear fleetingly in the early embryos of some species, presumably harking back to the deep evolutionary past. Abdominal segments 8–9 (or 7–9) are typically modified as the **anogenital tagmata**, or **terminalia**, the exposed parts being the genitalia. The female median gonopore occurs behind sternum 7 in Ephemeroptera and Dermaptera, and behind sternum 8 or 9 in all other orders. The anus is always on segment 11 (which may be fused with segment 10).

There is enormous complexity in both clasping and intromittent organs among the Hexapoda, and a correspondingly sharp disagreement exists over the

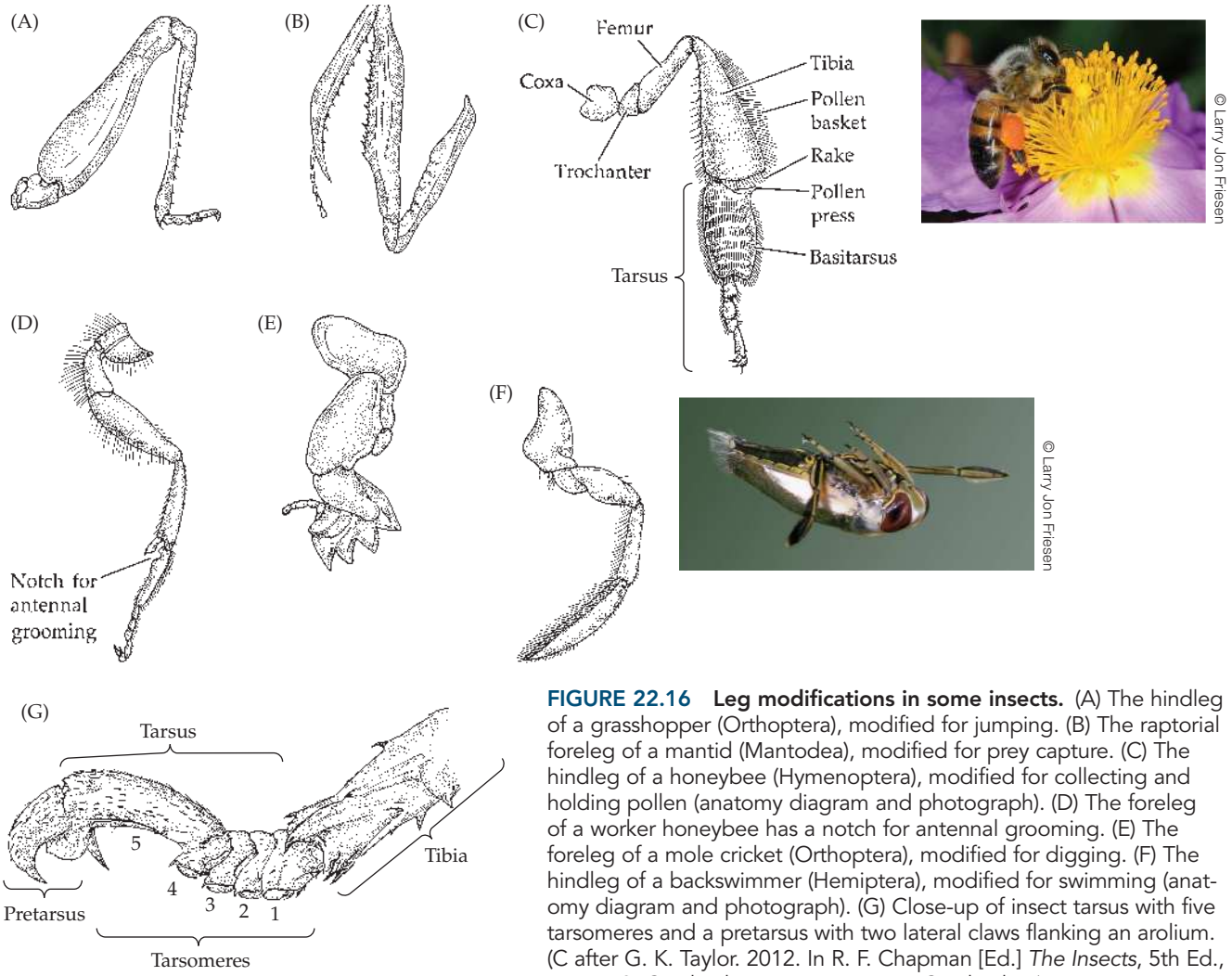

FIGURE 22.16 Leg modifications in some insects. (A) The hindleg of a grasshopper (Orthoptera), modified for jumping. (B) The raptorial foreleg of a mantid (Mantodea), modified for prey capture. (C) The hindleg of a honeybee (Hymenoptera), modified for collecting and holding pollen (anatomy diagram and photograph). (D) The foreleg of a worker honeybee has a notch for antennal grooming. (E) The foreleg of a mole cricket (Orthoptera), modified for digging. (F) The hindleg of a backswimmer (Hemiptera), modified for swimming (anatomy diagram and photograph). (G) Close-up of insect tarsus with five tarsomeres and a pretarsus with two lateral claws flanking an arolium. (C after G. K. Taylor. 2012. In R. F. Chapman [Ed.] *The Insects*, 5th Ed., pp. 1–13. Cambridge University Press, Cambridge.)

homologies and terminology of these structures. In general, females discriminate among males on the basis of sensory stimuli produced by the male genitalia; hence selection pressure has been a powerful force in the evolution of these structures (in both sexes). The most primitive male architecture can be seen in apterygotes and Ephemeroptera, in which the penes are paired and contain separate ejaculatory ducts. In most other insects, however, the intromittent organ develops late during embryogenesis by fusion of the genital papillae to form a median, tubular, often eversible endophallus, with the joined ejaculatory ducts opening at a gonopore at its base. The external walls may be sclerotized or modified in a wide variety of ways, and the whole organ is known as the **aedeagus**. Some workers consider the aedeagus to be derived from segment 9; others regard it as belonging to segment 10. A pair of sensory cerci (sing. cercus) often projects from the last abdominal segment.

Locomotion

Walking Like the other terrestrial arthropods, hexapods rely on their sclerotized exoskeleton for support on land. Their limbs provide the physical support needed to lift the body clear of the ground during locomotion. In order to accomplish this, the limbs must be long enough to hold the body high off the ground, but not so high as to endanger stability. Most hexapods maintain stability by having the legs in positions that suspend the body in a slinglike fashion and keep the overall center of gravity low (Figure 20.19).

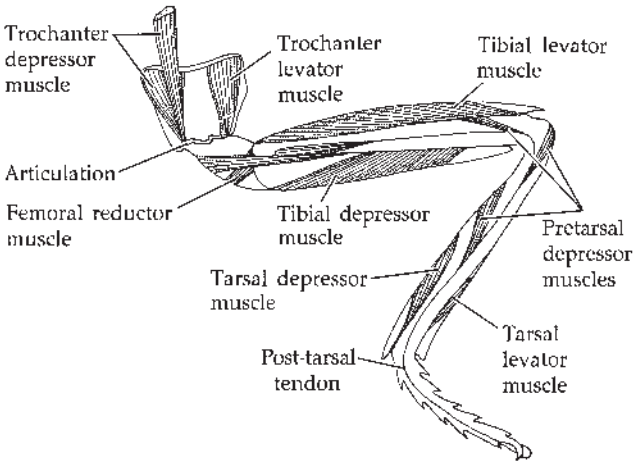

FIGURE 22.17 The musculature of an insect leg.

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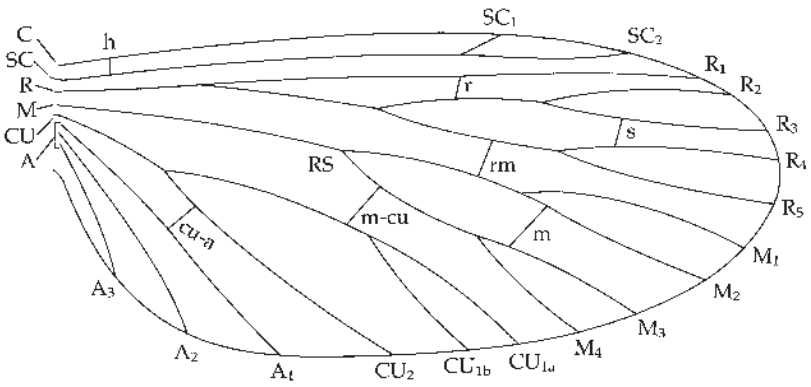


FIGURE 22.18 The nomenclature of basic wing venation in insects. Although the cells formed within the veins also have names, only the names of the veins are given here. Longitudinal veins are coded with capital letters, cross veins with lowercase letters. Longitudinal veins: costa (C); subcosta (SC); radius (R); radial sector (RS); media (M); cubitus (CU); anal (A). Cross veins: humeral (h); radial (r); sectorial (s); radiomedial (rm); medial (m); mediocubital (m-cu); cubitoanal (cu-a).

The basic structure of arthropod limbs was described in Chapter 20. In hexapods (and crustaceans) the anterior–posterior limb movements take place between the coxae and the body proper (in contrast to most arachnids, in which the coxae are immovably fixed to the body and limb movement occurs at more distal joints). Like the power controlled by the range of gears in a combustion engine automobile, the power exerted by a limb is greatest at low speeds and least at higher speeds. At lower speeds the legs are in contact with the ground for longer periods of time, thus increasing the power, or force, that can be exerted during locomotion. In burrowing forms the legs are short, and the gait is slow and powerful as the animal forces its way through soil, rotting wood, or other material. Longer limbs reduce the force but increase the speed of a running gait, as do limbs capable of swinging through a greater angle. Limbs long in length and stride are typical features of the fastest-running insects (e.g., tiger beetles, Carabidae, Cicindelinae).

One of the principal problems associated with increased limb length is that the field of movement of one limb may overlap that of adjacent limbs. Interference is prevented by the placement of the tips of adjacent legs at different distances from the body (Figure 22.19). Thus fast-running insects usually have legs of slightly different lengths. Insects usually move their legs in an alternating tripod sequence. Balance is maintained by always having three legs in contact with the ground.

Like many spiders, some insects can walk on water, and they do so in much the same way—by balancing the pull of gravity on their featherweight bodies with the physical principles of buoyancy and surface tension. Insects (and spiders) that walk on water don't get wet because their exoskeletons are coated with waxes that repel water molecules. The water surface, held taut by surface tension, bends under each leg to create a depression, or dimple, that works to push the animal upward in support. Water walking occurs in many insect groups, notably the Hemiptera (e.g., water striders), Coleoptera (e.g., whirligig beetles), and Collembola (some springtails).[5]

Many insects are superb jumpers (e.g., fleas, springtails, most orthopterans), but the click beetles (Elateridae) are probably the champions. It has been calculated that a typical click beetle (e.g., *Athous haemorrhoidalis*), when springing into the air to escape a predator, generates a g-force of 400, with a peak deceleration of 2,300 g.

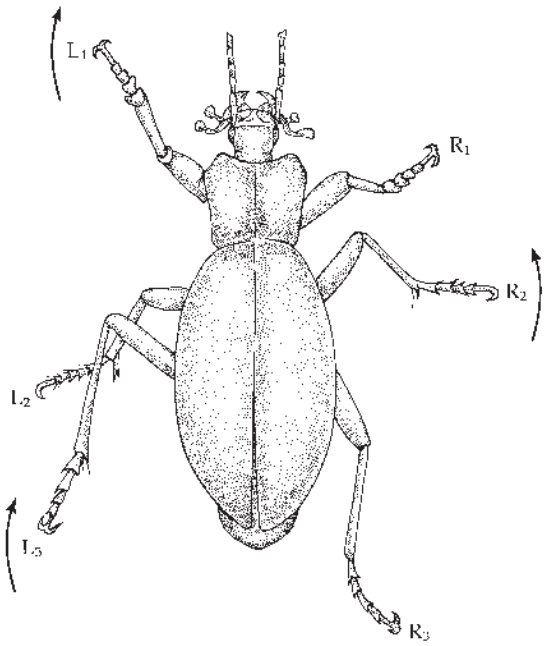


FIGURE 22.19 A beetle walking. The alternating tripod gait consists of alternate stepping with two sets of three legs; thus the body is always supported by a triad of legs. Here, three legs (L_1, R_2, and L_3) are moving forward while the other three (R_1, L_2, and R_3) are on the ground.

Flight Among the many remarkable advances of insects, flight is perhaps the most impressive. Insects were the first flying animals, and throughout the history of life on Earth, no other invertebrates have learned the art of true flight. The wingless insects belong to groups that have secondarily lost the wings (e.g., fleas, lice, certain scale insects), to life stages that have lost the wings, or to primitive taxa (the apterygotes) that arose prior to the evolution of wings. In three orders,

[5]On an undisturbed surface, water molecules are attracted to their neighbors beside and below, resulting in a flat skin of molecules that exerts only horizontal tensile forces; it is this "elasticity" of the surface that we call surface tension.

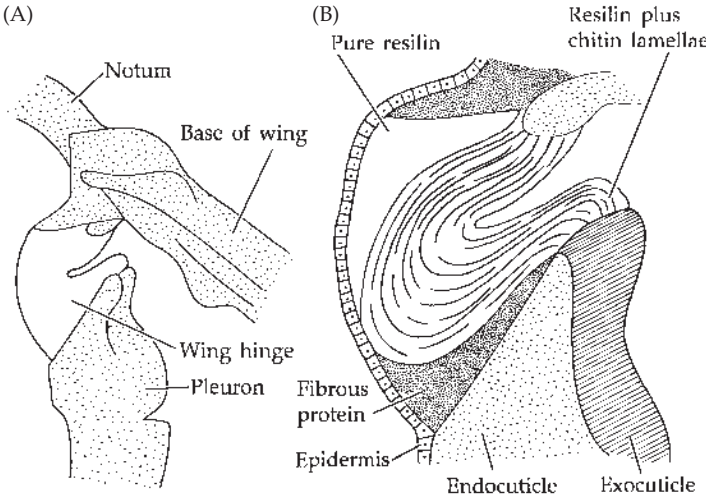
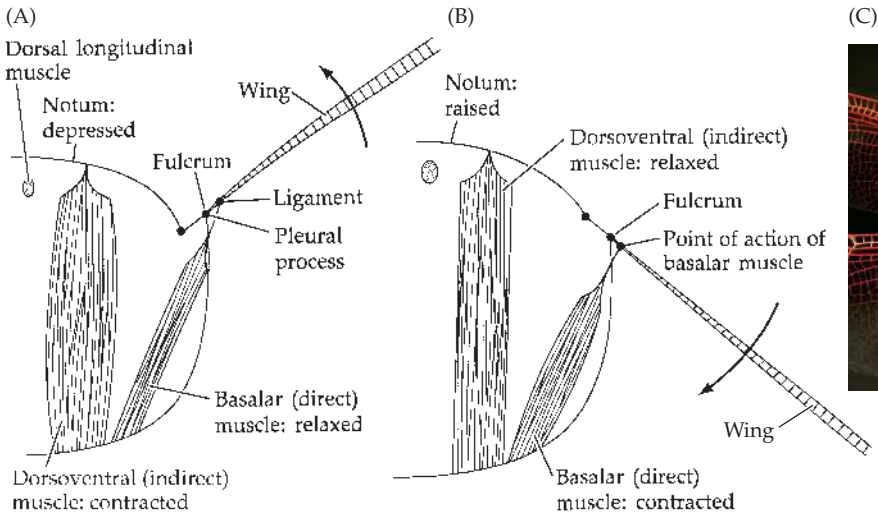


FIGURE 22.20 A typical insect wing hinge arrangement. This transverse section through the thoracic wall of a grasshopper shows the base of the wing and the wing hinge. (A) Entire hinge area. (B) Enlargement of hinge section.

the wings are effectively reduced to a single pair. In beetles, the forewings are modified as a protective dorsal shield (**elytra**). In dipterans, the hindwings are modified as organs of balance (**halteres**). The halteres beat with the same frequency as the forewings, functioning as gyroscopes to assist in flight performance and stability—flies fly very well. In strepsipteran males (females are wingless), the forewings are reduced to clublike structures resembling the halteres of Diptera.

Compared with an insect, an airplane is a simple study in aerodynamics. Planes fly by moving air over a fixed wing surface, the leading edge of which is tilted upward, forcing the air to travel farther (thus faster) over the top of the wing than the bottom, resulting in a vortex that creates a lift. But conventional fixed-wing aerodynamic theory is insufficient to understand insect flight. Insect wings are anything but fixed. Insects, of course, fly by flapping their wings to create vortices, from which they gain lift, but these vortices slip off the wings with each beat, and new vortices are formed with each alternate stroke. Beating insect wings trace a figure eight pattern, and they also rotate at certain crucial moments. Thus, each cycle of flapping creates dynamic forces that fluctuate drastically. By complex actions of wing orientation, insects can hover; fly forward, backward, and sideways; negotiate highly sophisticated aerial maneuvers; and land in any position. To complicate matters even more, in the case of small insects (and most are small, the average size of all insects being just 3–4 mm), the complex mechanics of flight take place at very low Reynolds numbers (see Chapter 3), such that the insect is essentially "flying through molasses." As a result of these complex mechanics, insect flight is energetically costly, requiring metabolic rates as high as 100 times the resting rate.

Each wing articulates with the edge of the notum (thoracic tergite), but its proximal end rests on a dorsolateral pleural process that acts as a fulcrum (Figure 22.20). The wing hinge itself is composed in large part of resilin, a highly elastic protein that allows for rapid, sustained movement. The complex wing movements are made possible by the flexibility of the wing itself and by the action of a number of different muscle sets that run from the base of the wing to the inside walls of the thoracic segment on which it is borne. These direct flight muscles serve to raise and lower the wing and to tilt its plane at different angles (somewhat like altering the blade angles on a helicopter) (Figure 22.21). However,



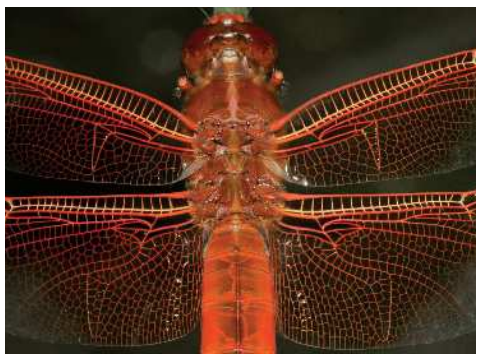


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FIGURE 22.21 Wing movements of a primitive insect such as a dragonfly, in which direct wing muscles cause depression of the wings. Dots represent pivot points, and arrows indicate the direction of wing movement. (A) The dorsoventral muscles contract to depress the notum as the basalar muscles relax, a combination forcing the wings into an upstroke. (B) The dorsoventral muscles relax as the basalar muscles contract, a combination pulling the wings into a downstroke and relaxing (and raising) the notum. (C) Thorax of a dragonfly showing wing attachment to the notum of thoracic segments 2 and 3.

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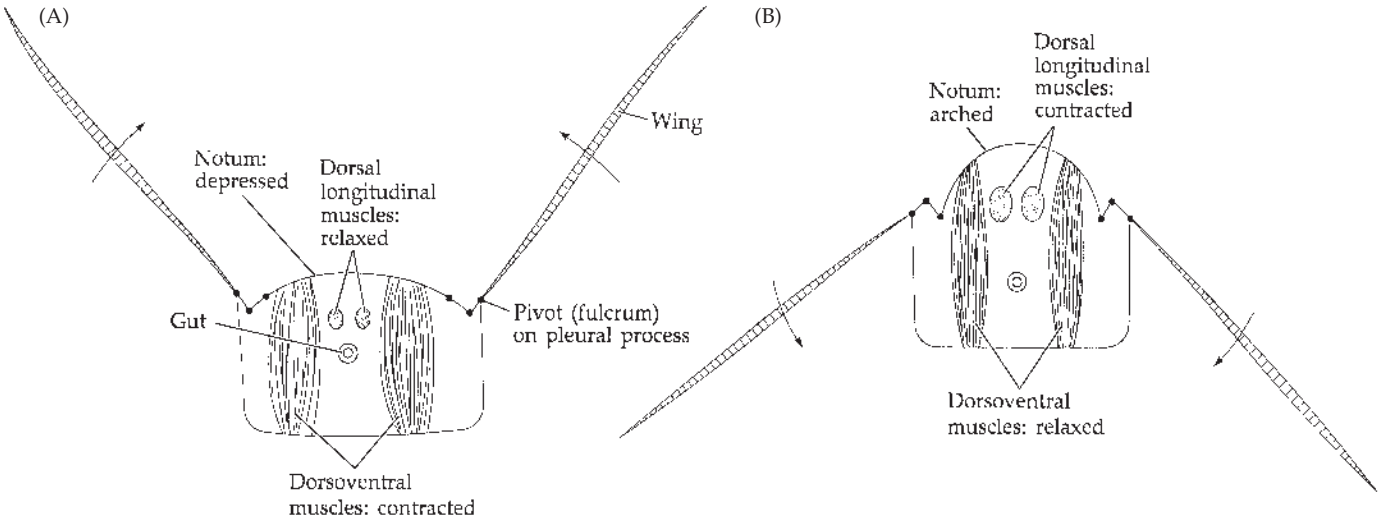

FIGURE 22.22 Wing movements of an insect such as a fly or hemipteran, in which both upward and downward movements of the wings are produced by indirect flight muscles. In these transverse sections of a thoracic segment, dots represent pivot points, and arrows indicate the direction of wing movement. Only two sets of muscles are shown. (A) The dorsoventral muscles contract, depressing the thoracic notum and forcing the wings into upstroke. (B) The dorsoventral muscles relax as the dorsal longitudinal muscles contract to "pop up" the notum, elevating it and forcing the wings into a downstroke.

except in palaeopterans (Odonata and Ephemeroptera), the direct flight muscles are not the main source of power for insect wing movements. Most of the force comes from two sets of indirect flight muscles, which neither originate nor insert on the wings themselves (Figures 22.21 and 22.22).

Dorsal longitudinal muscles run between apodemes at the anterior and posterior ends of each winged segment. When these muscles contract, the segment is shortened, which results in a dorsal arching of the segment roof and a downstroke of the wings. Dorsoventral muscles, which extend from the notum to the sternum (or to basal leg joints) in each wing-bearing segment, are antagonistic to the longitudinal muscles. Contraction of the dorsoventral muscles lowers the roof of the segment. In doing so, it raises the wings. Thus, wing flapping in most insects is primarily generated by rapid changes in the walls and overall shape of the mesothorax and metathorax. Other, smaller thoracic muscle sets serve to make minor adjustments to this basic operation.

Insects with low wing-flapping rates (e.g., dragonflies, orthopterans, mayflies, and lepidopterans) are limited by the rate at which neurons can repeatedly fire and muscles can execute contractions. However, in insects with high wing-flapping rates (e.g., dipterans, hymenopterans, and some coleopterans), an entirely different regulatory mechanism has evolved. Once flight has been initiated and a high wing-flapping rate attained (up to 100 beats/second), myogenic control takes over. This mechanism exploits the elastic-mechanical properties of the exoskeleton. When one set of indirect muscles contracts, the thorax is deformed. Upon relaxation of the muscles, there is an elastic rebound of the thoracic exoskeleton, which stretches the second set of indirect muscles and thus directly stimulates their contraction. This contraction establishes a second deformation, which in turn stretches and stimulates the first muscle group. Once initiated, this mechanism is nearly self-perpetuating, and the nonsynchronous firing of neurons serves only to keep it in action.

Not all insects utilize wings to travel through the air. Many small and immature insects are effectively dispersed by wind power alone. Some first-instar lepidopterans use silk threads for dispersal (as do spiders and mites). Tiny scale insects are commonly collected in aerial nets. In fact, studies have revealed the existence of "aerial plankton" consisting of insects and other minute arthropods, extending to altitudes as high as 14,000 feet. Most are minute winged forms, but wingless species are also common.

The Origin of Insect Flight

For many decades, two competing views of insect wing origin have dominated. In general, these views can be termed the novel structure hypothesis and the appendage hypothesis. The former holds that wings evolved by way of gene co-option to form a new structure (e.g., a gradual expansion of lateral, or paranotal, folds of the thoracic tergite, hence giving this view the name "tergal origin hypothesis"), which eventually became articulated and muscled to form wings. The latter hypothesizes that wings evolved from preexisting articulated structures on the thoracic appendages,

such as gills or protopodal exites on the legs. And some recent work has even suggested a "dual origin," with cells from both the tergal and pleural regions contributing to the wings.

The paranotal lobe hypothesis was first proposed by Müller in 1873, saw a resurgence of popularity in the middle of the twentieth century, and has lost favor in recent years. It suggests that wings originated as lateral aerodynamic flaps of the thoracic nota that enabled insects to alight right side up when jumping or when blown about by the wind. These stabilizing paranotal lobes later evolved hinged structures and muscles at their bases. The occurrence of fixed paranotal lobes in certain ancient fossil insects has been cited in support of the paranotal lobe hypothesis (Figure 22.23). However, recent studies suggest that these primitive paranotal lobes might have been used for other purposes, such as covering the spiracular openings or gills in amphibious insects, protecting or concealing the insects from predators, courtship displays, or thermoregulation by absorption of solar radiation.

The appendage hypothesis (also known as the "gill or branchial theory," "exite theory," or "leg theory") also dates back to the nineteenth century but was resurrected by the great entomologist V. B. Wigglesworth in the 1970s and was championed by J. Kukalová-Peck since the 1980s. It is the more favored hypothesis of wing origin today, based on recent paleontological work, microscopic anatomy, and molecular developmental biology. It suggests that insect wings are derived from thoracic appendages—from protopodal exites, in Wigglesworth and Kukalová-Peck's view. These proto-wing appendages might have first functioned as aquatic gills or paddles, or as terrestrial gliding structures. The paired abdominal gills of mayflies have been suggested as serial homologues of such "proto-wings." In Kukalová-Peck's version of this hypothesis, the first protopodal leg article (the epicoxa) fused with the thoracic pleural membrane early in the evolution of the Arthropoda, as did the second article (the precoxa) in the ancient hexapods, with both migrating dorsally off the leg and onto the body proper. In insects, the epicoxa eventually fused with the tergite, its exite enlarging to form the proto-wing and eventually the true wing. The precoxa formed the pleural sclerite providing the ventral articulation of the wing. Wing veins might have evolved from cuticular ridges that served to strengthen these structures and, eventually, to circulate blood through them.[6]

Kukalová-Peck's theory of wing evolution finds support in molecular developmental studies, which have shown that the cells that give rise to the wing primordium derive from the same cluster of cells that form the leg primordium, from which they segregate, migrating dorsally to a position below the tergum. Recent studies on gene expression also support the origin of wings from legs. The genes *pdm* and *apterous* are expressed in the wing (and leg) primordia of all insects. Expression of both genes appears to be necessary for normal wing formation. In malacostracan crustaceans (but not in branchiopod crustaceans) these same genes are expressed, in a similar manner, in the formation of the leg rami (the exopod and endopod).

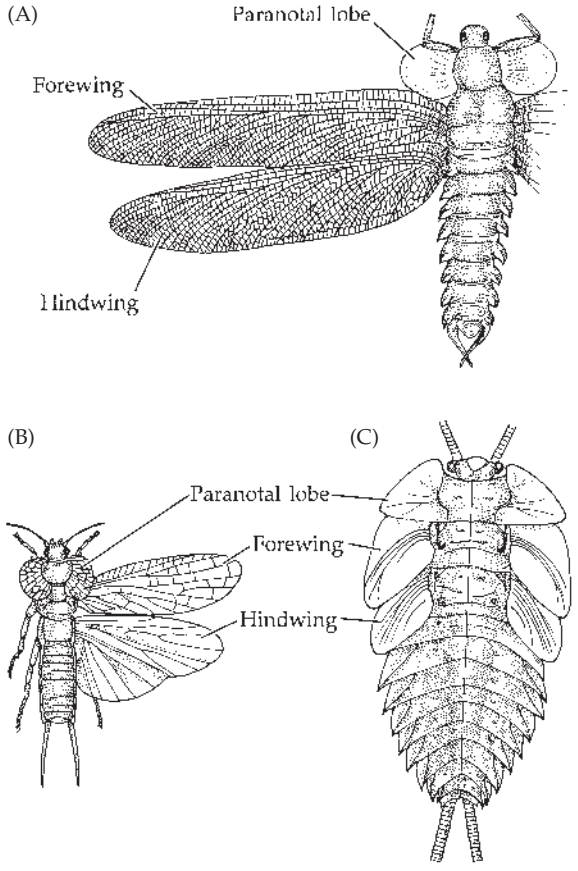

FIGURE 22.23 Fossil insects with paranotal lobes on the prothorax. (A) *Stenodictya lobata*, a Paleozoic palaeodictyopteran. (B) *Lemmatophora typa* (Mesozoic). (C) Nymphal stage of *Rochdalia parkeri*, a Paleozoic terrestrial palaeodictyopteran in which all three thoracic segments appear to have had "articulated" thoracic lobes.

Feeding and Digestion

Feeding Every conceivable kind of diet is exploited by species within the Hexapoda, whose feeding strategies include herbivory, carnivory, and scavenging, as well as a magnificent array of commensalism and parasitism. This "nutritional radiation" has played a key role in the phenomenal evolution among the Insecta. A comprehensive survey of insect feeding biology alone could easily fill a book this size. Setting aside symbiotic relationships for a moment, in the most general sense insects can be classified as (1) biters-chewers, (2) suckers, or (3) spongers (Figure 22.24).

[6]Unspecialized coxal exites can be seen on the legs of some living archaeognathans (bristletails) and in numerous extinct hexapods.

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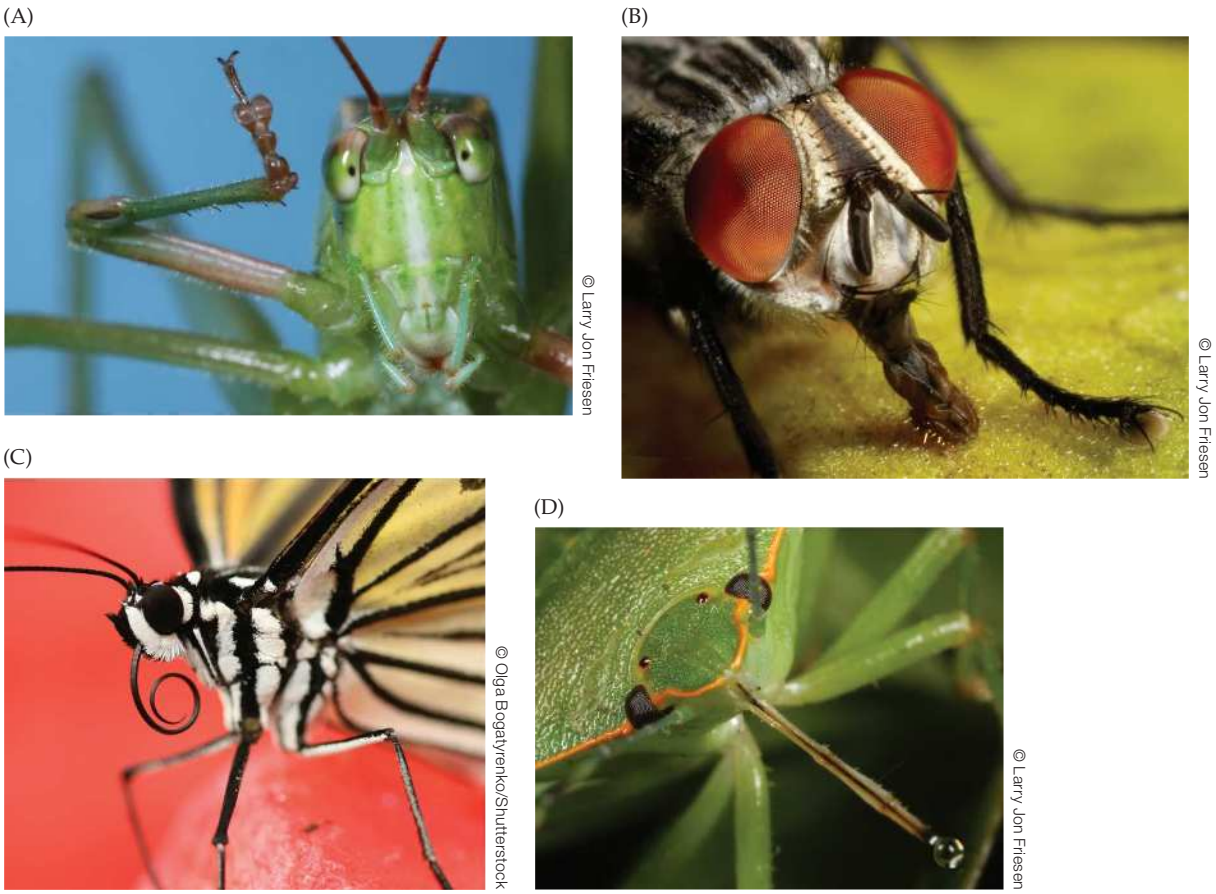

FIGURE 22.24 Mouthparts specialized for different modes of feeding. (A) Biting-chewing mouthparts of a grasshopper. Note the well-developed leglike palps. (B) Sponging mouthparts of a fly. (C) Sucking mouthparts of a butterfly. (D) Piercing mouthparts of a true bug.

Biters-chewers, such as the grasshoppers, have the least-modified mouthparts, so we describe them first. The maxillae and labium of these insects have well-developed leglike palps (Figure 22.24A) that help them hold food in place, while powerful mandibles cut off and chew bite-size pieces. The mandibles lack palps (in all hexapods) and typically bear small, sharp teeth that work in opposition as the appendages slide against each other in the transverse (side-to-side) fashion characteristic of most arthropod jaws. Biting-chewing insects may be carnivores, herbivores, or scavengers. In many plant eaters, the labrum bears a notch or cleft in which a leaf edge may be lodged while being eaten. Some of the best examples of this feeding strategy are seen among the Orthoptera (locusts, grasshoppers, crickets), and most people have witnessed the efficient fashion in which these insects consume their garden plants! Equally impressive are the famous leafcutter ants of the Neotropics, which can denude an entire tree in a few days. Leafcutter ants have a notable feeding adaptation: when cutting leaf fragments, they produce high-frequency vibrations with an abdominal stridulatory organ. This stridulation is synchronized with movements of the mandible, generating complex vibrations. The high vibrational acceleration of the mandible appears to stiffen the material being cut, just as soft material is stiffened with a vibratome for sectioning in a laboratory. Leafcutters don't eat the leaves they cut; instead, they carry them into an underground nest, where they use them to grow a fungus on which they feed. Several other insect groups have evolved associations with fungi, and in almost every case these relationships are mutualistic and obligate—neither partner can live without the other.

In sucking insects the mouthparts are markedly modified for the consumption of liquid foods, generally plant saps, nectars, animal blood, or cell fluids (Figure 22.24C,D). Sucking mouthparts and liquid diets have clearly evolved many times in different insect lines—further testimony to the frequency of evolutionary convergence in arthropods and the developmental adaptability of their appendages. In some sucking insects, such as mosquitoes, feeding is initiated by piercing the victim's epidermal tissue; this mode of feeding is referred to as piercing-sucking. Other insects, such as the butterflies and moths that feed on flower nectar, do not pierce anything and are merely suckers—but some carnivore lepidopterans, like the vampire moths, do pierce to draw blood!

In all sucking insects the mouth itself is very small and hidden. The mouthparts, instead of being adapted for handling and chewing solid pieces of food, are elongated into a needlelike beak adapted for a liquid diet. Different combinations of mouth appendages constitute the beak in different taxa. True bugs (Hemiptera), which are piercer-suckers, have a beak composed of five elements: an outer troughlike element (the labium) and, lying in the trough, four very sharp stylets (the two mandibles and two maxillae). The stylets are often barbed to tear the prey's tissues and enlarge the wound. The labrum is in the form of a small flap covering the base of the grooved labium. When piercer-suckers feed, the labium remains stationary, and the stylets do the work of puncturing the plant (or animal) and drawing out the liquid meal.

Different variations of piercing-sucking mouthparts are found in other insect taxa. In mosquitoes, midges, and certain biting flies (e.g., horseflies) there are six long, slender stylets, which include the labrum-epipharynx and the hypopharynx as well as the mandibles and first maxillae (Figure 22.15A). Other biting flies, such as the stable fly, have mosquito-like mouthparts but lack mandibles and maxillae altogether. Fleas (Siphonaptera) have three stylets: the labrum-epipharynx and the two mandibles. Thrips have unusual mouthparts: the right mandible is greatly reduced, making the head somewhat asymmetrical, and the left mandible, first maxillae, and hypopharynx make up the stylets.

Most lepidopterans are nonpiercing sucking insects in which the paired first maxillae are enormously elongated, coiled, and fused to form a tube through which flower nectar is sucked (Figure 22.24C); the mandibles are vestigial or absent (Figure 22.15D). The mouthparts of bees are similar: the first maxillae and labium are modified together to form a nectar-sucking tube, but the mandibles are retained and used for wax manipulation during hive construction (Figure 22.15C). The collected nectar is stored in a special "sac" in the foregut and carried back to the hive, where it is converted into honey, which is stored as a food reserve. Bees in an average hive consume about 500 pounds of honey per year—we humans get the leftovers.

Associated with sucking mouthparts are various mechanisms for drawing liquid food into the mouth. Most piercer-suckers rely largely on capillary action, but others have developed feeding "pumps." Often the pump is developed through elongation of the preoral cavity, or **cibarium**, which by extension of the cuticle around the mouth becomes a semiclosed chamber connecting with the alimentary canal (Figure 22.25). In these cases, cibarial muscles from the clypeus are enlarged to make a powerful pump. In lepidopterans, dipterans, and hymenopterans the cibarial pump is combined with a pharyngeal pump, which operates by means of muscles arising on the front of the head. Specialized salivary glands are also often associated with sucking mouthparts. In some hemipterans a salivary pump forces saliva through the feeding tube and into the prey, softening tissues and predigesting the liquid food. In mosquitoes, saliva carries blood thinners and anticoagulants (and often parasites such as *Plasmodium*, which causes malaria).

In spongers, such as most flies (order Diptera), the labium is typically expanded distally into a **labellum** (Figures 22.15E and 22.24B). Fluid nutrients are transported by capillary action along minute surface channels from the labellae to the mouth. In many spongers,

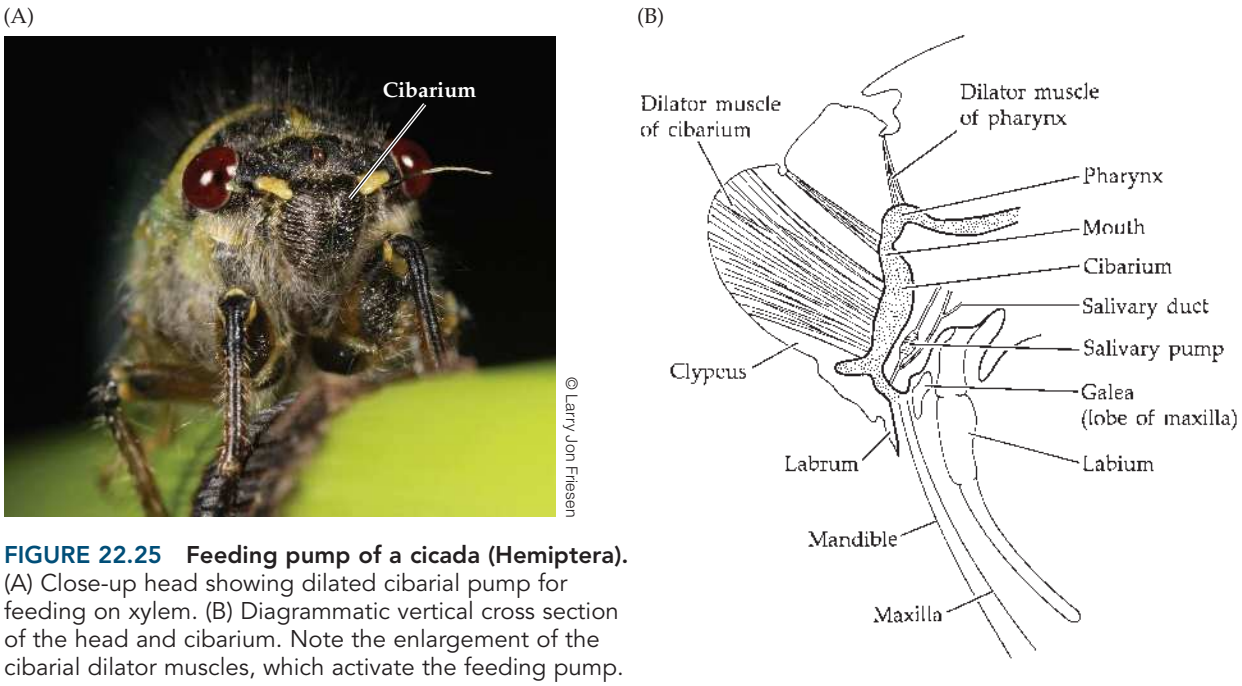

FIGURE 22.25 Feeding pump of a cicada (Hemiptera). (A) Close-up head showing dilated cibarial pump for feeding on xylem. (B) Diagrammatic vertical cross section of the head and cibarium. Note the enlargement of the cibarial dilator muscles, which activate the feeding pump.

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such as houseflies, saliva is exuded onto the food to partly liquefy it. In strict spongers, the mandibles are absent. In biting spongers, such as horseflies, the mandibles serve to slice open a wound in the flesh, thus exposing the blood and cellular fluids to be sponged up by the labellae.

Many insects are scatophagous, feeding on animal feces. Most of these groups have biting mouthparts, but some (such as certain flies) have sucking mouthparts. Perhaps the most famous of the scatophagous insects are the dung beetles, or tumblebugs (certain beetles in the families Scarabaeidae and Histeridae). These remarkable insects harvest animal dung by biting or slicing off pieces with specialized head or leg structures and working them into a ball. They may roll the dung ball a considerable distance and eventually bury it in the soil, whereupon females deposit eggs within it. Larvae are thus assured of a ready food supply. Dung balls may even be maneuvered by a pair of dung beetles pushing and pulling in a cooperative effort.

There are many symbiotic insects, and two orders are composed entirely of wingless parasites, most of which spend their entire lives on their hosts: some Psocodea (lice) and Siphonaptera (fleas). Bird lice are common, and lice are also found on dogs, cats, horses, cattle, and other mammals. Biting lice have broad heads and biting mouthparts used to chew epithelial cells and other structures on the host's skin. Sucking lice have narrow heads and piercing-sucking mouthparts, which they use to suck blood and tissue fluids from their host, always a mammal. Unlike most arthropod parasites, lice (of both types) spend their entire lives on the bodies of their hosts, and transmission to new hosts is by direct contact. For this reason most lice show a high degree of host specificity. Eggs, or nits, are attached by the female to the feathers or hair of the host, where they develop without a marked metamorphosis. Many lice, particularly those whose diet is chiefly keratin, possess symbiotic intracellular bacteria that appear to aid in the digestion of their food. These bacteria are passed to the offspring by way of the insects' eggs. Similar bacteria occur in ticks, mites, bedbugs, and some blood-sucking dipterans.

None of the biting lice are known to infest people or to transmit human disease microorganisms, although one species acts as an intermediate host for certain dog tapeworms. The sucking lice, on the other hand, include two genera that commonly infest humans (*Pediculus* and *Phthirus*). The latter genus includes the notorious *P. pubis*, the human pubic crab louse (which often occurs on other parts of the body as well). The genus *Pediculus* includes four species that parasitize primates, including *P. humanus* and its two morphotypes, the body louse and the head louse. A number of sucking lice are vectors for human disease organisms. The most common reaction to infestation with lice—a condition known as **pediculosis**, or being lousy—is simple irritation and itching caused by the anticoagulant injected by the parasite during feeding. Chronic infestation with lice among certain footloose travelers is manifested by leathery, darkened skin—a condition known as **vagabond's disease**.

Fleas (order Siphonaptera) are perhaps the best known of all insect parasites. Nearly 1,500 species from birds and mammals have been described. Unlike lice, fleas are holometabolous, passing through egg, larval, pupal, and adult stages. Some species of fleas live their entire lives on their host, although eggs are generally deposited in the host's environment and larvae feed on local organic debris. Larvae of domestic fleas, including the rare human flea (*Pulex irritans*), feed on virtually any organic crumbs they find in the household furniture or carpet. Upon metamorphosis to the adult stage, fleas may undergo a quiescent period until an appropriate host appears. A number of serious disease organisms are transmitted by fleas, and at least 8 of the 60 or so species of fleas associated with household rodents are capable of acting as vectors for bubonic plague bacteria.

Other insect orders contain primarily free-living insects but include various families of parasitic or micropredatory forms, or groups in which the larval stage is parasitic but the adults are free-living. Most of these "parasites" do not live continuously on a host and have feeding behaviors that fall into a gray zone between true obligate parasitism and predation. Such insects are sometimes classed as intermittent parasites, or micropredators. Bedbugs (Hemiptera, Cimicidae), for example, comprise about 100 species of minute flattened insects that feed on the blood of birds and mammals. However, most live in the nest or sleeping area of their host, emerging only periodically to feed. The common human bedbugs (*Cimex lectularius* and *C. hemipterus*) hide in bedding, in cracks, in thatched roofs, or under rugs by day and feed on their host's blood at night. They are piercer-suckers, much like the sucking lice. Bedbugs are not known to transmit any human diseases, although when present in large numbers, they can be troublesome (in South America, as many as 8,500 bugs have been found in a single adobe house). Mosquitoes (family Culicidae), on the other hand, are vectors for a large number of disease-causing microorganisms, including *Plasmodium* (responsible for malaria), yellow fever, viral encephalitis, dengue, and lymphatic filariasis (with its gross symptom, elephantiasis, resulting from blockage of lymph ducts). Kissing bugs (Hemiptera, Reduviidae, Triatominae) also have a casual host relationship. They live in all kinds of environments but often inhabit the burrows or nests of mammals, especially rodents and armadillos, as well as birds and lizards. They feed on the blood of these and other vertebrates, including dogs, cats, and people. Their host specificity is low. Several species are vectors of mammalian trypanosomiasis (*Trypanosoma cruzi*, the causative agent of Chagas' disease). The tendency of

some species to bite on the face (where the skin is thin) has resulted in the common name, "kissing bugs."

In the dipteran family Calliphoridae, larvae are saprophagous, coprophagous, wound feeding, or parasitic. The parasitic species include among their hosts earthworms, locust egg cases, termite colonies, and nestling birds, and several species parasitize humans and domestic stock (e.g., *Cochliomyia americana*, the tropical American screwworm).

Many insect parasites of plants cause an abnormal growth of plant tissues, called a gall. Some fungi and nematodes also produce plant galls, but most are caused by mites and insects (especially hymenopterans and dipterans). Parasitic adults may bore into the host plant or, more commonly, deposit eggs in plant tissues, where they undergo larval development. The presence of the insect or its larva stimulates the plant tissues to grow rapidly, forming a gall. The adaptive significance (for insects) of galls remains unclear, but one popular theory is that their production interferes with the production of defensive chemicals by the plant, thus rendering gall tissues more palatable. A somewhat similar strategy is used by leaf miners, specialized larvae from several orders (e.g., Coleoptera, Diptera, Hymenoptera) that live entirely within the tissues of leaves, burrowing through and consuming the most digestible tissues.

An interesting predatory strategy is that of New Zealand glowworms (*Arachnocampa luminosa*), which live in caves and in bushes along riverbeds. These larvae of small flies produce a bright bioluminescence in the distal ends of the Malpighian tubules, which lights up the posterior end of the body. (The light peaks at 485 nm wavelength.) Each larva constructs a horizontal web from which up to 30 vertical "fishing lines" descend, each with a regularly spaced series of sticky droplets. Small invertebrates (e.g., flies, spiders, small beetles, hymenopterans) attracted to the light are caught by the fishing lines, hauled up, and eaten. Harvestmen (Opiliones), the main predators of glowworms, use the light to locate their prey!

Digestive system Like the guts of all arthropods, the long, usually straight hexapod gut is divisible into an ectodermal foregut, endodermal midgut, and ectodermal hindgut (Figure 22.26). Salivary glands are associated with one or several of the mouth appendages (Figure 22.27). The salivary secretions soften and lubricate solid food, and in some species they contain enzymes that initiate chemical digestion. In moth caterpillars and in larval bees and wasps, the salivary glands secrete silk used to make pupal cells.

All hexapods, as well as most other arthropods that consume solid foods, produce a **peritrophic membrane** in the midgut (Figure 22.26B). This sheet of thin chitinous material may line the midgut or pull free to envelop and coat the food particles as they pass through the gut. The peritrophic membrane serves to protect the delicate midgut epithelium from abrasion. It is permeated by microscopic pores that allow passage of enzymes and digested nutrients. In many species, production of this membrane also takes place in the hindgut, where it encapsulates the feces as discrete pellets.

Along with their vast range of feeding habits, insects have evolved a number of specialized digestive structures. The foregut is typically divided into a well-defined pharynx, esophagus, crop, and proventriculus (Figures 22.26 and 22.27). The pharynx is muscular, particularly in the sucking insects, in which

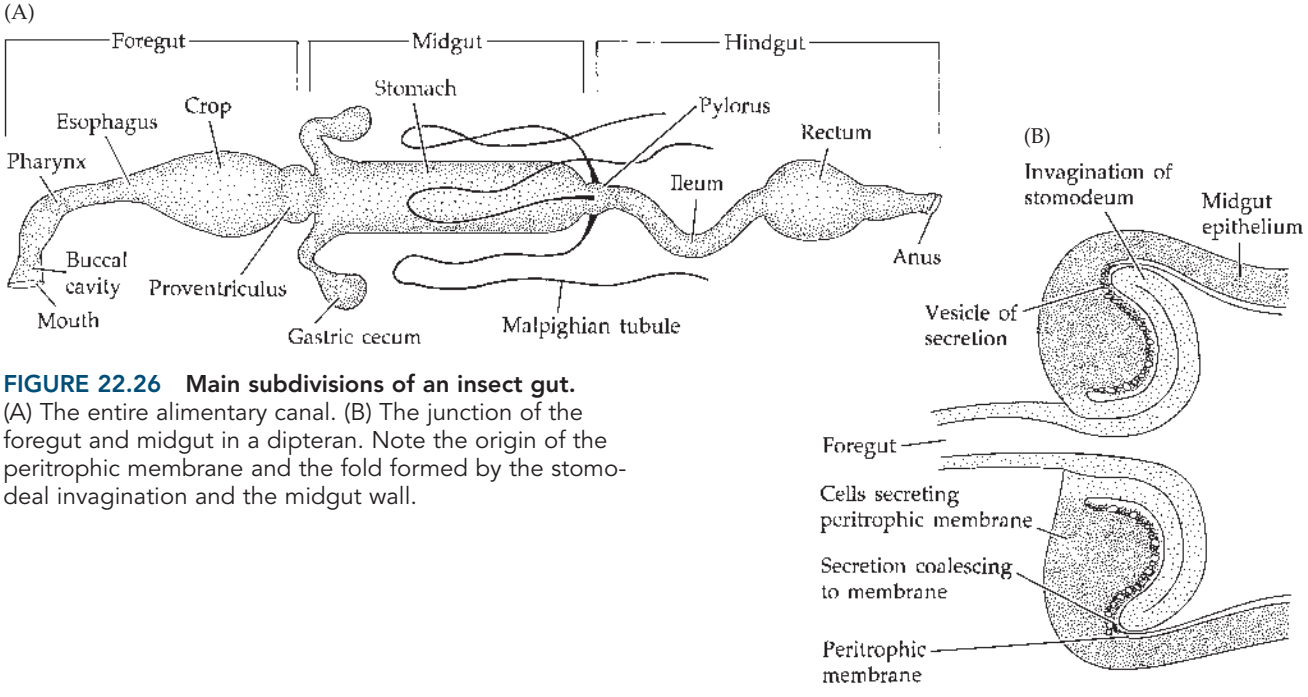

FIGURE 22.26 Main subdivisions of an insect gut. (A) The entire alimentary canal. (B) The junction of the foregut and midgut in a dipteran. Note the origin of the peritrophic membrane and the fold formed by the stomodeal invagination and the midgut wall.

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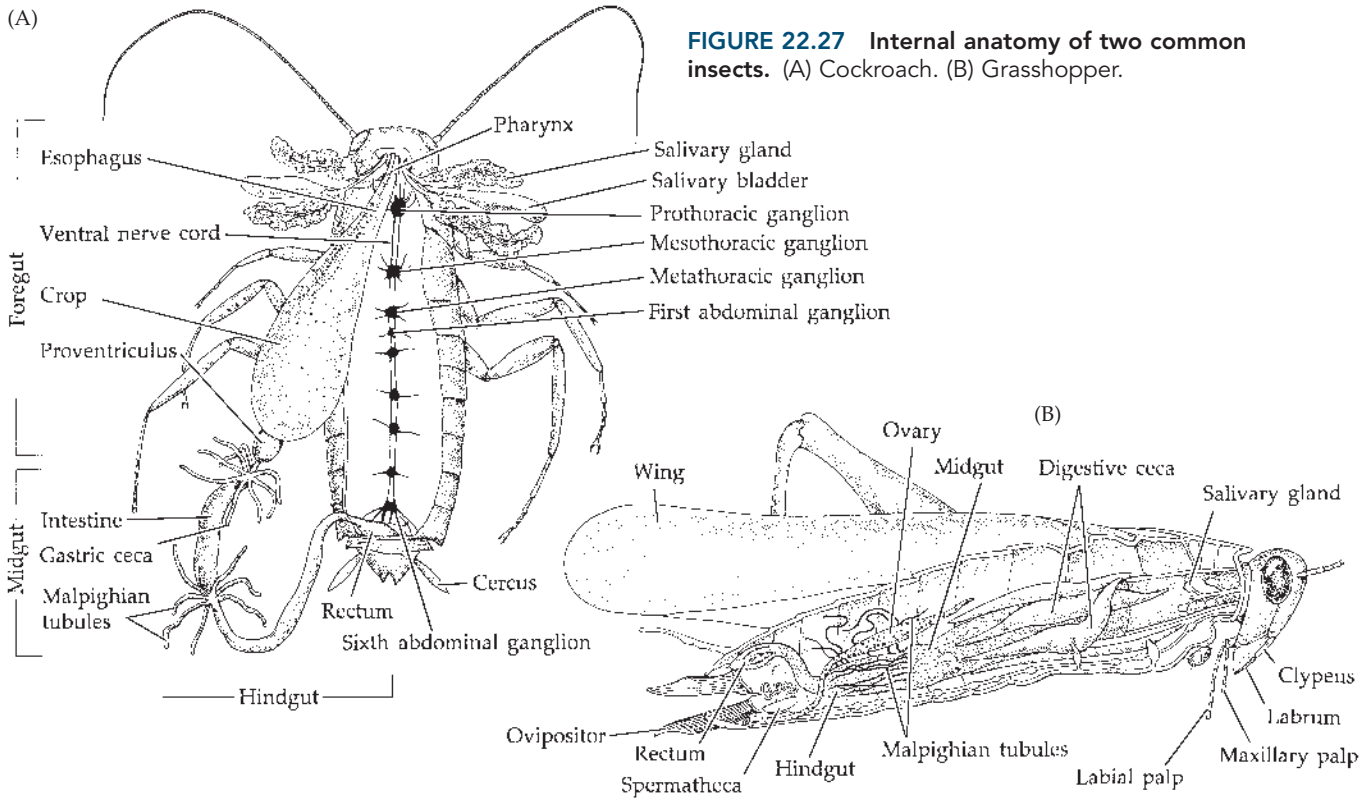

FIGURE 22.27 Internal anatomy of two common insects. (A) Cockroach. (B) Grasshopper.

it commonly forms a **pharyngeal pump**. The crop is a storage center whose walls are highly extensible in species that consume large but infrequent meals. The **proventriculus** regulates food passage into the midgut, either as a simple valve that strains the semifluid foods of sucking insects or as a grinding organ, called a gizzard or gastric mill, that masticates the chunks ingested by biting insects. Well-developed gastric mills have strong cuticular teeth and grinding surfaces that are gnashed together by powerful proventricular muscles.

The midgut (= stomach) of most insects bears gastric ceca that lie near the midgut-foregut junction and resemble those of crustaceans. These evaginations serve to increase the surface area available for digestion and absorption. In some cases the ceca also house mutualistic microorganisms (bacteria and protists). The insect hindgut serves primarily to regulate the composition of the feces and perhaps to absorb some nutrients. Digestion of cellulose by termites and certain wood-eating roaches is made possible by enzymes produced by protists and bacteria that inhabit the hindgut.

Clusters of fat cells create a **fat body** in the hemocoel of many insects, which is most conspicuous in the abdomen but also extends into the thorax and head. The fat body is an organ unique to the insects and is often likened to the vertebrate liver and the chloragogenous tissue in annelids. The fat body not only stores lipids, proteins, and carbohydrates, but also synthesizes proteins. Many insects do not feed during their adult life; instead, they rely on stored nutrients accumulated in the larval or juvenile stages and stored in the fat body.

Circulation and Gas Exchange

The hexapod circulatory system includes a dorsal tubular heart that pumps the hemocoelic fluid (blood) toward the head. The heart narrows anteriorly into a vessel-like aorta, from which blood enters the large hemocoelic chambers, through which it flows posteriorly, eventually returning to the pericardial sinus and then to the heart via paired lateral ostia (Figure 22.28). In most insects the heart extends through the first nine abdominal segments; the number of ostia is variable. Accessory pumping organs, or **pulsatile organs**, often occur at the bases of wings and of especially long appendages, such as the hindlegs of grasshoppers, to assist in circulation and maintenance of blood pressure.

The heart is a rather weak pumping organ, and blood is moved primarily by routine muscular activity of the body and appendages. Hence, circulation is slow and system pressure is relatively low. Like many arachnids, some hexapods use the hydraulic pressure of the hemocoelic system in lieu of extensor muscles. In this way, for example, butterflies and moths unroll their maxillary feeding tubes.

Many types of hemocytes (blood cells) have been reported from insects and several are apparently important in wound healing and clotting. Nutrients, wastes, and hormones can be efficiently carried by this system, but most insects do not have oxygen-transporting proteins in their blood. However, hemocyanin does occur in several hexapod groups, especially in embryonic stages or in hypoxic environments. Hemocyanin is apparently absent in Protura, Diplura, Ephemeroptera,

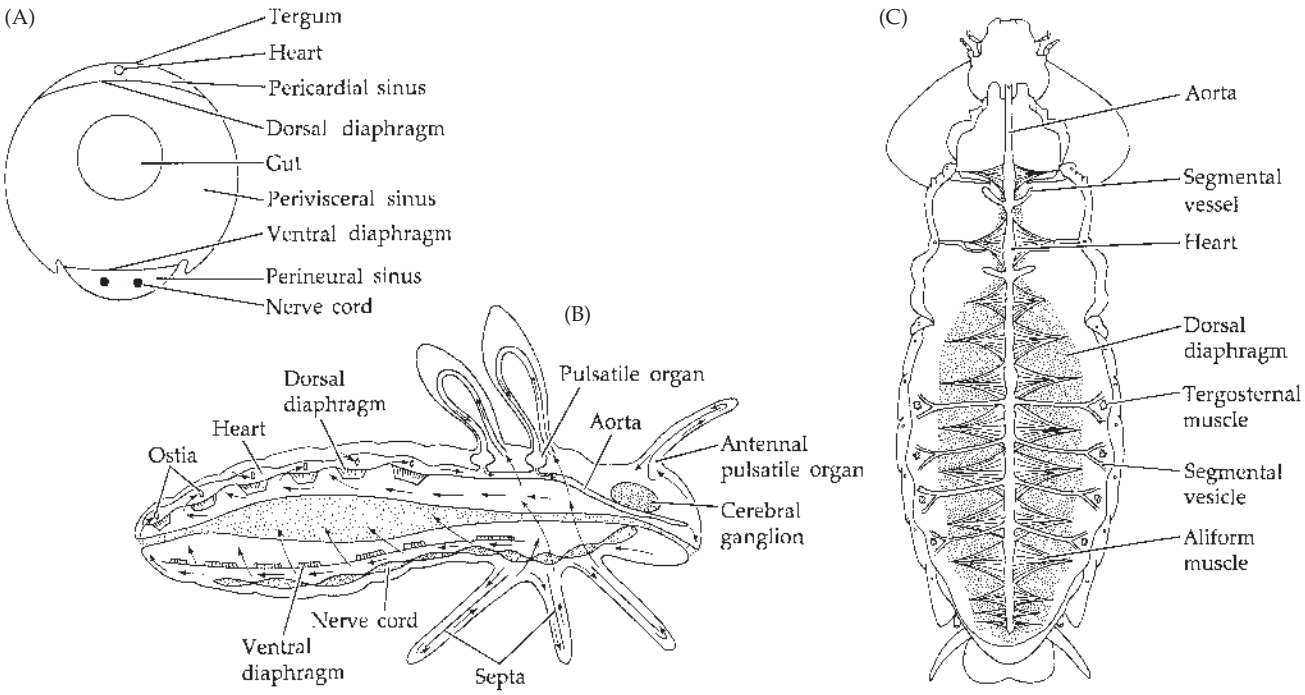

FIGURE 22.28 The circulatory system of insects. (A) An insect abdomen (cross section). Note the division of the hemocoel into three chambers (a dorsal pericardial sinus, a ventral perineural sinus, and a central perivisceral sinus). These chambers are separated by diaphragms lying on frontal planes. (B) Blood circulation in an insect with a fully developed circulatory system (longitudinal section). Arrows indicate the circulatory course. (C) A cockroach (ventral dissection). Note the dorsal and segmental vessels. The dorsal diaphragm and aliform (heart) muscles are continuous over the ventral wall of the heart and vessels, but they are omitted from the diagram for clarity. (B after V. B. Wigglesworth. 1972. *The Principles of Insect Physiology*. Springer, Dordrecht. https://link.springer.com/chapter/10.1007/978-94-009-5973-6_10)

Odonata, Hemiptera, and all holometabolous insect orders. The active lifestyles of these terrestrial animals require special structures to carry out the tasks of respiratory gas exchange and excretion. These structures are the tracheal system and the Malpighian tubules, described below.

Desiccation is one of the principal dangers faced by terrestrial invertebrates. Adaptations to terrestrial life always involve some degree of compromise between water loss and gas exchange with the atmosphere. Even though the general body surface of insects may be largely waterproof, the gas exchange surfaces cannot be.

In some minute hexapods, such as Collembola, gas exchange occurs by direct diffusion across the body surface. However, the vast majority of hexapods rely on a tracheal system (Figure 22.29). As explained in Chapter 20, **tracheae** are extensive tubular invaginations of the body wall, opening through the cuticle by pores called spiracles. Up to ten pairs of spiracles can occur on the pleural walls of the thorax and abdomen. Since tracheae are epidermal in origin, their linings are shed with each molt. The cuticular wall of each trachea is sclerotized and usually strengthened by rings or spiral thickenings called **taenidia**, which keep the tube from collapsing but allow for changes in length that may accompany body movements. The tracheae originating at one spiracle commonly anastomose with others to form branching networks penetrating most of the body. In some insects it appears that air is taken into the body through the thoracic spiracles and released through the abdominal spiracles, thus creating a flow-through system.

Each spiracle is usually recessed in an atrium, whose walls are lined with setae or spines (**trichomes**) that prevent dust, debris, and parasites from entering the tracheal tubes (Figure 22.29C). A muscular valve or other closing device is often present and is under control of internal partial pressures of O_2 and CO_2. In resting insects most of the spiracles are generally closed. Ventilation of the tracheal system is accomplished by simple diffusion gradients, as well as by pressure changes induced by the animal itself. Almost any movement of the body or gut causes air to move in and out of some tracheae. Telescopic elongation of the abdomen is used by some insects to move air in and out of the tracheal tubes. Many insects have expanded tracheal regions called tracheal pouches, which function as sacs for air storage.

Because the blood of hexapods does not transport oxygen, the tracheae must extend directly to each organ of the body, where their ends actually penetrate the tissues. Oxygen and CO_2 thus are exchanged directly

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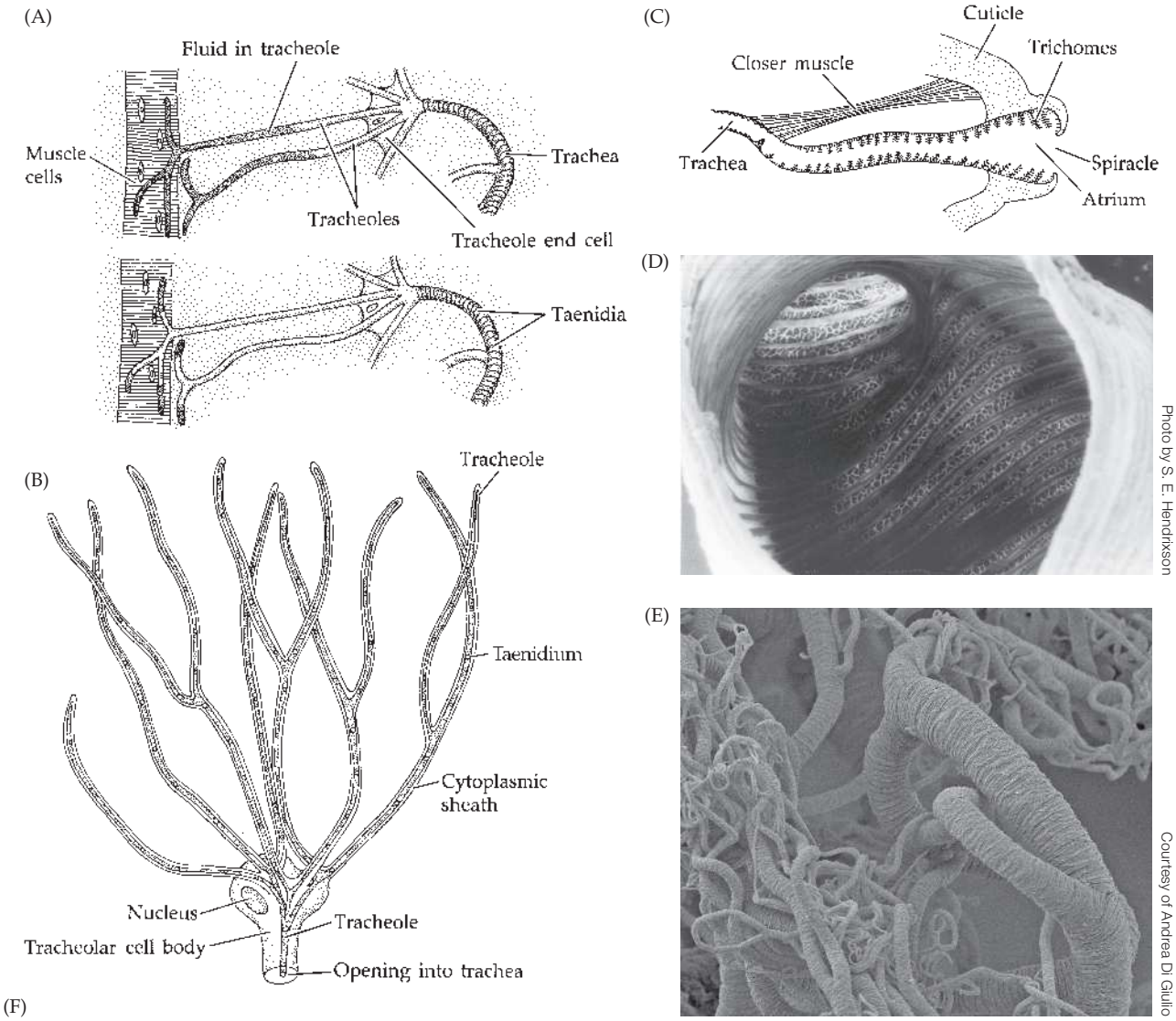

FIGURE 22.29 The tracheal system of insects. (A) Tracheoles and flight muscle cells. Note the region where the tracheoles become functionally intracellular within the muscle fibers. The upper figure depicts a situation in which the muscle cells are well oxygenated, oxygen demand is low, and fluid accumulates in the tracheoles. The lower figure depicts muscle cells that are oxygen deficient. Decreased fluid volumes in the tracheoles allow the tissues increased access to oxygen. (B) A tracheole end cell. The taenidia are rings that serve to keep the lumen of the tracheoles open. (C) A generalized insect spiracle (longitudinal section). Note the dust-catching spines (trichomes) within the atrium. (D) View inside a prothoracic trachea of the honeybee, *Apis mellifera*. (E) SEM of trachea and tracheoles of a carabid beetle. (F) Dragonfly nymph molting into an adult. Note the long white tracheae being pulled out of the exuvia by the emerging adult.

between cells and the small ends of the tracheae, the tracheoles. In the case of flight muscles, where oxygen demand is high, the tracheal tubes invade the muscle fibers themselves. **Tracheoles**, the innermost parts of the tracheal system, are thin-walled, fluid-filled channels that end as a single cell, the tracheole end cell (= tracheolar cell) (Figure 22.29). The tracheoles penetrate every organ in the body. Unlike tracheae, tracheoles are not shed during ecdysis. The tracheoles are so minute (0.2–1.0 μm) that ventilation is impossible, and gas transport here relies on aqueous diffusion. This ultimate constraint on the rate of gas exchange may be the primary reason terrestrial arthropods never achieved extremely large sizes.

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FIGURE 22.30 Aquatic nymph of a mayfly, *Paraleptophlebia* (Ephemeroptera), with lateral abdominal gills.

In aquatic insects the spiracles are usually nonfunctional, and gases simply diffuse across the body wall directly to the tracheae. A few species retain functional spiracles; they hold an air bubble over each opening, through which oxygen from the surrounding water diffuses. The air bubbles are held in place by secreted waxes and by patches of hydrophobic hairs in densities that may exceed 2 million per square millimeter. Most aquatic insects, particularly larval stages, have **gills**—external projections of the body wall that are covered by thin, unsclerotized cuticle and contain blood, tracheae, or air bubbles (Figure 22.30). The gills contain channels that lead to the main tracheal system. In some aquatic insects, such as dragonfly nymphs, the rectum bears tiny branched tubules called **rectal accessory gills**. By pumping water in and out of the anus, these insects exchange gases across the increased surface area of the thin gut wall. There are analogous examples of hindgut respiratory irrigation in other, unrelated invertebrate groups (e.g., thalassematids, holothurians).

Excretion and Osmoregulation

The problem of water conservation and the nature of the circulatory and gas exchange systems in terrestrial arthropods necessitated the evolution of entirely new structures to remove metabolic wastes. Like the gas exchange surfaces, the excretory system is a site of potential water loss because nitrogenous wastes initially occur in a dissolved state. These problems are compounded in small terrestrial organisms, such as many hexapods, because of their large surface-area-to-volume ratios. And water loss problems are even more severe in flying insects because flight is probably the most metabolically demanding of all locomotor activities.

In most terrestrial arthropods, the solution to these problems is Malpighian tubules. In the Hexapoda, these unbranched outgrowths of the gut arise near the junction of the midgut and hindgut (Figures 22.26, 22.27, and 22.31). Their blind distal ends extend into the hemocoel and lie among various organs and tissues. Up to several hundred Malpighian tubules may be present.

In the absence of sufficient blood pressure for typical excretory filtration, hexapods use osmotic pressure to achieve the same result. Various ions, especially potassium ions, are actively transported across the Malpighian tubule epithelium from the blood into the tubule lumen (Figure 22.31). The osmotic gradient maintained by this ion transport mechanism enables water and solutes to move from the body cavity into the tubules, and thence into the gut. Water and other metabolically valuable materials are selectively reabsorbed into the blood across the wall of the hindgut, while the Malpighian filtrate left behind is mixed with the other gut contents. Reabsorption of water, amino acids, salts, and other nutrients may be enhanced by the action of special cells in thickened regions called rectal glands. The soluble potassium urate from the Malpighian tubules has, at this point in the gut, been precipitated out as solid uric acid as a result of the low pH of the hindgut (pH 4–5). Uric acid crystals cannot be reabsorbed into the blood; hence they pass out of the gut with the feces. Insects also possess special cells called nephrocytes or pericardial cells that move about in certain areas of the hemocoel, engulfing and digesting particulate or complex waste products.

The hexapod cuticle is sclerotized or tanned to various degrees, adding a small measure of waterproofing. Some insects have mineralized cuticular areas, and one

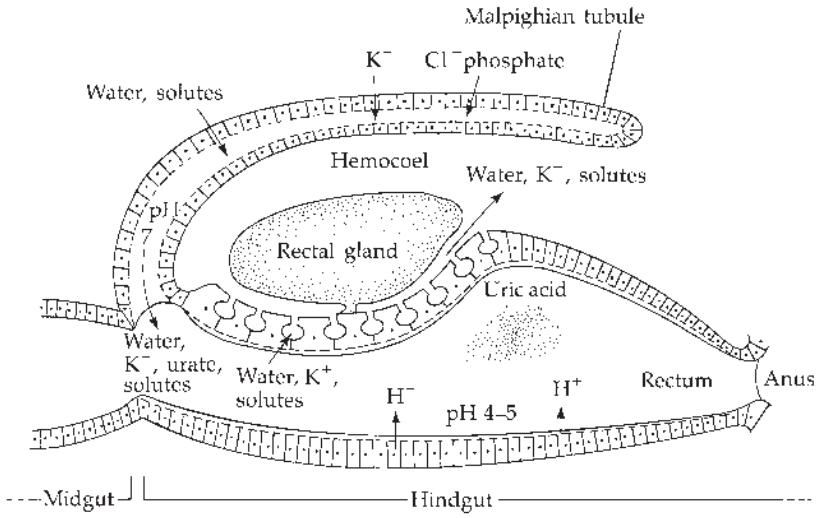

FIGURE 22.31 A single Malpighian tubule opening into the hindgut at its junction with the midgut. Arrows indicate the flow of materials.

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leafcutter ant has been shown to be fully calcified (*Acromyrmex echinatior*). But more importantly, a waxy layer occurs within the epicuticle, which greatly increases resistance to desiccation and frees insects to fully exploit dry environments. In many terrestrial arthropods (including primitive insects) an eversible coxal sac (not to be confused with the coxal glands of arachnids) projects from the body wall near the base of each leg. It is thought that the coxal sacs assist in maintaining body hydration by taking up water from the environment (e.g., dewdrops). Many insects collect environmental water by various other devices. Some desert beetles (Tenebrionidae) collect atmospheric water by "standing on their heads" and holding their bodies up to the moving air so that humidity can condense on the abdomen and be channeled to the mouth for consumption.

Insects that inhabit desert environments have a much greater tolerance of high temperatures and body water loss than do insects in mesic environments, and they are particularly good at water conservation and producing insoluble nitrogenous waste products. They also have behavioral traits, such as nocturnal activity cycles and dormancy periods that enhance water conservation. Upper lethal temperatures for desert species commonly range to 50°C. The spiracles are often covered by setae or depressed below the cuticular surface. Many xeric insects also undergo periods of dormancy (i.e., diapause or aestivation) during some stage of the life cycle, characterized by a lowering of the basal metabolic rate and cessation of movement, which allow them to withstand prolonged periods of temperature and moisture extremes. Some even utilize evaporative cooling to reduce body temperatures. The long-chain hydrocarbons that waterproof the epicuticle also are more abundant in xeric insects.

Nervous System and Sense Organs

The hexapod nervous system conforms to the basic arthropod plan described in Chapter 20 (Figures 22.32 and 22.33). The two ventral nerve cords, as well as the segmental ganglia, are often largely fused. In dipterans, for example, even the three thoracic ganglia are fused into a single mass. The largest number of free ganglia occurs in the primitive wingless insects, which have as many as eight unfused abdominal ganglia. Giant fibers have also been reported from several insect orders.

Like the "brains" of other arthropods, the paired cerebral ganglia of insects comprise three distinct regions: the protocerebrum (which innervates the eyes), the deutocerebrum (innervates the antennae), and the tritocerebrum (which does not innervate any appendages and thus was called the intercalary segment). The subesophageal ganglion is composed of the fused ganglia of the fourth, fifth, and perhaps the sixth head segments and innervates the mouthparts, salivary glands, and some other local musculature.

Insects possess a hypocerebral ganglion between the cerebral ganglion and the foregut. Associated with this ganglion are two pairs of glandular bodies called the **corpora cardiaca** and the **corpora allata** (Figure 22.33). These two organs work in concert with the prothoracic glands and certain neurosecretory cells in the protocerebrum. The whole complex is a major endocrine center that regulates growth, metamorphosis, molting, and other functions (see Chapter 20).

Hexapods typically possess simple ocelli in the larval, juvenile, and often adult stages. When present in adults, they usually form a triad or a pair on the anterodorsal surface of the head. The compound eyes are well developed, resembling those of Crustacea; they are image-forming eyes. Most adult insects have a pair of compound eyes (Figure 22.34), which bulge out to some extent, giving these animals a wide field of vision in almost all directions. Compound eyes are greatly reduced or absent in parasitic groups and in many cave-dwelling forms. The general anatomy of the arthropod compound eye was described in Chapter 20, but several distinct structural trends are found in hexapod eyes, as we describe here.

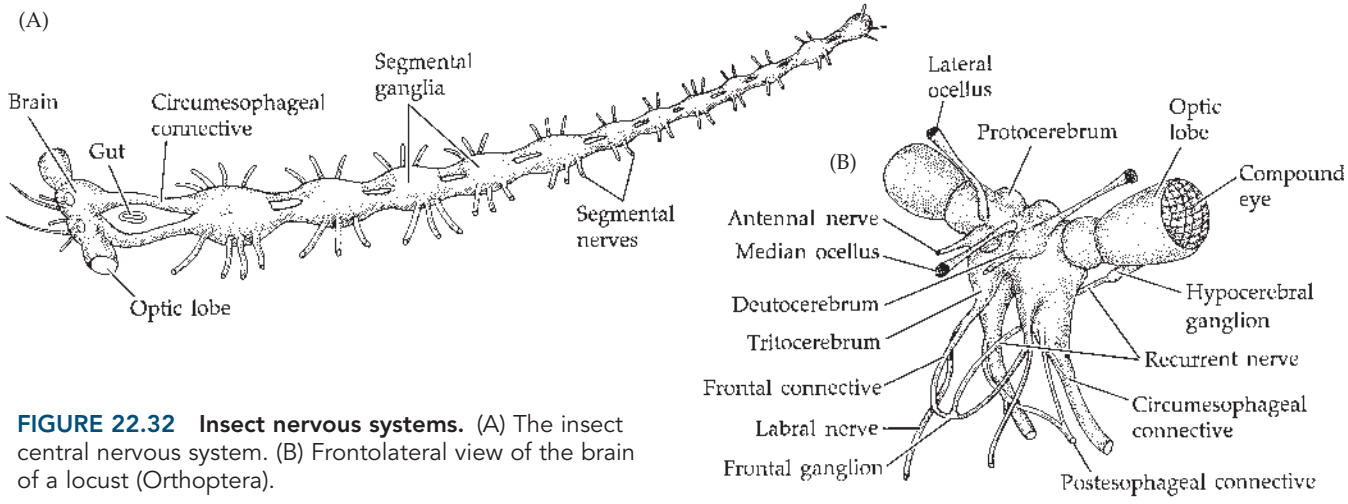


FIGURE 22.32 Insect nervous systems. (A) The insect central nervous system. (B) Frontolateral view of the brain of a locust (Orthoptera).

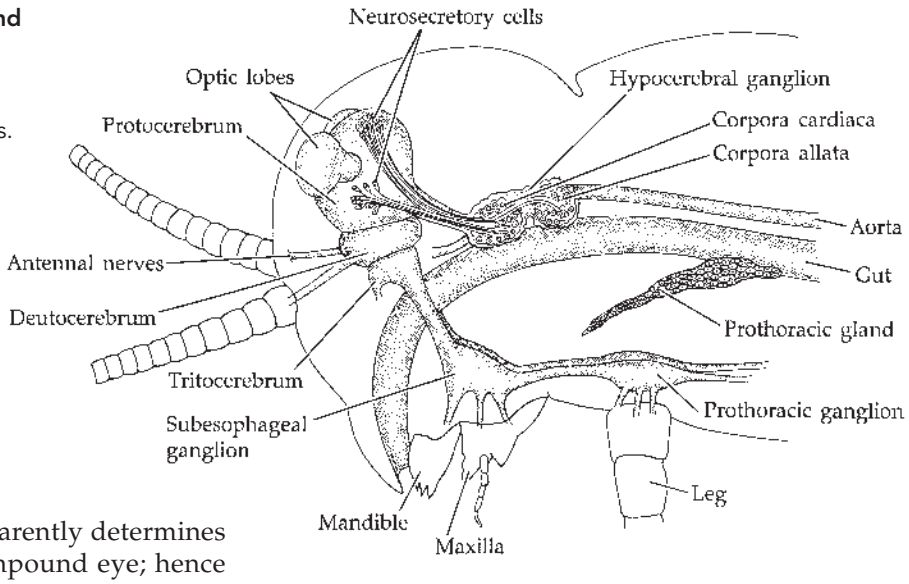
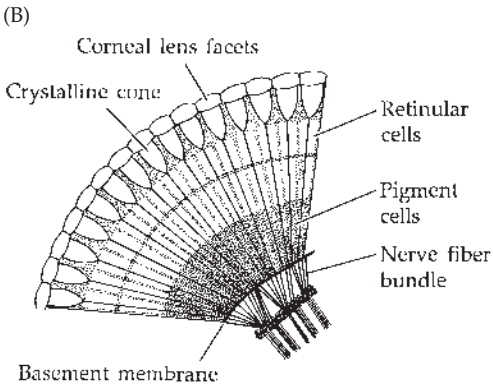


FIGURE 22.33 Endocrine organs and central nervous system in the head and thorax of a generalized insect. These organs all play roles in the control of molting and metamorphosis.

The number of ommatidia apparently determines the overall visual acuity of a compound eye; hence large eyes are typically found on active, predatory insects such as dragonflies and damselflies (order Odonata), which may have over 10,000 ommatidia in each eye. On the other hand, workers of some ant species have but a single ommatidium per eye (ants live in a world of chemical communication)! Similarly, larger facets capture more light and are typical of nocturnal insects. In all cases, a single ommatidium consists of two functional elements: an outer light-gathering part composed of a lens and a crystalline cone, and an inner sensory part composed of a rhabdome and sensory cells (Figure 22.34C).

In some insects the outer surface of the cornea (lens) is covered with minute conical tubercles about 0.2 μm tall and arranged in a hexagonal pattern. It is thought that these projections decrease reflection from the surface of the lens, thus increasing the proportion of light transmitted through the facet. Insect eyes in which the crystalline cone is present are called **eucone eyes** (Figure 22.34B). Immediately behind the crystalline cone (in eucone eyes) are the elongate sensory neurons, or retinular cells. Primitively, each ommatidium probably contained eight retinular cells arising from three successive divisions of a single cell. This number is found in some insects today, but in most it is reduced to six or seven, with the other one or two persisting as short basal cells in the proximal region of each ommatidium. Arising from each retinular cell is a neuronal axon that passes out through the basement membrane at the back of the eye into the optic lobe. There is no true optic nerve in insects; the eyes connect

Courtesy of David McIntyre



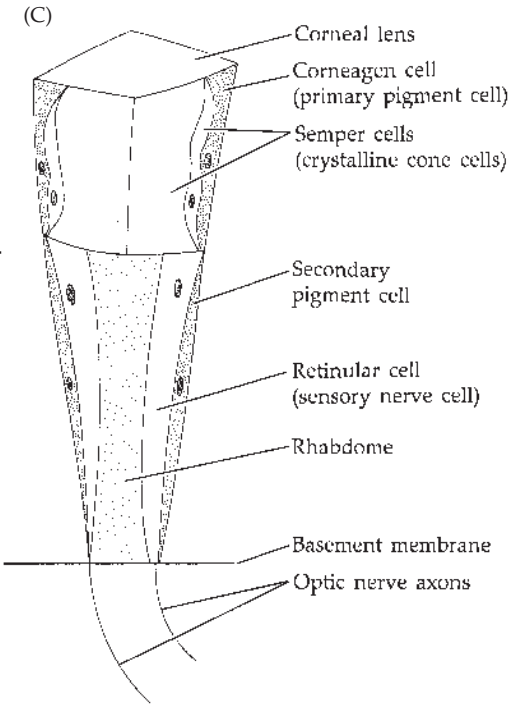


FIGURE 22.34 Compound eyes of insects. (A) Close-up of the compound eyes of a tachinid fly (Diptera) with many ommatidia. (B) A generalized insect compound eye (cross section). (C) A single ommatidium from a eucone compound eye.

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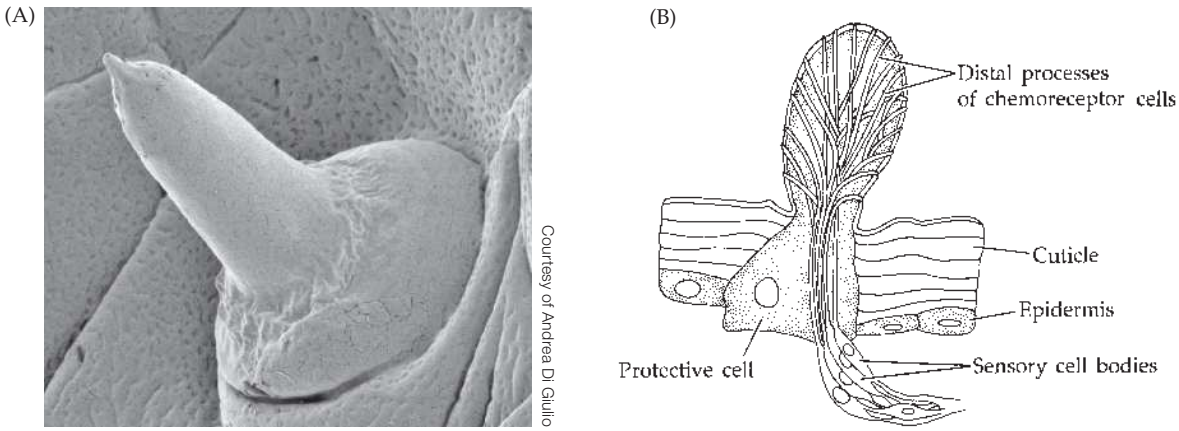
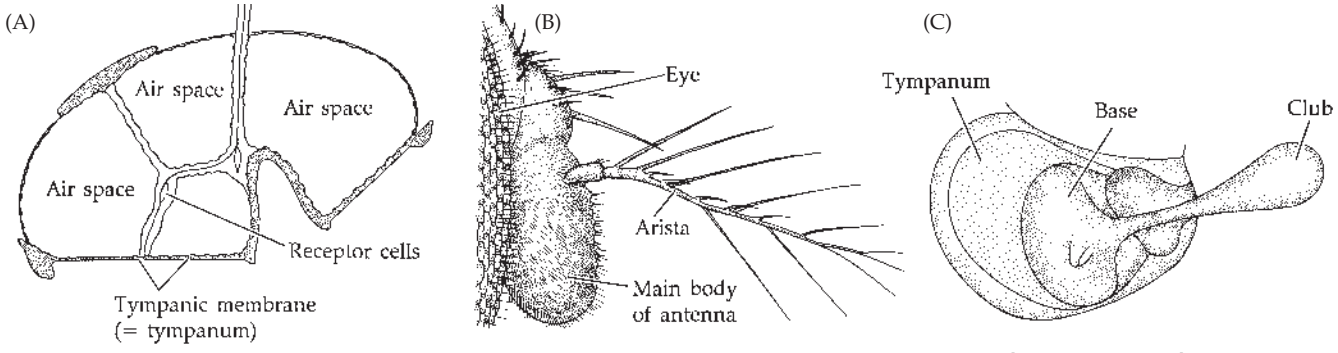


FIGURE 22.35 Chemosensory peg organs. (A) SEM of a peg organ from an antenna of a beetle. (B) Diagram of a peg organ in cross section from the antenna of a grasshopper.

directly with the optic lobe of the brain. The rhabdomeres consist of tightly packed microvilli that are about 50 nm in diameter and hexagonal in cross section. The retinular cells are surrounded by 12 to 18 secondary pigment cells, which isolate each ommatidium from its neighbors.

The general body surface of hexapods, like that of other arthropods, bears a great variety of microscopic sensory setae, known collectively as **sensilla** (sing., sensillum). The incredible diversity of these cuticular surface structures has only begun to be explored, primarily by scanning electron microscopy. Sensilla are most heavily concentrated on the antennae, mouthparts, and legs. Most appear to be tactile or chemosensory. Club-shaped or peg-shaped chemosensory setae, usually called **peg organs** and resembling the aesthetascs of crustaceans, are particularly common on the antennae of hexapods (Figure 22.35).

Insects have internal proprioceptors called **chordotonal organs**. These structures stretch across joints and monitor the movement and position of various body parts. Phonoreceptors also occur in most insect orders. These structures may be simple modified body or appendage setae, or antennae, or complex structures called **tympanic organs** (Figure 22.36). Tympanic organs generally develop from the fusion of parts of a tracheal dilation and the body wall, which form a thin tympanic membrane (= tympanum). Receptor cells in an



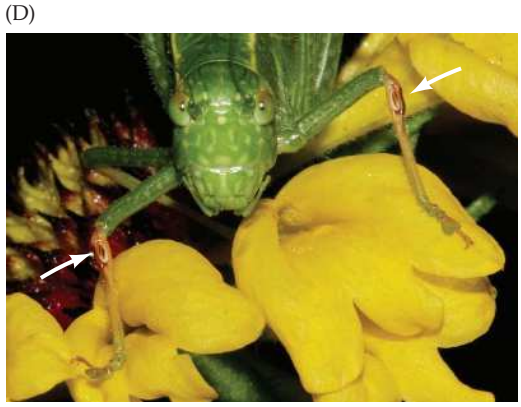


FIGURE 22.36 Insect "ears": insect auditory organs (phonoreceptors) differ widely in their anatomy and location. (A) The "ear" of noctuid moths (Lepidoptera) is a pressure receiver used to detect the ultrasonic cries of hunting bats. It is similar to most insect "ears" in comprising a tympanic membrane backed by a tracheal air space. Two receptor cells attach to the tympanum. (B) In *Drosophila* (Diptera), a feathery seta called an arista arises on the third antennal segment. The arista detects air movements, thus responding to sound through interaction with vibrating air particles. It is used to detect the calling song of the species. (C) In the "ear" of a water boatman (Hemiptera), the tympanum is covered by the base of a club-shaped cuticular body that protrudes outside the body. The club performs rocking movements that allow some frequency analysis of the songs of other water boatmen. (D) Tympani (arrows) on the tibiae of katydid forelegs. (C after J. Prager. 1976. *J Comp Physiol* 110: 33–50. https://link.springer.com/article/10.1007/BF00656780)

underlying air sac, or attached directly to the tympanic membrane, respond to vibrations in much the same fashion as they do in the cochlea of the human inner ear. Many insects can discriminate among different sound frequencies, but others may be tone-deaf. Tympanic organs may occur on the abdomen, the thorax, or the forelegs. Several insects that are prey to bats have the ability to hear the high frequencies of bat echolocation devices, and they have evolved flight behaviors to avoid these flying mammals. For example, some moths, when they hear a bat's echolocation (generally above the range of human ears), will fold their wings and suddenly drop groundward as an evasive maneuver. Praying mantises, whose sonar detection device is buried in a groove on the ventral side of the abdomen, throw out the raptorial forelimbs and elevate the abdomen. These movements cause the insect to "stall" and go into a steep roll, which it pulls out of at the last minute with a "power dive" that effectively avoids bat predators.

Sound communication in insects, like light communication in fireflies (and some ostracods), is a species-specific means of mate communication. Several insect groups (e.g., some orthopterans, coleopterans, dipterans, and hemipterans) possess sound-producing structures. Male flies of the genus *Drosophila* create species-specific mating songs by rapidly vibrating the wings or abdomen. These "love songs" attract conspecific females for copulation. It has been demonstrated that the rhythm of the male's song is encoded in genes inherited from his mother, on the X chromosome, whereas the song's "pulse interval" is controlled by genes on autosomal chromosomes.

Cicadas may possess the most complex sound-producing organs in the animal kingdom (Figure 22.37). The ventral metathoracic region of male cicadas bears two large plates, or opercula, that cover a complex system of vibratory membranes and resonating chambers. One membrane, the tymbal, is set vibrating by special muscles, and other membranes in the resonating chambers amplify the tymbal's vibrations. The sound leaves the cicada's body through the metathoracic spiracle.

Numerous families of beetles and bugs utilize water surfaces as a substratum both for locomotion and for communication by waves or ripples. Such insects produce a signal with simultaneous vertical oscillations of one or more pairs of legs and sometimes also with distinct vertical body motions. The wave patterns produced are species-specific. Potential prey trapped on a surface film may also be recognized in this fashion, just as spiders recognize prey by web vibrations. Limited data suggest that the receptor organs for ripple communication are either specialized sensilla on the legs or special proprioceptors between joints of the legs or antennae, perhaps similar to the tarsal organs of scorpions.

A number of insects are bioluminescent, the most familiar being beetles of the family Lampyridae, known as lightning bugs or fireflies. In the tropics, where they are especially abundant, fireflies are sometimes kept in containers and used as natural flashlights, and women may wrap them in gauze bags worn as glowing hair ornaments. The light of luminescent insects ranges from green through red and orange, depending on the species and the precise chemical nature of the luciferin-luciferase system involved. Light-producing organs are typically composed of clusters of light-producing cells, or **photocytes**, backed by a layer of reflecting cells and covered with a thin, transparent epidermis. The photocytes are richly supplied with tracheae, oxygen being necessary for the chemical reaction. Each species of firefly, and of most other glowing insects, has a distinct flash pattern, or code, to facilitate mate recognition and communication.

One of the most sophisticated communication behaviors among insects may be the famous honeybee "waggle dance." Each day forager bees leave their colony to locate new food sources (e.g., fresh flower blooms). They fly meandering in search forays until a good source is located. Then they return to the hive along a straight flight path (a "bee line"), possibly using memorized ground structure for guidance; while doing so, they are thought to imprint a navigational "map" from the colony to the food source. Most behaviorists believe that this information is communicated to hive mates in a complex tail-wagging dance that allows other bees from the hive to fly directly to the new feeding ground. The forager bee also carries food odors

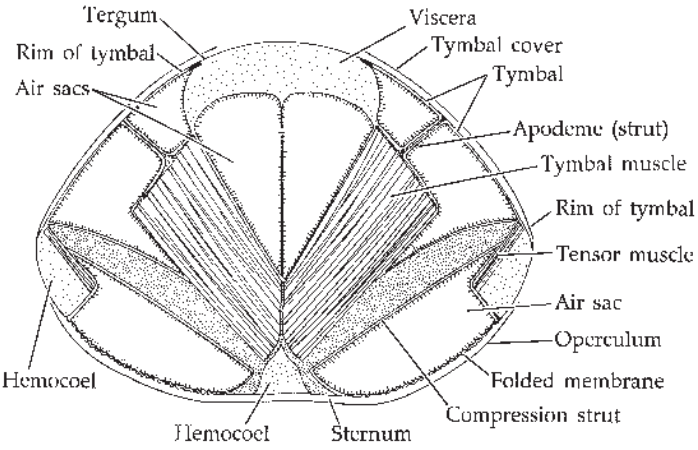


FIGURE 22.37 Sound production structure in cicadas (Hemiptera) from the first abdominal segment (section). Sound is produced by buckling of the tymbal, a thin disc of cuticle. The tymbal muscle is connected to the tymbal by a strut. Contraction of this muscle causes the tymbal to buckle inward, thereby producing a click that is amplified by resonance in the underlying air sacs. On relaxation, the elasticity of the muscle causes the tymbal to buckle out again. On the underside of this abdominal segment, a folded membrane can be stretched to tune the air sacs to the resonant frequency of the tymbal.

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(nectar samples), pollen, and various other odors clinging to the hairs on her body. She can also mark the food source with a pheromone produced in a special gland, called the **Nasanov gland**. All of these clues help her hive mates find the new food source. Karl von Frisch was the first person to document all these attributes of bee foraging early in the twentieth century.

A large body of research on bee navigation has accumulated since the pioneering "dancing bee studies" of von Frisch. We now know that honeybees (and solitary bees) have outstanding vision. Much of the bee's daily activity, including navigation and flower recognition, relies strongly on ultraviolet vision. Bees appear to utilize a hierarchical series of flight orientation mechanisms; when the primary mechanism is blocked, a bee can switch to a secondary system. The primary navigation system utilizes the pattern of polarized ultraviolet sunlight in the sky. This pattern depends on the location of the sun as determined by two coordinates, the azimuth and the elevation. Bees and many other animals that orient to the sun have a built-in ability to compensate for both hourly changes (elevation) and seasonal changes (azimuth) in the sun's position with time. On cloudy days, when the sun's light is largely depolarized, bees cannot rely on their ultraviolet celestial navigation mechanism and thus may switch to their second-order navigational system: navigation by landmarks (foliage, rocks, and so on) that were imprinted during the most recent flight to the food source. Limited evidence suggests that some form of tertiary backup system may also exist.

Thus, if the honeybee dance model is correct,[7] honeybees must simultaneously process information concerning time, the direction of flight relative to the sun's azimuth, the movement of the sun, the distance flown, and local landmarks (not to mention complications due to other factors, such as crosswinds) and in doing so reconstruct a straight-line heading to inform their hive mates. If recent evidence is correct, bees (like homing pigeons) may also detect Earth's magnetic fields with iron compounds (magnetite) located in their abdomens. Bands of cells in each abdominal segment of the honeybee contain iron-rich granules, and nerve branches from each segmental ganglion appear to innervate these tissues.[8]

In some insects the ocelli are the principal navigation receptors. Some locusts and dragonflies and at least one ant species utilize the ocelli to read compass information from the blue sky. As in bees, the pattern of polarized light in the sky seems to be the main compass cue. In some species, both ocelli and compound eyes may function in this fashion. Many (probably most) insects also see ultraviolet light.

Perhaps the most famous insect navigators are North America's monarch butterflies (*Danaus plexippus*). Each autumn, monarchs migrate up to 4,000 km from breeding grounds in the eastern United States and Canada to overwintering sites in the mountains of Michoacán, in central Mexico (one of two major migratory populations in North America, both of which are threatened by habitat loss). They make this remarkable journey by orienting with a sun compass, using the sun's changing azimuth (and knowledge of the relative time of day) to direct their movements. On cloudy days, when a precise solar azimuth is unobtainable, monarchs still manage to orient towards the south-southwest, suggesting that they also have a backup mechanism of orientation, such as a geomagnetic compass. Monarchs are one of a small group of animal species for which a sun compass orientation mechanism has been shown to exist. Not all monarchs migrate, and many resident year-round breeding populations are established throughout the Americas. Less well understood are the migrations of dragonflies, some of which exceed that of monarchs in distance traveled.

Many insects release noxious quinone compounds to repel attacks. Perhaps best known in this regard are certain Tenebrionidae, many of which stand on their heads to do so. But the champions of this chemical warfare strategy are definitely the bombardier beetles, members of the carabid subfamilies Brachininae and Paussinae, which expel quinone compounds at temperatures reaching 100°C (Figure 22.7C).

Reproduction and Development

Reproduction Hexapods are dioecious, and most are oviparous. A few insects are ovoviviparous, and many can reproduce parthenogenetically. Most insects rely on direct copulation and insemination. Reproductively mature insects are termed adults or **imagos**. Female imagos have one pair of ovaries, formed of clusters of tubular ovarioles (Figure 22.38A). The oviducts unite as a common duct before entering a genital chamber. Seminal receptacles (spermathecae) and accessory glands also empty into the genital chamber. The genital chamber opens, via a short **copulatory bursa** (= vagina), on the sternum of the eighth, or occasionally the seventh or ninth, abdominal segment. The male reproductive system is similar, with a pair of testes, each formed by a number of sperm tubes (Figure 22.38B). Paired sperm ducts dilate into seminal vesicles (where sperm are stored) and then unite as a single ejaculatory duct. Near this duct, accessory glands discharge seminal fluids into the reproductive tract. The lower end of the ejaculatory

[7] The honeybee dance hypothesis is not without its detractors, and some workers doubt its existence altogether; see the General References section for this chapter for a glimpse at the history of the honeybee dance controversy.

[8] Many animals possess magnetotactic capabilities, including some molluscs, hornets, salmon, tuna, turtles, salamanders, homing pigeons, cetaceans, and humans. Magnetotactic bacteria also exist, which swim to the north in the Northern Hemisphere, to the south in the Southern Hemisphere, and in both directions at the geomagnetic equator. In all these cases, iron oxide crystals in the form of magnetite have been shown to underlie the primary detection devices. However, in honeybees, the iron-containing structures are trophocytes that contain paramagnetic magnetite. These magnetotactic trophocytes surround each abdominal segment and are innervated by the central nervous system.

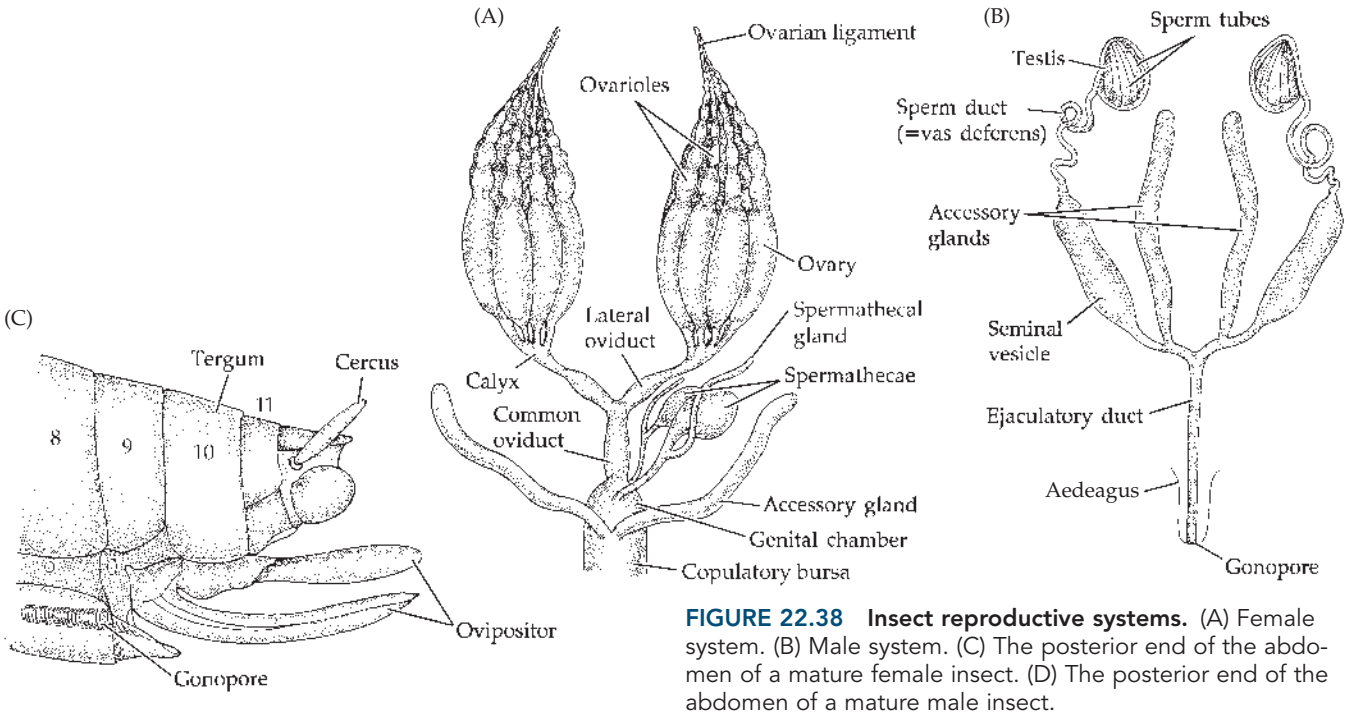

FIGURE 22.38 Insect reproductive systems. (A) Female system. (B) Male system. (C) The posterior end of the abdomen of a mature female insect. (D) The posterior end of the abdomen of a mature male insect.

duct is housed within a penis, which extends posteroventrally from the ninth abdominal sternite.

Courtship behaviors in insects are extremely diverse and often quite elaborate, and each species has its own recognition methods. Courtship may consist of simple chemical or visual attraction, but more typically it involves pheromone release, followed by a variety of displays, tactile stimulation, songs, flashing lights, or other rituals that may last for hours. The subject of insect courtship is a large and fascinating study of its own. Although the field of pheromone biology is still in its infancy, sexual attractant or aggregation pheromones have been identified from about 500 different insect species (about half of which are synthesized and sold commercially for pest control purposes).

Most insects transfer sperm directly as the male inserts either his **aedeagus** (Figure 22.38B,D) or a gonopod into the genital chamber of the female. Special abdominal claspers, or other articulated cuticular structures on the male, often augment his copulatory grip. Such morphological modifications are species specific and thus serve as valuable recognition characters, for both insect mates and insect taxonomists. Copulation often takes place in midflight. In some of the primitive wingless insects, and in the Odonata, sperm transfer is indirect. In these cases, a male may deposit his sperm on specialized regions of his body to be picked up by the female; or he may simply leave the sperm on the ground, where they are found and taken up by females. In bedbugs (order Hemiptera, family Cimicidae) males use the swollen penis to pierce a special region of the female's body wall; sperm are then deposited directly into an internal organ (**the organ of Berlese**). From there they migrate to the ovaries, where fertilization takes place as eggs are released.

Sperm may be suspended in an accessory gland secretion, or, more commonly, the secretion hardens around the sperm to produce a spermatophore. Females of many insect species store large quantities of sperm within the spermathecae. In some cases sperm from a single mating is sufficient to fertilize a female's eggs for her entire reproductive lifetime, which may last a few days to several years.

Insect eggs are protected by a thick membrane (the chorion) produced within the ovary. Fertilization occurs as the eggs pass through the oviduct to be deposited. Accessory glands contribute adhesives or secretions that harden over the zygotes. In many species, cuticular extensions around the gonopore of the female form an **ovipositor** (Figure 22.38C), with which she places the eggs in a brooding site that will afford suitable conditions for the young once they hatch (such as in a shallow underground chamber, in a plant stem, or within the body of a host insect). Although 50–100 eggs are usually laid at a time, as few as one and as many as several thousand are deposited by some species. The volume of eggs scales up to eight

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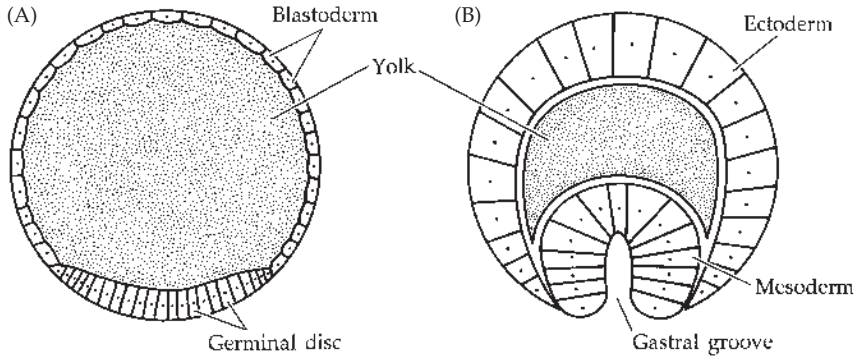

FIGURE 22.39 Early stages of insect development. (A) The blastoderm (blastula) of a generalized insect, subsequent to cytokinesis (cross section). Note the thickened germinal disc. (B) An early gastrula of a honeybee (cross section). Note the gastral groove and the proliferation of mesoderm.

orders of magnitude across insect groups, the smallest being those of the parasitoid wasp *Platygaster vernalis* (volume = 7×10^{-7} mm^3) and the largest those of the earth-boring beetle *Bolboleaus hiaticollis* (volume = 5×10^2 mm^3). Some insects, such as cockroaches, enclose several eggs at a time in a protective egg case.

Parthenogenesis is common in a variety of insect groups. It is used as an alternative form of reproduction seasonally by a number of insect taxa, particularly those living in unstable environments. In the Hymenoptera (bees, wasps, ants), it is also used as a mechanism for sex determination. In these cases, diploid fertilized eggs become females, and haploid unfertilized eggs develop into males. Infections by the bacterium *Wolbachia*, a frequent parasite of arthropod reproductive systems, are known to affect reproduction in many insect species. In some cases, infections result in infertility, whereas in others they transform males into functional females. But in some wasp species, *Wolbachia* infections eliminate males altogether by disrupting the first cell division of the egg, resulting in diploid eggs that can develop only as females—thus creating parthenogenetic strains of normally sexual wasps. Such asexual strains of wasps will revert back to dioecy if the *Wolbachia* dies out.[9]

Embryology As discussed in Chapter 20, the large centrolecithal eggs of arthropods are often very yolky, a condition resulting in modifications of the cleavage pattern. Most hexapods undergo meroblastic cleavage by way of intralecithal nuclear divisions, followed by migration of the daughter nuclei to the peripheral cytoplasm (= periplasm). Cytokinesis does not occur during these early nuclear divisions (up to 13 cycles), which thus generate a syncytium, or plasmodial phase of embryogenesis. The nuclei continue to divide until the periplasm is dense with nuclei, whereupon a syncytial blastoderm exists. Eventually, cell membranes begin to form, partitioning uninucleate cells from one another. At this point the embryo is a periblastula, comprising a yolky sphere containing a few scattered nuclei and covered by a thin cellular layer (Figure 22.39).

Along one side of the blastula a patch of columnar cells forms a germinal disc, sharply marked off from the thin cuboidal cells of the remaining blastoderm (Figure 22.39A). From specific regions of this disc, presumptive endodermal and mesodermal cells begin to proliferate as germinal centers. These cells migrate inward during gastrulation to lie beneath their parental cells, which now form the ectoderm. The mesoderm proliferates inward as a longitudinal gastral groove (Figure 22.39B). The cells of the developing gut usually surround and gradually begin absorbing the central yolky mass of the embryo, and paired coelomic spaces appear in the mesoderm.

As segments begin to demarcate and proliferate, each receives one pair of mesodermal pouches and eventually develops appendage buds. As the mesoderm contributes to various organs and tissues, the paired coelomic spaces merge with the small blastocoel to produce the hemocoelic space. The mouth and anus arise by ingrowths of the ectoderm that form the proctodeal foregut and hindgut, which eventually establish contact with the developing endodermal midgut.

Polyembryony occurs in a number of insect taxa, particularly parasitic Hymenoptera. In this form of development the early embryo splits to give rise to more than one developing embryo. Thus, from two to thousands of larvae may result from a single fertilized egg, which is often deposited in the body of another (host) insect.

Postembryonic development Within Hexapoda there are three main types of development: **ametabolous** (= direct, amorphic, or ametamorphic development), **hemimetabolous**, and **holometabolous** (indirect or complete metamorphosis). Figure 22.40 depicts these development types. Species in the most primitive wingless hexapod orders (entognathans, archaeognathans, and zygentomans) undergo ametabolous development. The young hatch out as juveniles closely resembling the adult, imago condition, but the overall body size increases with each successive molt. Winged insects undergo either hemimetabolous development

[9] *Wolbachia pipientis* are maternally transmitted, gram-negative, obligate intracellular bacteria found in filarial nematodes, crustaceans, arachnids, and at least 20% of all insect species. Many *Wolbachia* increase their prevalence in populations by manipulating host reproductive systems.

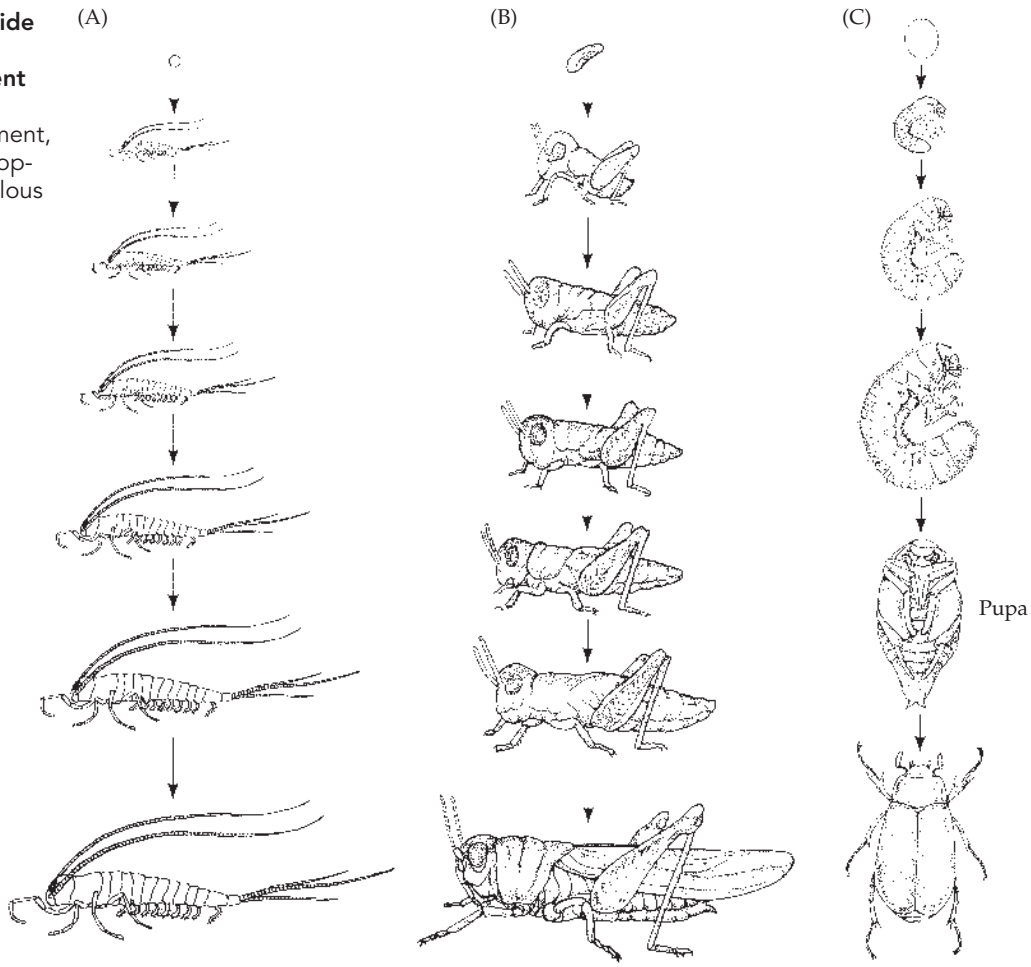

FIGURE 22.40 Side-by-side comparison of the three main types of development found in hexapods. (A) Ametabolous development, (B) hemimetabolous development, and (C) holometabolous development.

(Figures 22.40B and 22.41) or holometabolous development (Figures 22.40C and 22.42).

In hemimetabolous development, principal changes during growth are primarily in body size and proportions and in the development of wings and sexual structures. The juveniles of hemimetabolous insects are often called **nymphs** (terrestrial juveniles) or **naiads** (aquatic juveniles). Naiads occur in Plecoptera (stoneflies), Odonata (dragonflies and damselflies), and Ephemeroptera (mayflies), and they differ from other hemimetabolous groups in that these juveniles are quite different from the adult in body type and habitat. Nymphs and adults often live in the same general habitat; naiads and their respective adults do not. Nymphs and naiads possess compound eyes, antennae, and feeding and walking appendages similar to those of the adults. However, functional wings and sexual structures are always lacking, although juveniles have wing rudiments called wing pads or wing buds, and the wings themselves become exposed for the first time during the preadult molt.

Holometabolous insects hatch as vermiform larvae that bear no resemblance whatsoever to the adult forms. These larvae are so different from adults that they are often given separate vernacular names; for example, butterfly larvae are called caterpillars, fly larvae maggots, and beetle larvae grubs. Holometabolous larvae lack compound eyes (and often antennae), and their natural history differs markedly from that of adults. Their mouthparts may be wholly unlike those of adults, and external wing buds are never present. Often the greater part of a holometabolous insect's lifetime is spent in a series of larval instars. Larvae typically consume vast quantities of food and attain a larger size than adults. Termination of the larval stage is accompanied by **pupation**, during which (in a single molt) the pupal stage is entered (Figures 22.42 and 22.43). **Pupae** do not feed or move about very much. They often reside in protective niches in the ground, within plant tissues, or housed in a **cocoon**. Energy reserves stored during the long larval life are utilized by the pupa to undergo wholesale body transformation. Many larval tissues are broken down and reorganized to attain the adult form; external wings and sexual organs are formed. The remarkable transformation from larval stage to adult stage in holometabolous insects is one of the most impressive achievements of animal evolution (Figure 22.42). The opening photo of this chapter features the moth, *Rothschildia cincta*, taken soon after it eclosed from its silken cocoon, upon which

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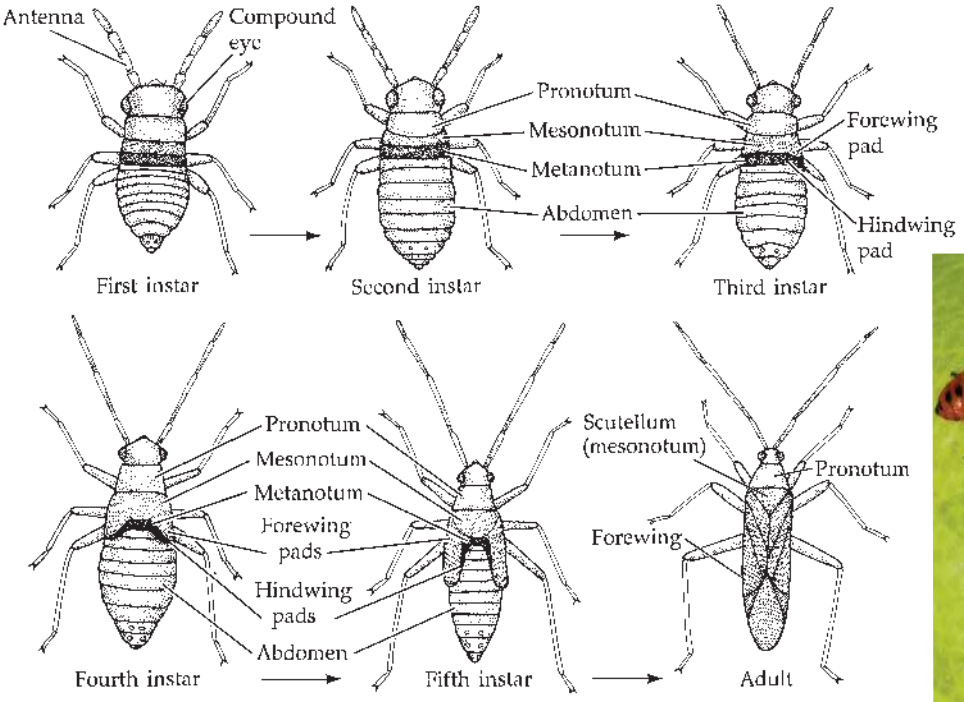

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FIGURE 22.41 Illustrations and photo of the life stages of milkweed bugs (Hemiptera), illustrating the main life stages of hemimetabolous development. Note the wing pads in instars 3–5. (After S. Reynolds.2013. In R. F. Chapman et al. [Eds.], *The Insects*, 5th Ed., pp. 398–459. Cambridge University Press, Cambridge.)

it rests after undergoing one of the most amazing transformations known.[10]

The role of ecdysone in initiating molting is described in Chapter 20. This hormone works in conjunction with a second endocrine product in controlling the sequence of events in insect metamorphosis. This second product, juvenile hormone, is manufactured and released by the corpora allata associated with the brain (Figure 22.33). When ecdysone initiates a molt in an early larval instar, the accompanying concentration of juvenile hormone in the hemolymph is high. A high concentration of juvenile hormone ensures a larva-to-larva molt. After the last larval instar is reached, the corpora allata ceases to secrete juvenile hormone. Low concentrations of juvenile hormone result in a larva-to-pupa molt. Finally, when the pupa is ready to molt,

[10]Dancers in some Native American tribes in northwestern Mexico and the southwestern United States create ankle rattles by adding small rocks inside dry *Rothschildia cincta* cocoons, which they string together and around their legs.

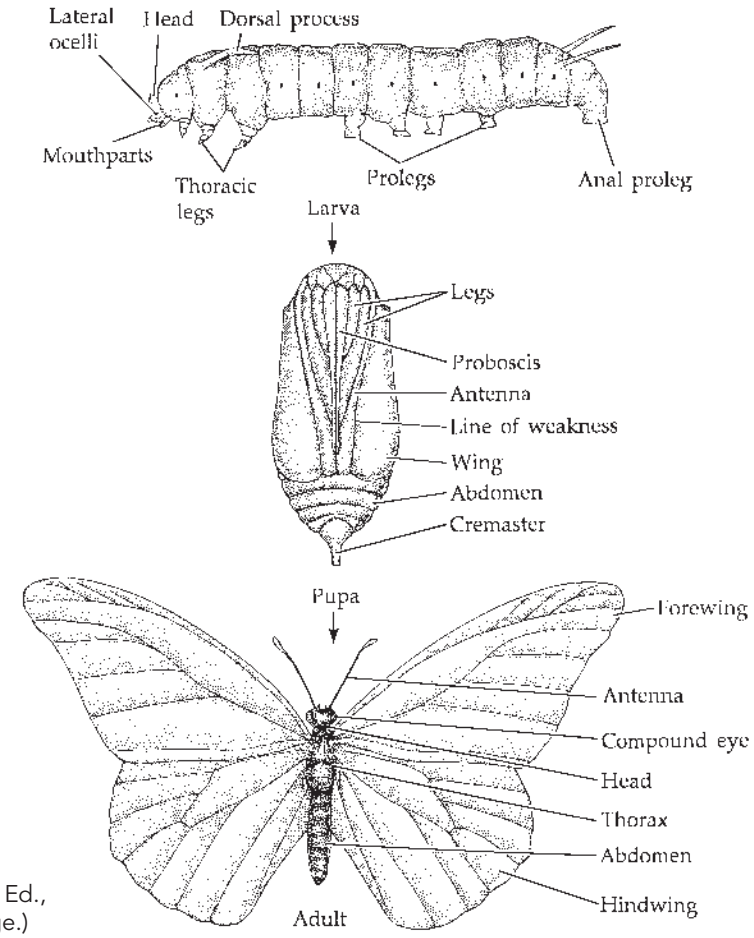

FIGURE 22.42 Life stages of a butterfly (Lepidoptera), illustrating the main life stages of holometabolous development. (After S. Reynolds. 2013. In R. F. Chapman et al. [Eds.], *The Insects*, 5th Ed., pp. 398–459. Cambridge University Press, Cambridge.)

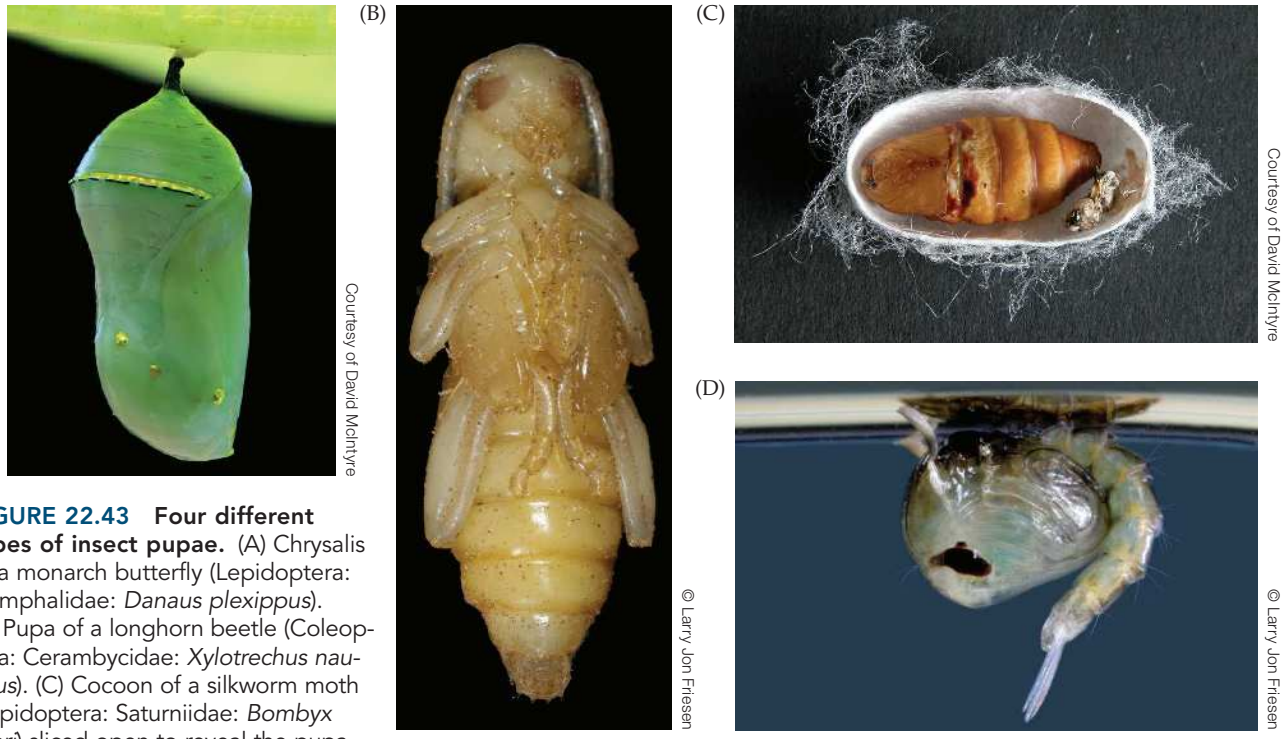

FIGURE 22.43 Four different types of insect pupae. (A) Chrysalis of a monarch butterfly (Lepidoptera: Nymphalidae: *Danaus plexippus*). (B) Pupa of a longhorn beetle (Coleoptera: Cerambycidae: *Xylotrechus nauticus*). (C) Cocoon of a silkworm moth (Lepidoptera: Saturniidae: *Bombyx mori*) sliced open to reveal the pupa inside. The shed skin (exuviae) of the final larval instar is visible to the right of the pupa inside the cocoon. (D) Pupa of a mosquito (Diptera: Culicidae).

juvenile hormone is absent from the hemolymph altogether; this deficiency leads to a pupa-to-adult molt. There is recent evidence that Hox genes (e.g., *Scr*) can control the number of larval molts, suggesting that such genes could underlie the evolution of life history traits in insects.

Hexapod Evolution

Hexapods (and arachnids and myriapods) were among the earliest animals to colonize and exploit terrestrial and freshwater ecosystems. The fossil record is good, with about 1,263 recognized families (by comparison, there are 825 recognized fossil families of tetrapod vertebrates). The oldest known fossil hexapods are from the Early Devonian (Pragian) Rhynie chert, which has led to the hypothesis that hexapods originated in the late Silurian with the earliest terrestrial ecosystems. The remarkable diversification of insects is undoubtedly related to the evolution of wings, and insects are the only group of invertebrates with the ability to fly. Whole genome duplications have also occurred in at least 14 hexapod orders (e.g., Lepidoptera, Odonata, Trichoptera), and these have likely contributed to insect radiations. Fossil winged insects exist from the Late Mississippian (~324Ma), which suggests a Carboniferous origin of insect flight. However, the description of *Rhyniognatha* (~412 Ma) from a mandible, potentially indicative of a winged insect, suggests a late Silurian to Early Devonian origin of winged insects. Divergence time estimates based on a molecular phylogenetic analysis of many nuclear, protein-coding genes (Misof et al. 2014) corroborate an origin of winged insect lineages during this time period, which implies that the ability to fly emerged soon after the establishment of complex terrestrial ecosystems. Since then, insects have shaped Earth's terrestrial ecosystems, coevolving with another hyperdiverse terrestrial group, the flowering plants, ultimately qualifying the Cenozoic to be called "the age of insects."

By the Carboniferous, various modern insect orders were flourishing, although many were quite unlike today's fauna. Some Carboniferous hexapods are notable for their gigantic size, such as silverfish (Zygentoma) that reached 6 cm in length and dragonflies (Odonata) with wingspans of about 70 cm. In addition to the living orders of insects, at least ten other orders arose and radiated in late Paleozoic and early Mesozoic times, then went extinct.

The Permian saw an explosive radiation of holometabolous insects, although many groups went extinct in the great end-Permian extinction event (Chapter 1). In fact, relatively few groups of Paleozoic insects survived into the Mesozoic, and many recent families first appeared in the Jurassic. By the Cretaceous, most modern families were extant, insect sociality had evolved, and many insect families had begun their intimate relationships with angiosperms. Tertiary insects were essentially modern and included many genera indistinguishable from the Recent (Holocene) fauna.

Our current view of the evolutionary relationships of hexapod orders is presented in Figure 22.44. This

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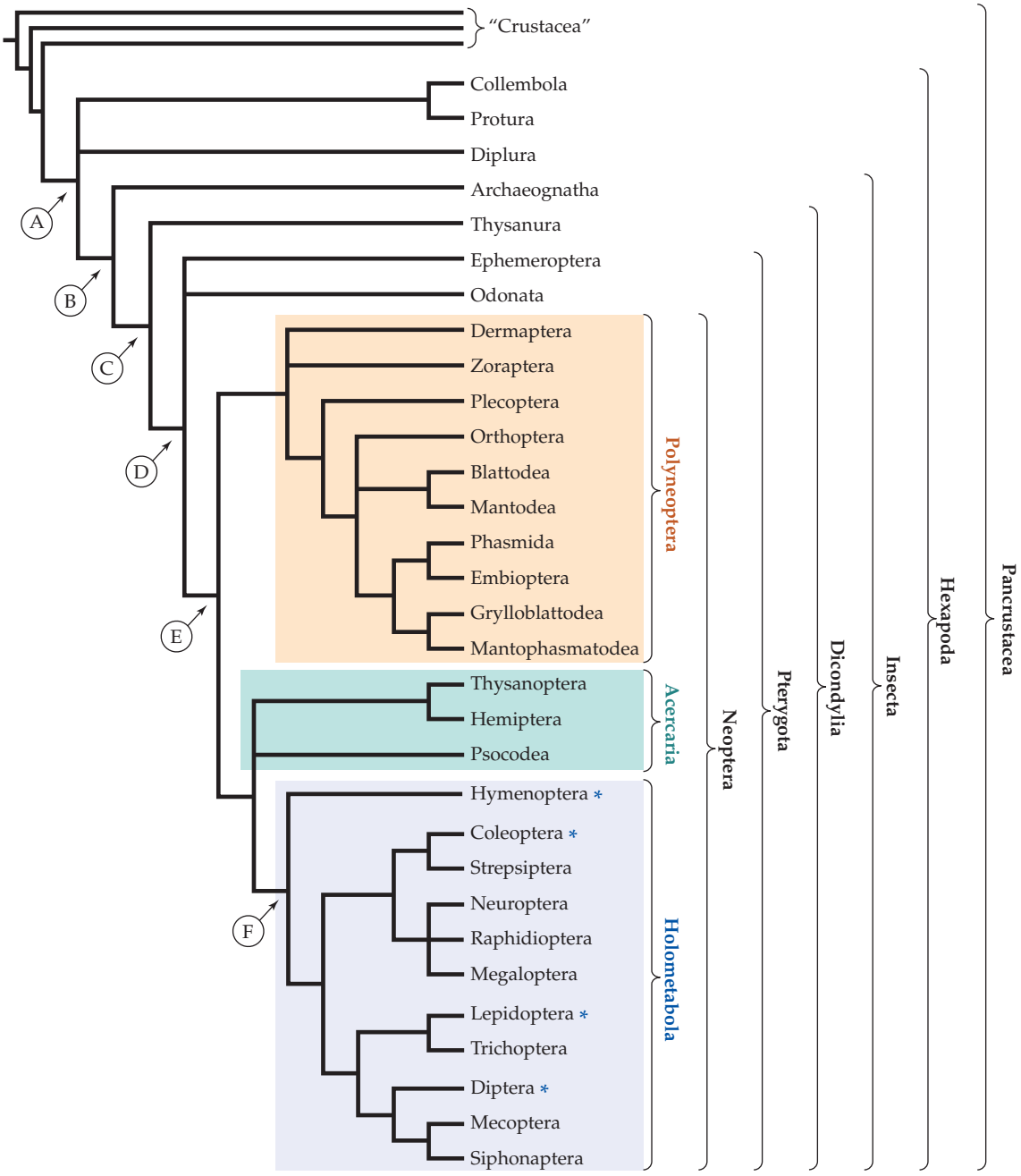

FIGURE 22.44 Phylogeny of the 31 orders of Hexapoda. Major clades are indicated to the right of the tree. The most recent common ancestor of extant taxa with traits that led to the success of the Hexapoda are denoted with circled letters to the left of the tree. These key innovations include (A) arthropod body subdivided into three tagmata: the head, 3-segmented thorax with one pair of uniramous legs on each segment, and an 11-segmented abdomen (synapomorphies of Hexapoda); (B) the evolution of external mouthparts (an apomorphy of the class Insecta); (C) the evolution of dicondylic mandibles (an apomorphy of the Dicondylia); (D) the evolution of wings (an apomorphy of Pterygota); (E) the evolution of wing folding (an apomorphy of Neoptera); (F) the evolution of holometabolous development, or complete metamorphosis (an apomorphy of the Holometabola). The most diverse insect orders, commonly known as the "big four," are denoted with asterisks. Crustacea, a paraphyletic group due to its exclusion of the Hexapoda, is shown at the base of the tree.

tree is based on Misof et al. (2014), presenting a molecular phylogenetic analysis of 1,478 single-copy nuclear, protein-coding genes (see Chapter 2 for detailed tree with divergence time estimates). This continues to be the most data-rich analysis of the hexapods conducted to date. The results of this analysis support many of the long-held views of hexapod evolution but also provide novel support for some parts of the tree that had been difficult to resolve based on smaller molecular sets and by analyses of morphological characters alone. As noted in Chapter 20, recent phylogenomic analyses suggest the Hexapoda and remipede crustaceans are sister groups.

The hexapods are divided between three entognathous orders and the Insecta. The three entognathous

orders (the Collembola, Protura, and Diplura) all have internalized mouthparts. Most current workers regard the Collembola + Protura to be a monophyletic group (called the Ellipura), and this relationship is strongly supported by the most recent analyses. However, whether the Diplura are more closely related to the Collembola + Protura or to the Insecta (a view persuasively argued by Kukalová-Peck) remains hotly debated, with recent analyses favoring the latter (e.g., Schwentner et al., 2017). Thus, the entognathous hexapods may or may not form a monophyletic group. Among the potential synapomorphies that may unite all three orders is entognathy itself (the overgrowth of the mouthparts by oral folds from the lateral cranial wall). In addition, the Malpighian tubules and compound eyes are reduced—compound eyes are degenerate in Collembola and absent in the extant Diplura and Protura. However, these reductions could be convergences resulting from small body size. Our evolutionary tree thus depicts an unresolved trichotomy at the base of the Hexapoda, and we treat the entognathous hexapods as a potentially paraphyletic group in our classification.

The monophyly of the Insecta (Archaeognatha, Zygentoma, and Pterygota) (Figure 22.44, node B) is undisputed. The principal synapomorphies of this group include the structure of the antenna, with its lack of muscles beyond the first segment (scape); the presence of a group of special chordotonal organs (vibration sensors) in the second antennal segment (pedicel) called the Johnston's organ; a well-developed posterior tentorium (forming a transverse bar); subdivision of the tarsus into tarsomeres; females with ovipositor formed by gonapophyses (limb-base endites) on segments 8 and 9; and long, annulated, posterior terminal filaments (cerci).

The Insecta have traditionally been divided into the wingless insects (Archaeognatha and Zygentoma) and the winged insects (Pterygota). However, on the basis of molecular studies and the presence of a dicondylic mandible, the Zygentoma (silverfish) are now thought to be the sister group of the Pterygota. They are classified together in a lineage known as the Dicondylia (see Figure 22.44, node C).

The Pterygota are, of course, distinguished by the presence of wings on the mesothorax and metathorax of adults. There is wide agreement that wings evolved only once in Hexapoda along the branch leading to the Pterygota (Figure 22.44, node D). However, the Pterygota comprise two groups, Palaeoptera and Neoptera, with fundamentally different wing types. The Palaeoptera ("ancient wings") include the Odonata (dragonflies and damselflies) and Ephemeroptera (mayflies), which are characterized by many-veined, netlike wings that cannot be folded over the back. It is still unclear whether or not the two palaeopterous orders, Ephemeroptera and Odonata, form a monophyletic group, and they are therefore depicted in a trichotomy with Neoptera in our summary tree (Figure 22.44, node D). The Neoptera ("modern wings") have reduced wing venation, but more importantly, they can rotate their wing joint and fold back their wings when they are not flying (Figure 22.44, node E). This is one of the most important evolutionary innovations in hexapods. Wing folding allows insects to protect their fragile wings, especially from abrasion, thereby allowing them to live in tight spaces such as crevices under bark, under rocks, and in burrows, nests, and tunnels.

The Neoptera is divided into three broad groups: Polyneoptera (10 orders); Acercaria, or Paraneoptera (3 orders); and the Holometabola, or Endopterygota (11 orders). Polyneopterans are a morphologically diverse group of insects with biting-chewing mouthparts and hemimetabolous development. The phylogenetic relationships among the orders within Polyneoptera, and the monophyly of the group itself have long been controversial. However, recent phylogenomic work recovered strong support that the polyneopteran orders form a monophyletic group.

The Acercaria includes the Thysanoptera, Hemiptera, and the Psocodea. Supported by many derived characters, the monophyly of this group is likely (but controversial), since Misof et al. (2014) found evidence that the Psocodea may be the sister group to Holometabola. Although this relationship appears to be well supported by their analyses (see Figure 2.6) with high bootstrap support values, this measure of support is of controversial utility for such large molecular data sets.

The monophyly of the Holometabola is well established. The 11 orders placed together in the Holometabola are united on the basis of holometabolous development (Figure 22.44, node F). The eminent success of the holometabolous lifestyle is demonstrated by the fact that holometabolous species outnumber hemimetabolous species ten to one. The most species-rich insect orders (Hymenoptera, Coleoptera, Lepidoptera, and Diptera), commonly known as the "big four," all undergo complete (holometabolous) metamorphosis. There is a popular theory among evolutionary biologists that views indirect development, including holometabolous development in insects, as selectively advantageous because it results in the ecological segregation of adults from young, thus avoiding intraspecific competition and allowing each stage to develop its own suite of specific survival strategies. We have seen that such transformations in development are common in marine and some freshwater invertebrates, but only the insects have managed to exploit this strategy so successfully on land.

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Chapter Summary

This chapter described the vast world of Hexapoda—the insects (Ectognatha) and three small orders of hexapods with internal mouthparts (Collembola, Protura, and Diplura). With nearly a million described hexapod species, and 10 to 100 times that number of undescribed species, we have only scratched the surface of hexapod diversity and biology. All hexapods have a distinct body plan comprising a head, a 3-segmented thorax, an abdomen of 11 (or fewer in groups with a reduced abdomen) segments, three pairs of thoracic legs, a single pair of antennae, three sets of "jaws" (mandibles, maxillae, and labium), an aerial gas exchange system composed of tracheae and spiracles, Malpighian tubules formed as proctodeal (ectodermal) evaginations, and, in the subclass Pterygota, wings. No other group of arthropods has a thorax fixed at 3 segments, each with a pair of walking legs, nor do any other invertebrates have wings. Hexapods are an ancient group, their origin likely being in the Lower Ordovician. Insects are not only extremely diverse, but also incredibly abundant in the terrestrial world. Insects coevolved with flowering plants, and many wild species of plants rely on them for pollination (as do about 80% of the world's crop species). Of the 31 recognized orders of Hexapoda, several stand out as megadiverse and are known among entomologists as "the big four": Coleoptera (beetles) with 387,100 described species, Diptera (flies) with 159,295 species, Lepidoptera (butterflies and moths) with 157,402 species, and Hymenoptera (bees and wasps) with 115,000 species. Within Hexapoda there are three main types of development: ametabolous (direct, or amorphic development), hemimetabolous, and holometabolous (indirect, or complete development, with distinct larval stages that undergo pupation to adulthood). Hexapods arose from a crustacean ancestor (thus making the Crustacea paraphyletic if the hexapods are excluded), and the two subclasses together comprise the Pancrustacea; Pancrustacea and Myriapoda together comprise the clade Mandibulata.

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CHAPTER 23

Phylum Arthropoda

Subphylum Myriapoda: Centipedes, Millipedes, and Their Kin

The arthropod subphylum Myriapoda includes four groups traditionally ranked as classes: Chilopoda (centipedes), Diplopoda (millipedes), Pauropoda (pauropods), and Symphyla (symphylans). All modern myriapods are terrestrial, but the lineage probably began its evolution in the aquatic realm. Although molecular clock phylogenies suggest a late Cambrian (500 Ma) monophyletic origin for the Myriapoda, the first fossil record of millipedes is from the Late Ordovician or early Silurian, and these are thought to represent marine species. The oldest reliable terrestrial myriapod fossils date only from the late Silurian (~425 Ma). Figure 23.1 illustrates a variety of myriapod types. More than 16,000 living species have been described so far.

Centipedes and millipedes are familiar arthropods, easily distinguished from all other terrestrial invertebrates by a body divided into just two tagmata, the head and the long, homonomous, and many-segmented trunk bearing many pairs of jointed legs. As in the Hexapoda, the head is equipped with one pair of antennae. The mouthparts are represented by the mandibles and the first maxillae; a second pair of maxillae is present in the centipedes and symphylans, but in millipedes and pauropods the corresponding segment bears no appendages.

Millipedes are slow-moving detritus feeders that generally spend their time burrowing through soil and litter, consuming plant remains and converting vegetable matter into humus. In tropical environments where earthworms are often scarce, millipedes may be the major soil-forming animals. Uniquely among the arthropods, most of their trunk segmental units bear two pairs of legs each and are commonly described as **diplosegments** (Figure 23.2F). When threatened, many millipedes roll up into a flat coil, and some can roll up

This chapter was revised by Alessandro Minelli.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

into perfect balls (like many isopods). Millipedes typically have many trunk segments, but some have only 9 to 12. Despite their vernacular name (from *milli*, "thousand," *pedes*, "feet"), which has equivalents in many languages, only one species has been found with a thousand legs, the newly discovered *Eumillipes persephone* (a subterranean species from Western Australia) that has 330 segments and 653 pairs of legs.

Millipedes are incapable of strong biting and at first sight seem only to rely on their calcified cuticle and their rolling ability for defense, but the majority possess repugnatorial glands with lateral openings (**ozopores**) that secrete volatile toxic liquids (Figure 23.2F). Their chemical weaponry is surprisingly diverse: it includes the benzoquinones, hydroquinones, phenol, and acetates of long-chain carboxylic acids produced

FIGURE 23.1 Representative myriapods. (A) The European centipede *Himantarium gabrielis*, whose leg count may reach 179 pairs. (B) The scutigeromorph centipede *Dendrothereua homa* from Yucatan, Mexico. (C) The African scolopendromorph centipede *Alipes grandidieri*. The tibia and tarsal articles of the terminal legs are conspicuously flattened and leaflike; stridulation is produced by friction between the articles. (D) *Desmoxytes purpurosea*, the shocking pink dragon millipede, a polydesmidan millipede discovered in Thailand in 2007. (E) The Southwestern desert millipede *Orthoporus ornatus*. (F) An unidentified pauropod from Tasmania (Australia). (G) An unidentified symphylan from Tasmania (Australia). (H) The European pincushion millipede *Polyxenus lagurus*, a typical representative of the penicillate millipedes. (I) A giant pill millipede from the Southern Hemisphere, a representative of the Sphaerotheriida clade of pentazonian millipedes.

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by juloids; and the benzoic acid, benzaldehyde, and hydrogen cyanide produced by polydesmoids. A few tropical species have toxins powerful enough to cause blisters on human skin. Pill millipedes, such as the common European species of *Glomeris*, lack lateral ozopores, but from along their dorsal midline they squeeze out drops of fluid containing quinazolinones, which belong to the same class of substances as the synthetic drug Quaalude (methaqualone), a powerful sedative. One common household species in North America and Europe (introduced long ago from Asia), the polydesmidan *Oxidus gracilis*, releases strong-smelling defensive chemicals when injured. Members of the subclass Penicillata, which are small, soft bodied, and without repugnatorial glands, have evolved a mechanical defense strategy of throwing stiff bristles from their posterior end at ants and other predators. Given their range of defensive tactics, it is not surprising that many millipedes have aposematic (warning) coloration, usually bright reds, yellows, and oranges, and that some soil-dwelling vertebrates (lizards and worm snakes) have evolved look-alike coloration (Batesian mimicry).

Millipedes in the family Xystodesmidae (order Polydesmida) produce hydrogen cyanide as a defensive chemical, and they use aposematic coloration to warn predators of their toxicity. Coloration patterns in these species include bright yellows, oranges, reds, and violet. One nocturnal genus in this family, *Motyxia*, known only from California, does not display conspicuous coloration. Remarkably, however, they produce a green bioluminescent glow at a dominant wavelength of 495 nm by way of a biochemical source of light produced in the exoskeleton. The source is a photoprotein with a chromophore containing a porphyrin as its functional group. This is the only known instance of light production via a photoprotein on land, all other examples being marine. The emitted light could be a sexual signal to attract mates, or an aposematic warning glow to announce the presence of a cyanide-based chemical defense.

In contrast to millipedes, most centipedes are fast-running predators, have one pair of legs per segment, and have poison claws at the tip of their first pair of legs, which are thus turned into a peculiar kind of maxillipeds called **forcipules** or **prehensors**. When threatened, centipedes usually strike out with the poison claws, with which they can inflict a painful bite. A few *Scolopendra* species have warning coloration—black and red banding. Lithobiomorph centipedes bear large numbers of unicellular repugnatorial glands on the last four pairs of legs, which they kick in the direction of an enemy—a behavior that throws out sticky droplets of noxious secretions. Despite their vernacular name (from *centi*, "hundred," *pedes*, "feet"), these creatures rarely have as many as 100 legs, and only in the order Geophilomorpha is this attained; the highest number of leg pairs recorded thus far (in *Gonibregmatus plurimipes*) is 191.

CLASSIFICATION OF THE SUBPHYLUM MYRIAPODA

CLASS CHILOPODA (CENTIPEDES)
- SUBCLASS NOTOSTIGMOPHORA
  - ORDER SCUTIGEROMORPHA
- SUBCLASS PLEUROSTIGMOPHORA
  - ORDER CRATEROSTIGMOMORPHA
  - ORDER GEOPHILOMORPHA
  - ORDER LITHOBIOMORPHA
  - ORDER SCOLOPENDROMORPHA

CLASS DIPLOPODA (MILLIPEDES)
- SUBCLASS PENICILLATA
  - ORDER POLYXENIDA
- SUBCLASS CHILOGNATHA
  - INFRACLASS PENTAZONIA
    - ORDER GLOMERIDESMIDA
    - ORDER GLOMERIDA
    - ORDER SPHAEROTHERIIDA
  - INFRACLASS HELMINTHOMORPHA
    - SUPERORDER COLOBOGNATHA
      - ORDER PLATYDESMIDA
      - ORDER POLYZONIIDA
      - ORDER SIPHONOCRYPTIDA
      - ORDER SIPHONOPHORIDA
    - SUPERORDER EUGNATHA
      - ORDER JULIDA
      - ORDER SPIROBOLIDA
      - ORDER SPIROSTREPTIDA
      - ORDER CALLIPODIDA
      - ORDER CHORDEUMATIDA
      - ORDER STEMMIULIDA
      - ORDER SIPHONIULIDA
      - ORDER POLYDESMIDA

CLASS PAUROPODA (PAUROPODS)

CLASS SYMPHYLA (SYMPHYLANS)

Myriapod Classification

Subphylum Myriapoda

Terrestrial mandibulate and tracheate arthropods provided with 1 pair of antennae; mandibles with

articulating endite; first maxillae free or fused together; second maxillae partly or wholly fused, or absent; postcephalic trunk of numerous, mostly similar segments (or diplosegments); appendages of head and trunk uniramous; most lineages with lateral compound eyes or groups of closely packed ocelli; exoskeleton without well-developed wax layer (except in some desert species); without endodermally derived digestive ceca; ectodermally derived (proctodeal) Malpighian tubules assist in excretion; often with organs of Tömösváry; copulation often indirect; development direct, but often with postembryonic increase in the number of segments and appendages. About 16,350 described, living species.

Class Chilopoda

With numerous freely articulating trunk segments, each with 1 pair of legs, the first pair modified as large poison claws held under the head like mouthparts; antennae simple, of fixed (14 in the Geophilomorpha, 17 in most Scolopendromorpha) or variable (in excess of 100 in some cave-dwelling Lithobiomorpha) number of articles; both pairs of maxillae may be medially coalesced; cuticle uncalcified; gonopore on last true body segment; spiracles lateral, except in Scutigeromorpha; with 15 to 191 leg-bearing body segments (number always odd in the adults); legs long, extending laterally such that the body is carried close to the ground; last pair of legs often sexually dimorphic, extending backward and not used for locomotion.

Centipedes of the subclass Notostigmophora have middorsal spiracles and very short tracheae that end on the dorsal vessel; hemolymph containing hemocyanin; a dome-shaped head, with compound eyes; and 15 pairs of long, thin legs. The subclass Pleurostigmophora includes centipedes with lateral spiracles, a flattened head, and a variable number of legs. The largest centipedes belong to the order Scolopendromorpha (having either 21 or 23 pairs of legs, with 39 or 43 only in one species, *Scolopendropsis duplicata*), although the highest leg count occurs in the long, thin geophilomorphs (27 to 191 pairs of legs). The globally distributed order Scolopendromorpha contains the species most people readily recognize as centipedes. North America, north of Mexico, is the only major inhabited region that has no native species of scutigeromorph centipedes, although the long-legged, swift-moving European species *Scutigera coleoptrata* has become widely introduced and is often encountered in houses. Approximately 3,300 living species of centipedes have been described.

Class Diplopoda

Trunk comprising 9 to 330 segmental units; most of these (diplosegments) with 2 pairs of legs, spiracles, ganglia, and heart ostia; each diplosegment with 1 tergite, 2 pleura, and 1 to 3 sternites; first trunk segment legless, modified as collum; diplosegments 2–4 (and also 5 in the order Spirobolida) with 1 pair of legs each; total number of leg pairs in adults ranging from 11 up to 653; antennae simple, generally 7-jointed; first maxillae fused into a gnathochilarium; second maxillae absent; gonopores opening on third trunk segment, on or near coxae of second pair of legs; cuticle usually calcified; many species capable of rolling into a tight coil; spiracles located ventrally, typically in front of leg coxae, and never valvular (i.e., they cannot be closed); legs ventrally positioned and generally short, such that the body is carried close to the ground. On some or most trunk segments many millipedes have lateral repugnatorial glands that secrete noxious chemicals that can irritate the skin and eyes. In addition to their defensive role against predator attacks, the secretions of julids have been shown to have antimicrobial and antioxidative effects. A few millipedes spray their secretions up to 40 cm. About 12,000 species of millipedes have been described.

The segmental nature of the trunk rings was recently challenged by insights obtained from gene expression studies demonstrating that dorsal and ventral halves of the body are decoupled in their early development. The body itself is usually elongate. Most common forms are either subcylindrical and wormlike, short legged, and capable of rolling into a tight spiral when disturbed, or broadly flattened and equipped with lateral wing- or keel-like cuticular extensions of the body wall, called **paranota**, that may cover the legs. Filamentous outgrowths (spinnerets) bearing the openings of silk-producing glands are sometimes present at the caudal end of the body. Female gonopores open on eversible vulvae, sometimes transformed into ovipositors or into sclerotized appendages (**cyphopods**). Male gonopores occur on the leg bases or on paired (rarely unpaired) penes. Sperm transfer is either direct or mediated by specialized copulatory legs called **gonopods**. Millipede gonopods are present only in males, though not in all groups. Helminthomorphan millipedes have one or two pairs of gonopods closely behind the body ring that bears the gonopores, whereas in pentazonian millipedes there are no gonopods but the last pair of legs (the **telopods**) are modified in males as pincers used to grasp the female during mating. Spiracles are situated close to the leg bases. In the subclass Penicillata, the exoskeleton is soft; in the Chilognatha, the cuticle is calcified, hard, and rigid.

The main subgroups of the Diplopoda are defined by the following characters:

- **Penicillata** Cuticle soft, not calcified; 9–11 diplosegments covered by tufts of bristles; males without copulatory appendages
- **Chilognatha** Cuticle calcified; wide tracheal pouches; sperm actively transferred by male into the female genital opening

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- **Pentazonia** Ventral plates (stigmatic plates, traditionally called sternites) of diplosegments divided along the midline; tracheae anastomosing; terminal leg pair of male (telopods) pincer shaped; intestine N shaped, that is, bent twice. Glomeridesmids are flattened millipedes with 21–22 diplosegments; they cannot roll into a ball. Glomerids and sphaerotheriids are short, round, 12- or 13-segmented millipedes that can roll into a perfect ball.
- **Helminthomorpha** More than 21 body rings; stigmatic plates undivided; lateral ozopores (often limited to some diplosegments and sometimes lost); unbranched tracheae arising in a cluster from the tracheal pouch
- **Colobognatha** Gnathochilarium without palps; adults protect egg clutch by curling around them; first postembryonic stage with four pairs of legs; ninth and tenth leg pair of adult males transformed into sexual appendages (gonopods)
- **Eugnatha** Mandible with two articulated basal articles; pleurites fused to tergites; eighth (sometimes also ninth) leg pair of adult males transformed into sexual appendages (gonopods). This is by far the largest group of millipedes, including common cylindrical species (e.g., orders Julida, Spirobolida, and Spirostreptida), as well as the Polydesmida, whose segments are often provided with lateral keels, or paranota, that give them a flattened zipperlike aspect.

Class Pauropoda

Minuscule (0.3–2 mm) whitish-brownish myriapods; eyeless; with 4- or 6-segmented biramous antennae with 3 flagella and a unique candelabra-shaped or globular sense organ; trunk of 11 segments, tergites weakly sclerotized except in a few families; 8–11 pairs of legs (none on the first trunk segment); tergites of trunk segments usually covering more than 1 segment each; first maxillae fused into a gnathochilarium; second maxillae absent; most species without tracheal or circulatory systems; gonopores on third trunk segment. Although found in all parts of the world, pauropods are not commonly noticed; they occur mainly in moist soils and woodland litter. About 850 species have been described.

Class Symphyla

Small (1–9 mm, but up to 30 mm in *Hanseniella magna*); eyeless; trunk with 14 segments, last fused to telson; first 12 trunk segments each with a pair of legs (the first pair occasionally vestigial); penultimate segment with spinnerets and a pair of long sensory hairs; dorsal surface with 15–24 tergal plates; soft uncalcified cuticle; antennae long, threadlike, of up to 50 segments; first maxillae medially coalesced; second maxillae completely fused to form a complex labium; 1 pair of spiracles opening on the head; tracheae supply first 3 trunk segments only; gonopores open on third trunk segment. Symphylans, generally uncommon, occur in soil and rotting vegetation. About 200 species have been described.

The Myriapod Body Plan

Myriapods differ from hexapods and most crustaceans in their retention of a largely homonomous trunk with paired segmental appendages. The head appendages and legs are similar to those of hexapods. Metamerism is also evident internally in structures such as the segmental heart ostia, tracheae, and ganglia. The key features that distinguish the Myriapoda are listed in Box 23A.

Centipedes (chilopods) bear one pair of walking legs per segment (Figure 23.2A–D). Most species are a few centimeters in length, although the smallest are just 3–4 mm long and some tropical giants attain lengths of nearly 30 cm.

In the millipedes (diplopods) the head is followed by a limbless segment called the **collum**, a heavily sclerotized collar between the head and trunk (Figure 23.2E). Each of the next three segmental units bears a single pair of legs. The trunk is articulated into diplosegments, each bearing a double complement of metameric organs (Figure 23.2F). Millipedes range in length from about 0.5 to 30 cm. The cuticle of millipedes is particularly robust, being well sclerotized and usually calcified.

BOX 23A Characteristics of the Subphylum Myriapoda

1. Body of two tagmata: head and multisegmented trunk
2. All appendages multiarticulate and uniramous
3. Head appendages, from anterior to posterior: antennae, mandibles, first maxillae, and second maxillae; second maxillae fused into a single flaplike structure called a "labium" or absent; first and second maxillae often bearing palps
4. With an aerial gas exchange system composed of tracheae and spiracles (possibly evolved multiple times and convergent with those in Hexapoda)
5. With one or two pairs of ectodermally derived (proctodeal) Malpighian tubules (convergent with those in Hexapoda)
6. Most with lateral compound eyes or with groups of closely packed ocelli
7. Gut simple, without digestive ceca
8. Gonochoristic; with direct development

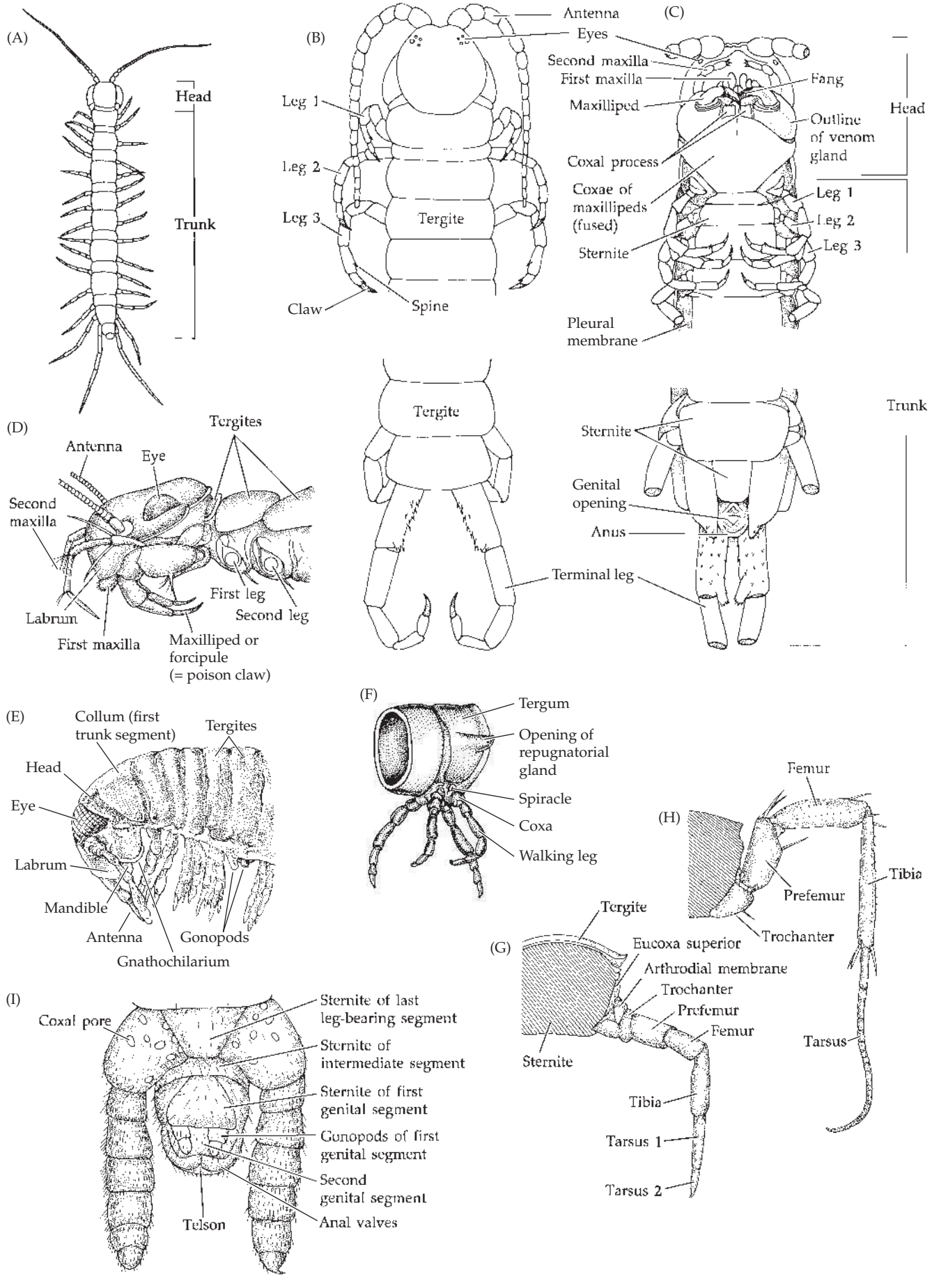
(A)
Head
Trunk
(B)
Antenna
Eyes
Leg 1
Leg 2
Leg 3
Tergite
Claw
Spine
(C)
Second maxilla
First maxilla
Maxilliped
Fang
Outline of venom gland
Head
Coxal process
Coxae of maxillipeds (fused)
Leg 1
Leg 2
Leg 3
Sternite
Pleural membrane
(D)
Tergites
Antenna
Eye
Second maxilla
First leg
Second leg
Labrum
First maxilla
Maxilliped or forcipule (= poison claw)
Tergite
Sternite
Trunk
Genital opening
Anus
Terminal leg
(E)
Collum (first trunk segment)
Tergites
Head
Eye
Labrum
Mandible
Antenna
Gonopods
Gnathochilarium
(F)
Tergum
Opening of repugnatorial gland
Spiracle
Coxa
Walking leg
(G)
Tergite
Eucoxa superior
Arthrodial membrane
Trochanter
Prefemur
Femur
Sternite
Tibia
Tarsus 1
Tarsus 2
(H)
Femur
Tibia
Prefemur
Trochanter
Tarsus
(I)
Coxal pore
Sternite of last leg-bearing segment
Sternite of intermediate segment
Sternite of first genital segment
Gonopods of first genital segment
Second genital segment
Anal valves
Telson

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FIGURE 23.2 General body anatomy of myriapods. (A) The two body regions of myriapods, head and trunk; shown is a lithobiomorph centipede. (B,C) A female scolopendromorph centipede (dorsal and ventral views), with middle body segments omitted. (D) Head of a scutigeromorph centipede in lateral view. (E) Anterior end of a millipede in lateral view. (F) A single diplosegment from the polydesmidan millipede *Gigantowales chisholmi* (Diplopoda). (G,H) Trunk segments in two centipedes shown as transverse sections; note the variation in limb morphology. (G) *Lithobius*. (H) *Scutigera*. (I) Ventral view of the terminal segments of a male geophilomorph centipede (*Strigamia*).(G–I from J. G. E. Lewis. 1981. *The Biology of Centipedes*. Cambridge University Press, New York.)

Pauropods are minute, soft-bodied, eyeless, soil-inhabiting myriapods (Figure 23.1F). They are less than 2 mm in length and have 12 trunk segments. As in millipedes, some segmental pairing occurs, and usually only six tergites are visible dorsally.

Symphylans (Figure 23.1G) are also minute, eyeless myriapods, only one species exceeding 1 cm in length. The trunk has 12 (rarely 11) pairs of legs. Some tergites are divided, and 15–24 tergites are usually visible dorsally. The thirteenth body segment bears spinnerets, a pair of long sensory hairs, and a tiny postsegmental telson. Like pauropods, symphylans inhabit loose soil and humus.

Head and Mouth Appendages

In myriapods, the eyes and protocerebrum are located in a preantennal position. The antennary segment bears the antennae and houses the deutocerebrum. The next segment (the premandibular segment) houses the tritocerebrum but lacks appendages. The three following segments carry, in turn, the mandibles and the first and second pairs of maxillae. The second maxillae are fused as a "labium" in symphylans but have been lost altogether in millipedes and pauropods. In millipedes and pauropods the first maxillae fuse to form a flaplike gnathochilarium. The ganglia of the mandibular and maxillary segments are generally fused to form the subesophageal ganglion. The antennae of millipedes are primarily composed of seven distinct antennomeres and a short, retractile tip bearing four apical sensory cones. As in the other mandibulates, the mouth region of Myriapoda is bordered by a labrum anteriorly and by a hypopharynx posteriorly. The latter arises as a flaplike (or tonguelike) outgrowth of the body wall through which the salivary glands open.

Locomotion

Myriapods rely on their well-sclerotized exoskeleton for body support. In centipedes, the legs extend laterally, keeping the body close to the ground to maintain stability while at the same time providing for long strides and generally rapid locomotion. In millipedes, the legs arise ventrally and are typically short, again keeping the body close to the ground while providing for powerful, though slow, locomotion.

The basic design of arthropod limbs was described in Chapter 20. The power exerted by a limb is greatest at low speeds and least at high speeds. At lower speeds the legs are in contact with the ground for longer periods of time, and in the case of myriapods more legs are contacting the ground at any given moment. In burrowing forms, such as many millipedes, the legs are short, and the gait is slow and powerful as the animals bulldoze their way through soil or rotting wood. In centipedes, which mostly run at high speeds, less than half the limbs may touch the ground at any given moment, and for shorter periods of time (Figure 23.3). Longer limbs increase the speed of a running gait, and limbs long in length and stride are typical features of the fastest-running centipedes and symphylans. The legs of most myriapods move in clear metachronal waves from posterior to anterior (Figure 23.3A–C).

Locomotor repertoires typically evolve in concert with the overall habits of animals, particularly feeding behaviors. Most centipedes are surface-dwelling predators that must move quickly to capture their prey. *Scutigera* is a centipede that qualifies as a world-class runner, reaching speeds up to 42 cm/sec when in pursuit of prey. On the other hand, most millipedes are detritivores that burrow through soil, leaf litter, or rotten timber in search of food.

One group of centipedes lacks the high-speed modifications of their relatives. Large geophilomorphs such as the European *Himantarium* burrow, aided by dilation of the body and use of the trunk musculature in a fashion similar to that of earthworms. This peristalsis-like motion is rare in arthropods because of their rigid exoskeleton. However, geophilomorphs have enlarged areas of flexible cuticle on the sides of the body between the tergites and sternites; these enlarged areas (pleura) allow them to significantly alter their body diameter. Other centipedes have smaller, flexible pleural areas that allow some degree of lateral undulatory motion.

Thanks to a well-developed musculature and to the soft integument, pauropods are able to both elongate the body and shorten it by a high degree of contraction, allowing them to creep in narrow irregular spaces; adult pauropods also run swiftly in short rushes.

Feeding and Digestion

Most centipedes are active, aggressive predators on smaller invertebrates, particularly worms, snails, and other arthropods. Their first trunk appendages (**prehensors** or **forcipules**), located ventral to the mouth field (Figure 23.2D), are raptorial limbs used to stab prey and inject poison. The poison is produced in large venom glands, generally located in the basal articles

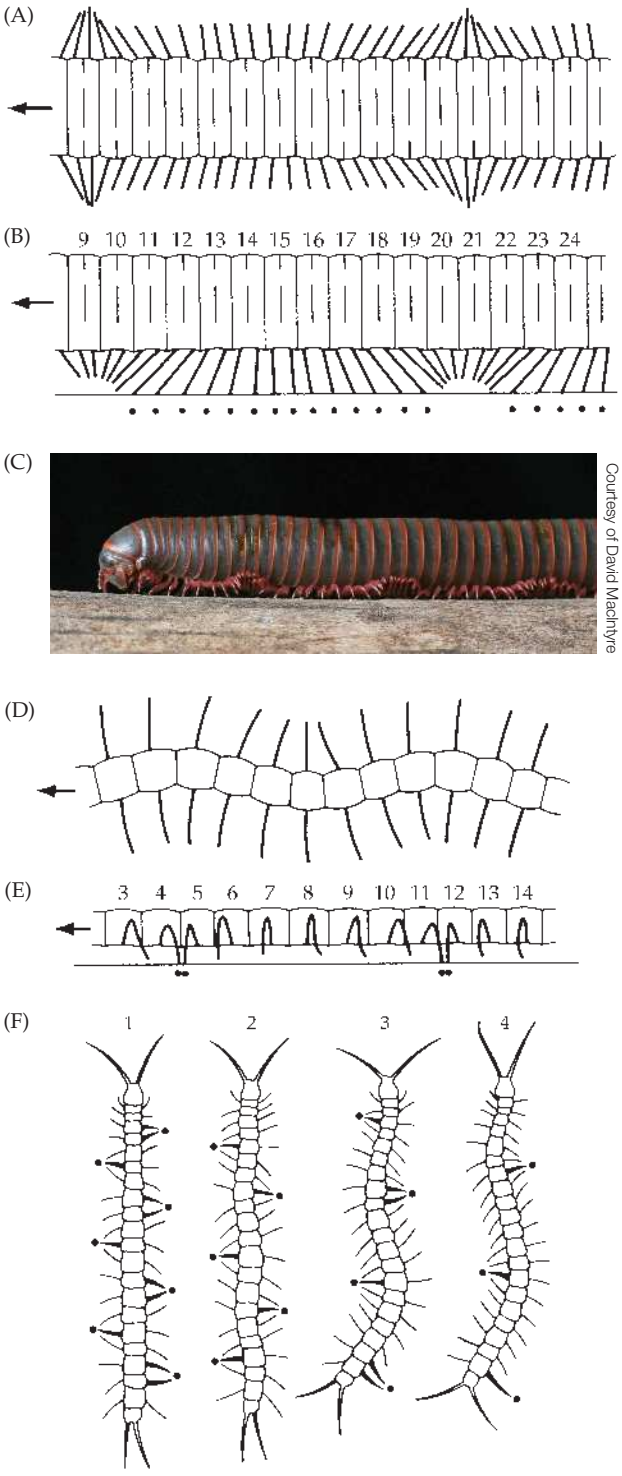

FIGURE 23.3 Locomotion in millipedes and centipedes. (A,B) Schematic of a typical millipede (such as *Spirostreptus* or *Gymnostreptus*) in motion. The dorsal view (A) shows left and right leg sets exactly in phase with each other. The lateral view (B) of the same animal shows that the majority of the limb tips are on the ground at once, an arrangement yielding a slow but powerful gait. (C) A millipede (*Narceus americanus*) in motion. Also see chapter opener photo of *N. americanus* (the giant North American millipede). (D,E) Schematic of a typical centipede (such as *Scolopendra* or *Cryptops*) in motion. The dorsal view (D) shows the limb pairs in opposite phase and the undulations of the body that accentuate stride length. The lateral view (E) of the same animal illustrates that fewer than one-third of the limb tips are on the ground at any one time, an arrangement yielding the short, swift strokes typical of a rapid but weak gait. Arrows indicate the animal's direction of travel; dots are points of leg-tip contact with the substratum. (F) Locomotion in a scolopendrid centipede at various speeds. Parts 1–4 show the body waves and leg actions at increasing speeds. Limbs shown with heavy lines are in their power strokes, with the tips against the substratum (dots); limbs depicted by thin lines are in various stages of their recovery strokes. Notice that at maximum speed the animal is still supported by a tripod stance. (F after S. M. Manton. 1965. *Zool J Linn Soc* 46: 252–483.)

of the forcipules. The poison is so effective that large centipedes, such as the tropical *Scolopendra*, can subdue small vertebrates. Chemically, centipede toxins are extremely diverse, especially in the Scolopendromorpha. As many as 39 toxins have been found in the venom of the Florida blue centipede *Scolopendra viridis*. The bite of even the most dangerous centipede is normally not fatal to people, but the venom can cause a reaction similar to that accompanying a serious wasp or scorpion sting.

The feeding strategy of millipedes is quite different. Most millipedes have a preference for dead and decaying plant material, although some species (e.g., *Blaniulus guttulatus*) have been reported to cause damage to cultivated plants. Millipedes play an important role in the recycling of leaf litter in many parts of the world. Most bite off a large piece of plant tissue with their powerful mandibles, mix it with saliva as they chew it, and then swallow it. Some, such as siphonophorids, are believed to feed on the juices of living plants and fungi. A few millipedes (some callipodidans and a few chordeumatidans) have evolved predaceous lifestyles.

The feeding biology of pauropods is not well understood, but most appear to feed on fungi and decaying plant and animal matter. *Millotauropus*, however, feeds on springtails and their eggs.

Symphylans are primarily herbivores, although a few have adopted a carnivorous, scavenging lifestyle. Many symphylans consume live plants. One species, *Scutigerella immaculata*, is a serious pest in plant nurseries and flower gardens, where it has been reported at abundances exceeding 90 million per acre.

Like the guts of all arthropods, the long, usually straight myriapod gut is divisible into an ectodermal foregut, endodermal midgut, and ectodermal hindgut (Figure 23.4). There are no digestive ceca branching off the gut. Salivary glands are associated with the mouth appendages. The mouth leads inward to a long esophagus, which is sometimes expanded posteriorly as a storage area, or crop and gizzard (as in most centipedes). The gizzard often contains cuticular spines

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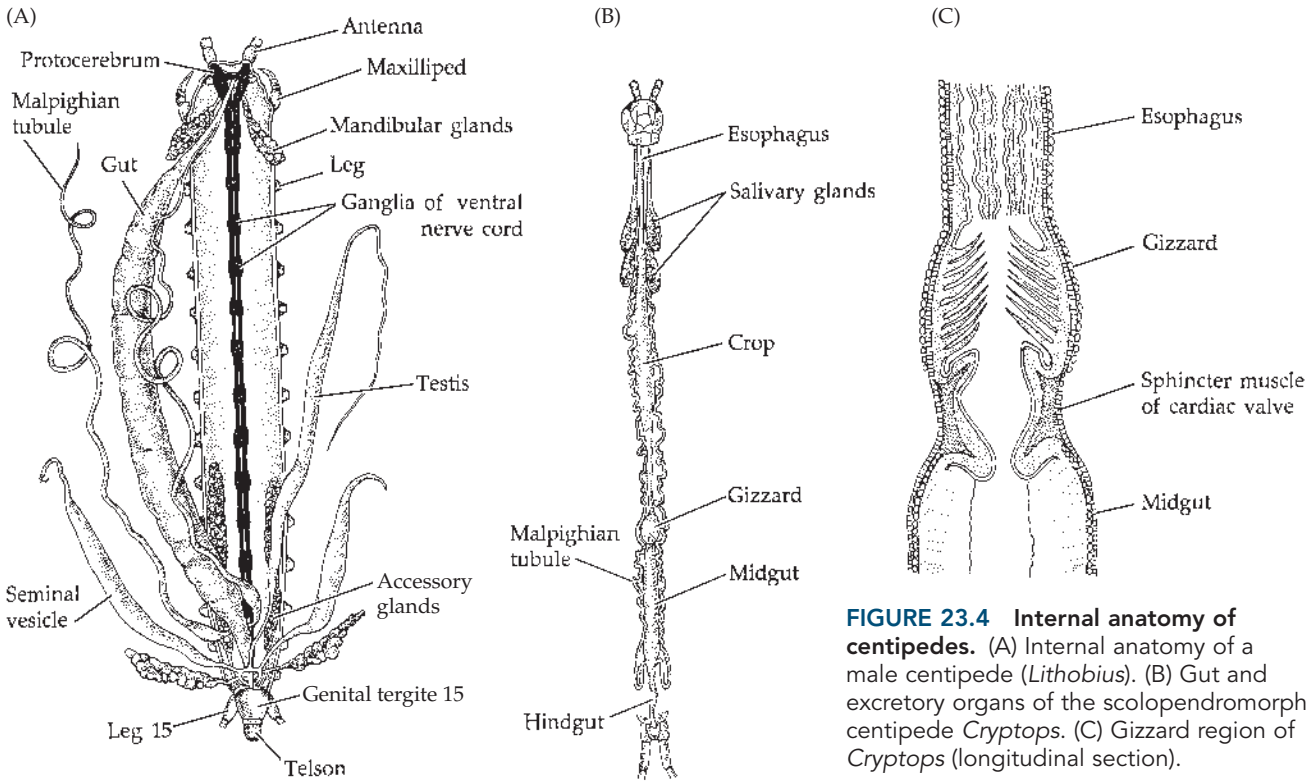

FIGURE 23.4 Internal anatomy of centipedes. (A) Internal anatomy of a male centipede (*Lithobius*). (B) Gut and excretory organs of the scolopendromorph centipede *Cryptops*. (C) Gizzard region of *Cryptops* (longitudinal section).

that help strain large particles from the food entering the midgut, where absorption occurs (Figure 23.4C). As in other arthropods, the gut of myriapods produces a peritrophic membrane—a sheet of thin, porous, chitinous material that lines and protects the midgut and that may pull free to envelop and coat food particles as they pass through the gut.

Circulation and Gas Exchange

The myriapod circulatory system includes a dorsal tubular heart that pumps the hemocoelic fluid (blood) toward the head. The heart narrows anteriorly to a vessel-like aorta, from which blood flows posteriorly through large hemocoelic chambers before returning to the pericardial sinus and then back to the heart via paired lateral ostia. Circulation is slow, and system pressure is relatively low. In millipedes, the heart bears two pairs of ostia in each diplosegment; one pair of ostia occurs in each segment in centipedes. The copper-containing respiratory pigment hemocyanin has been found in the blood of scutigeromorph centipedes and a few millipedes and symphylans, but not in pauropods, which are arguably too small to get benefit from the presence of a respiratory pigment.

Most myriapods rely on a tracheal system for gas exchange (Figure 23.5). As explained in Chapter 20, tracheae are extensive tubular invaginations of the body wall opening through the cuticle by pores called spiracles. The tracheae originating at one spiracle often anastomose with others to form branching networks penetrating most of the body. Spiracles are placed segmentally, although not necessarily on all segments: in the lithobiomorphs and in most scolopendromorphs, spiracle-bearing segments alternate with segments without spiracles. In the scutigeromorph centipedes, the respiratory openings are dorsal and lead to thick bundles of very short tracheae that terminate at the heart. Millipedes usually bear two pairs of spiracles per diplosegment, just anterior to the leg coxae. In the symphylans a single pair of spiracles opens on the sides of the head, and the tracheae supply only the first three trunk segments. Except for a few species retaining primitive characters, pauropods lack a tracheal system.

Each spiracle is usually recessed in an atrium, the walls of which are lined with setae or spines (trichomes) that prevent dust, debris, and parasites from entering the tracheal tubes. The spiracles are often surrounded by a sclerotized rim or lip, the **peritrema**, which also aids in excluding foreign particles. A muscular valve or other closing device is present in many centipedes and under control of internal partial pressures of O_2 and CO_2. As in insects, ventilation of the tracheal system is accomplished by simple diffusion gradients, as well as by pressure changes induced by the animal's movements. The blood of myriapods appears to play a limited role in oxygen transport (except in the very active scutigeromorphs).

The innermost parts of the tracheal system are the tracheoles, which are thin-walled, fluid-filled channels that end as a single cell, the tracheole end cell (= tracheolar cell). Unlike the cuticular wall of the tracheae, the wall of

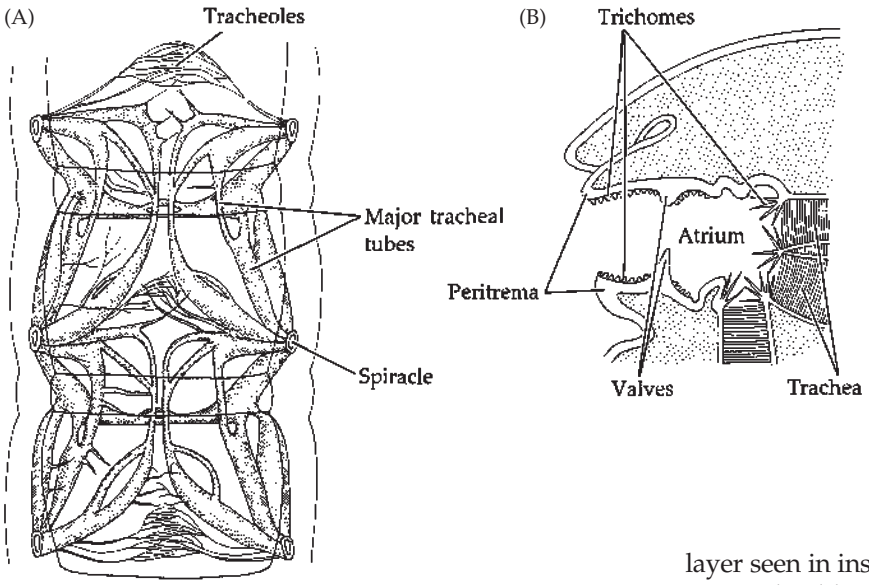

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FIGURE 23.5 The tracheal system of centipedes. (A) Tracheal system of three body segments of a scolopendromorph centipede, *Scolopendra cingulata* (dorsal view). (B) A spiracle of *S. cingulata* (transverse section). (C) Lateral view of three trunk segments of the Asian *S. subspinipes*, showing alternation of longer and shorter segments and the spiracles, each of which is placed between the margin of a longer tergite and the basis of its corresponding leg. (B after J. G. E. Lewis. 1981. *The Biology of Centipedes*. Cambridge University Press, New York.)

the tracheoles is not shed during ecdysis. The tracheoles are so minute (0.2–1.0 mm) that ventilation is impossible and gas transport here relies on aqueous diffusion.

Excretion and Osmoregulation

When myriapods invaded land, the problem of water conservation necessitated the evolution of entirely new structures to remove metabolic wastes—Malpighian tubules (Figure 23.4). These excretory organs function much as those of insects (Chapter 22), and the Malpighian tubules of myriapods and hexapods represent a striking case of convergent evolution. Myriapods usually possess only one pair of Malpighian tubules, but there are three tubules in Craterostigmomorpha and four in Scutigeromorpha. In those species that are largely confined to moist habitats and nocturnal activity patterns, a significant portion of the excretory wastes may be ammonia rather than uric acid.

The myriapod cuticle is sclerotized and calcified to various degrees, adding a measure of waterproofing, but aside from a few species, such as the spirostreptid *Orthoporus ornatus* of American deserts, it lacks the waxy layer seen in insects. For this reason, myriapods rely to a considerable extent on behavioral strategies to avoid desiccation. Many live in humid or wet environments or are active only during cool periods. Other myriapods stay hidden in cool or moist microhabitats, such as under rocks, during hot hours of the day or dry periods.

A few geophilomorph centipedes live in intertidal habitats, under rocks or in algal mats. A few millipedes have semiaquatic habits, for example, the littoral julidan *Thalassisobates littoralis* that lives among the stranded decaying matters on the shores of the Mediterranean Sea. However, this species does not spend much time underwater, unlike some subterranean species from caves in southern Europe or the Amazonian *Myrmecodesmus adisi*, whose juveniles spend up to 11 months underwater. A few geophilomorph centipedes, also from periodically inundated Amazonian forests, tolerate month-long submersion. When underwater, these myriapods apparently rely on plastron respiration; in other words, they use water-dissolved oxygen that reaches their tracheae via minute air bubbles trapped into the spiracles or retained by a specialized integument. Although the tracheal system of myriapods (except for the unique sort present in scutigeromorph centipedes) greatly resembles that of insects, there is evidence that it evolved independently.

Nervous System and Sense Organs

The myriapod nervous system conforms to the basic arthropod plan described in Chapter 20. Very little secondary fusion of ganglia occurs, and the ventral nerve cord retains much of its primitive double nature, with a pair of fused ganglia in each segment. Millipedes possess two pairs of fused ganglia in each diplosegment.

As in other arthropods, the cerebral ganglion of myriapods comprises three distinct regions: the preantennal protocerebrum (associated with the eyes, if these are present), the deutocerebrum (associated with the antennae), and the tritocerebrum (Figure 23.6). A

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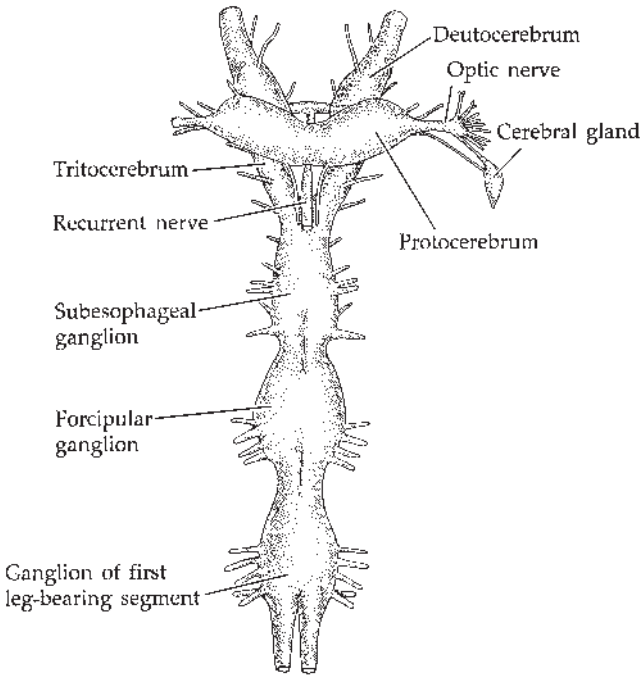

FIGURE 23.6 The brain and anterior ganglia of a centipede. *Lithobius forficatus* (dorsal view). (After J. G. E. Lewis. 1981. *The Biology of Centipedes*. Cambridge University Press, New York.)

subesophageal ganglion controls the mouthparts, salivary glands, and some local musculature.

Myriapods typically possess eyes, although these are lacking in all pauropods, symphylans, and geophilomorphs and in many scolopendromorphs among the centipedes, as well as in siphoniulids, siphonophoridans, and polydesmidans among the millipedes. Many troglobitic (cave-dwelling) species belonging to other groups, especially to the lithobiomorph centipedes, are also blind. Centipedes can possess a few or many independent eyes (Figure 23.7). In the scutigeromorph centipedes, up to

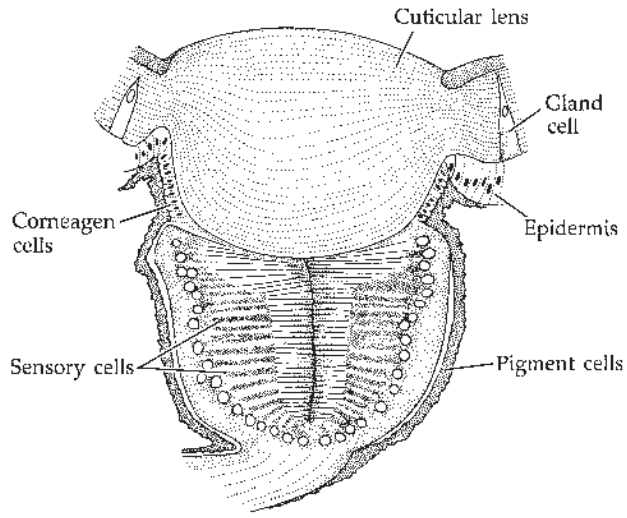

FIGURE 23.7 An eye of a centipede (section).

200 of these eyes cluster to form a compound eye. However, the eyes of living centipedes appear to function only in the detection of light and dark, and not in image formation. Many millipedes have a compound eye of up to about 90 ommatidia on each side of the head. Some millipedes also possess integumental photoreceptors, and many eyeless species exhibit negative phototaxis.

Centipedes and millipedes are noted for their highly sensitive antennae, which are richly supplied with tactile and chemosensory setae. In many species, an **organ of Tömösváry** (Figure 23.8) is located at the base of each antenna. Each part of this paired organ consists of a disc with a central pore where the ends of sensory neurons converge. The exact role of this organ has yet to be clearly established, and speculation has run the gamut from chemosensation to pressure or humidity sensation or the detection of sound or vibration.

Reproduction and Development

Myriapods are gonochoristic and oviparous, although parthenogenesis occurs in several families of millipedes and in some centipedes, pauropods, and symphylans. Many myriapods, like most arachnids, rely on indirect copulation and insemination. Packets of sperm (spermatophores) are deposited in the environment, or they are held by the male and picked up by the female. All myriapods have direct development, with the young hatching (except in pauropods) as "miniature adults," although often with fewer body segments.

Chilopoda Female centipedes possess a single elongate ovary located above the gut, whereas males have from 1 to 26 testes similarly placed (Figure 23.9). The oviduct joins with the openings from several accessory glands and a pair of seminal receptacles just internal to the gonopore, which is situated on the genital segment (the legless segment in front of the telson). The gonopore of females is usually flanked by a pair of small grasping appendages, or gonopods, that manipulate the males' sperm packets. In males the testes join the ducts of several accessory glands and a pair of seminal vesicles near the gonopore, which opens on the ventral surface of the genital segment. The male gonopore also lies between a pair of small gonopods.

Sperm are packed into spermatophores, which are transferred to the female. In some cases (e.g., scutigeromorphs), males deposit spermatophores directly on the ground and the females simply pick them up. In most species, however, males deposit a spermatophore on a silken **nuptial net**, which is spun from modified genital glands (Figure 23.10). Mating pairs of centipedes typically perform courtship behavior, stroking each other with their antennae and often moving the large (up to several millimeters) spermatophore into the nuptial net. Eventually the female picks up the spermatophore with her gonopods and inserts it into her gonopore.

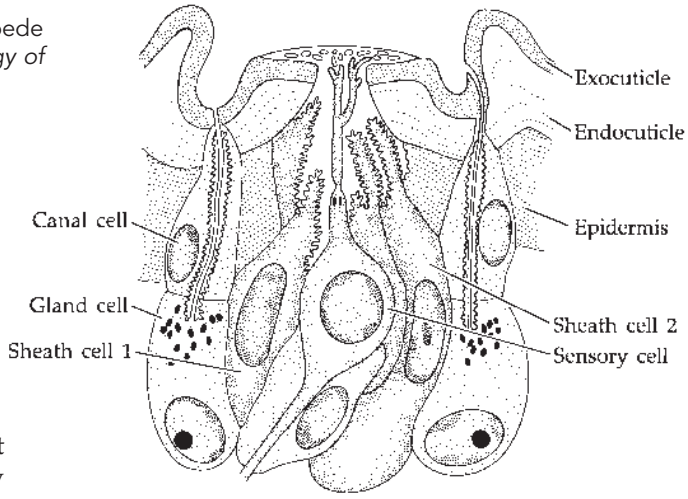

FIGURE 23.8 The organ of Tömösváry. From the centipede *Lithobius forficatus*. (After J. G. E. Lewis. 1981. *The Biology of Centipedes*. Cambridge University Press, New York.)

Fertilization occurs as the eggs pass through the gonoduct. Females often coat the fertilized eggs with moisture and fungicides before depositing them in the ground or in rotting vegetation.

In Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha, the female remains coiled around her brood until hatching, ventrally in the case of craterostigmomorphs and scolopendromorphs (Figure 23.10D), and dorsally in most geophilomorphs. Parental caretaking is almost unknown in the other myriapod classes, except for a few polyzoniidan and platydesmidan millipedes that also exhibit brood care. In a few platydesmidan millipedes, embryo brooding is provided by the male.

Scutigeromorphs, lithobiomorphs, and craterostigmomorphs hatch with 4, 7, and 12 pairs of legs, respectively, and obtain the final number of 15 leg pairs following one (craterostigmomorphs) or a few molts but continue molting until they reach maturity and beyond (hemianamorphosis). Scolopendromorphs and geophilomorphs, however, develop by epimorphosis. That is, they reach the final number of body segments during the embryonic development; no segment or leg pair is added during the postembryonic life.

Diplopoda Millipedes possess a single pair of elongate gonads in both sexes. Unlike those of centipedes, millipede gonads lie between the gut and the ventral nerve cord. The gonopores open on the third (genital) trunk segment. In females each oviduct opens separately into a genital atrium near the coxae of the second pair of legs. A groove in the vulva leads into one or more seminal receptacles. In many millipede groups (but not in polydesmidans), males possess a pair of penes, or **gonapophyses**, also on the coxae of the second pair of legs.

The mandibles are used to transfer sperm in the "pill millipedes," but more commonly one or two pairs of legs are modified as copulatory appendages, or gonopods. Usually, gonopods replace the anterior pair or both pairs of legs of the seventh trunk segment; only in the Colobognatha do the gonopods replace the posterior leg pair of trunk segment 7 and the anterior leg pair of trunk segment 8. Males bend the anterior body

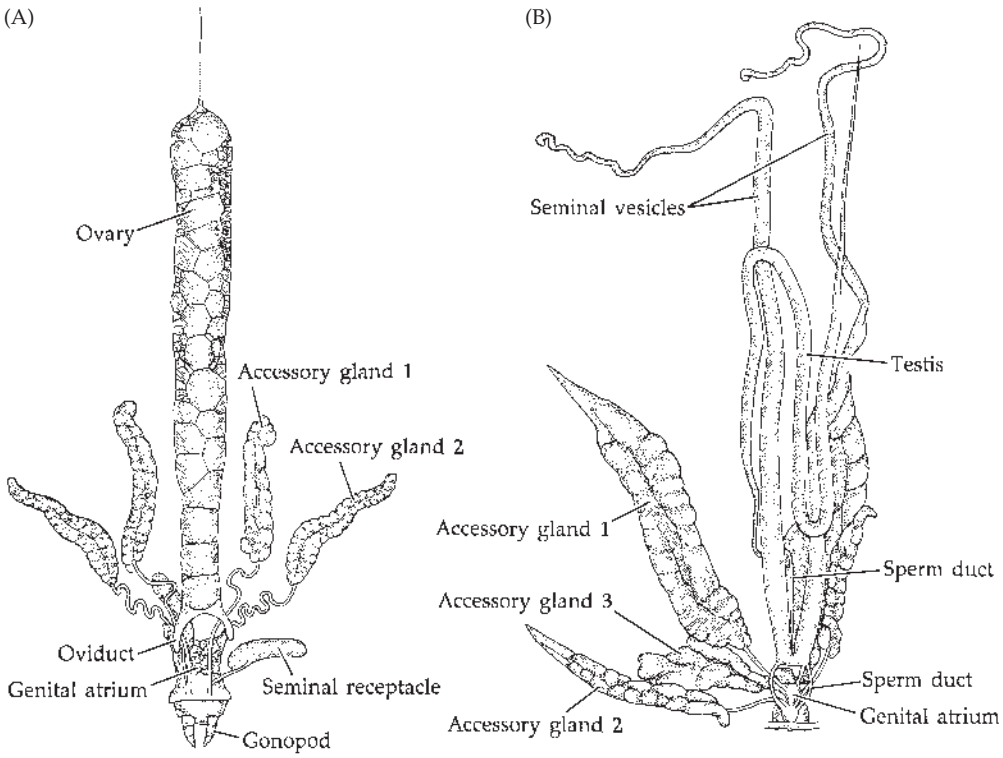

FIGURE 23.9 Reproductive systems of the centipede *Lithobius forficatus*. (A) Female system. (B) Male system.

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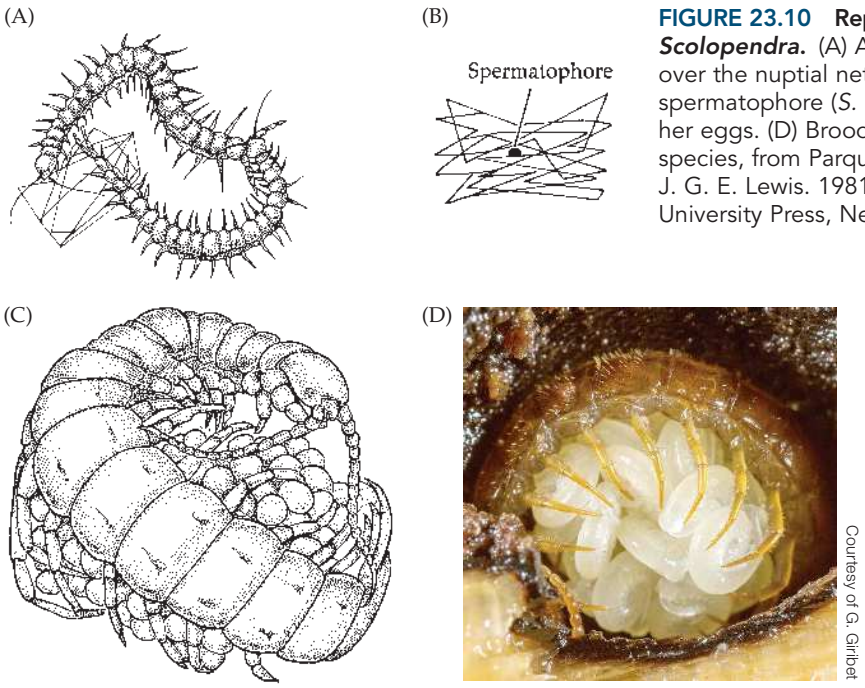

Courtesy of G. Giribet

FIGURE 23.10 Reproductive behavior in the centipede *Scolopendra*. (A) A male and female in mating position over the nuptial net (*S. cingulata*). (B) A nuptial net with a spermatophore (*S. cingulata*). (C) A female *S. cingulata* and her eggs. (D) Brooding female of an unidentified *Cryptops* species, from Parque Nacional Puyehue, Chile. (C after J. G. E. Lewis. 1981. *The Biology of Centipedes*. Cambridge University Press, New York.)

segments back under the trunk until the penes and gonopods make contact, whereupon the latter pick up a spermatophore in preparation for mating.

In most millipedes, mating occurs by indirect copulation, in which the male and female genital openings never actually make contact, although the male and female may embrace with their legs and mandibles and may coil their trunks together. Sometimes a pair remains in such an embrace for up to two days. Pheromones are known to play an important role in many species. Antennal tapping, head drumming, and stridulation may be included in the mating repertoire (Figure 23.11). Males of the family Sphaerotheriidae produce sounds during courtship by rubbing the telopods against the back edge of the body. The *Sphaerotherium* (Sphaeotheriida) male usually stridulates when in contact with a female to initiate mating, probably to prevent the female from rolling into a ball or to stimulate her to unroll if she has already done so.

Males often have an array of secondary sexual characteristics, including strong modifications of the first pair of legs. In species of the genus *Chordeuma* (Chordeumatida) in Europe, dorsal glands on trunk ring XVI of the male produce a secretion upon which females feed prior to mating.

Fertilization takes place as the eggs are laid. In pentazonian millipedes, the last pair of male legs is modified into strong claspers, used to hold the female in place. In these millipedes, males mold soil into a small cup into which they ejaculate sperm. The sperm-filled cup is then passed to the female, who is firmly held by the male's large claspers. Eggs are usually laid in the soil, although some species also produce silk bags to house the eggs. Some species fashion a nest of soil and humus reinforced

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FIGURE 23.11 Rusty millipede (*Trigoniulus corallinus*), Hawaii. The large, shield-like plate behind the head of this millipede is the first trunk ring, the collum, a segment without appendages. The next four diplosegments (2–5) have a single pair of legs, whereas ring 6 has two pairs of legs. Notice, too, that ring 7 of the male (on top) appears to lack legs. In fact this ring's diminutive appendages are hidden and specialized for sperm transfer to the female if she accepts him as a mate. All remaining rings from diplosegment 8 to the last diplosegment of the body have two pairs of walking legs. The close contact between male (above) and female might suggest mating, but during sperm transfer the partners actually take a different position. This photograph likely shows a preliminary act (i.e., mechanical stimulation by the male) and mating will follow if the female accepts the male.

with parental feces, or the entire nest may be composed of fecal material. One to 300 eggs are laid at a time.

Most newborn millipedes have only three pairs of legs; new segments and leg pairs are added at each molt, according to one of three possible developmental schedules. In Pentazonia (as in the pill millipede *Glomeris*: Glomerida) the final number of segments and leg pairs is obtained after some molts, but the millipede must undergo further molts without segmental increase before achieving adult size and sexual maturity (hemianamorphosis). In polydesmidans and other helminthomorphs, the achievement of the final number of segments and leg pairs coincides with obtaining the adult condition and no further molt occurs (teloanamorphosis). In the remaining helminthomorphs, new segments and leg pairs are added at every molt, and the animal continues molting even after reaching sexual maturity (euanamorphosis).

The males of some European julids may undergo periodomorphosis: specific environmental conditions may induce sexually mature males to molt to intercalary males with regressed gonopods, thereby suspending reproductive activity. This is resumed after one or more additional molts, with newly differentiated gonopods.

Pauropoda In female pauropods a single ovary lies beneath the gut, but in the males the testes are located above the gut. As in millipedes, the gonopore of the female (a median, unpaired opening) and the gonopores of the male (two paired openings) are on the third trunk segment. Females take up a spermatophore, often after the male has suspended it from one or a few silk threads spanning two stones or leaves. Fertilization is internal. The yolky eggs are laid in decaying wood. Postembryonic development begins with a motionless "pupoid stage" with minute oral and anal openings and inarticulated traces of the antennae and of the first two pairs of legs. The next molt produces the first active juvenile, with three pairs of legs. The development then proceeds by anamorphosis through four juvenile stages and one adult stage.

Symphyla Symphylans display one of the more unusual methods of fertilization in the animal kingdom. Paired gonads discharge through gonopores on the third trunk segment in both sexes. Males deposit spermatophores in the environment. At least some symphylans construct stalklike structures, topped with spermatophores. When a female encounters one of these sperm packages, she bites off the spermatophores and stores the sperm in her preoral cavity. When her own eggs are ripe, the female removes them from her gonopore with her mouthparts and cements them to moss or some other substrata. Fertilization occurs during this process as she coats each egg with the stored sperm. Young symphylans hatch with only about half the adult number of trunk segments and appendages.

During postembryonic development, first-order and second-order molts regularly alternate until maturity is reached. A new two-segment unit is added after each first-order molt, but only one more pair of legs is differentiated, the other pair differentiating after the subsequent second-order molt, at which time no new segments are added. Mature symphylans continue to molt throughout life (up to 40 times in *Scutigerella immaculata*), without further addition of segments or legs.

Embryonic Development

The yolky eggs of myriapods rely almost entirely on meroblastic cleavage. Most myriapods undergo early cleavage by intralecithal nuclear divisions, followed by a migration of the daughter nuclei to the peripheral cytoplasm (= periplasm). Here they continue to divide until the periplasm is dense with nuclei, whereupon cell membranes begin to form, partitioning uninucleate cells from one another. At this point the embryo is a periblastula, comprising a yolky sphere that has a few scattered nuclei and is covered by a thin cellular layer, or blastoderm.

Along one side of the blastula a patch of columnar cells forms a germinal disc, sharply marked off from the thin cuboidal cells of the remaining blastoderm. From specific regions of this disc, presumptive endodermal and mesodermal cells begin to proliferate as germinal centers. These cells migrate inward during gastrulation to lie beneath their parental cells, which now form the ectoderm. The mesoderm proliferates inward as a longitudinal gastral groove; the cells of the developing gut usually surround and gradually begin absorbing the large central yolky mass of the embryo.

Segments begin to demarcate and proliferate and eventually develop appendage buds. The mouth and anus arise by ingrowths of the ectoderm that form the fore- and hindguts, which eventually establish contact with the developing endodermal midgut.

Variations on this basic scheme occur in groups with secondary yolk reduction, such as in pauropods and symphylans. In these groups a largely holoblastic cleavage takes place, and a coeloblastula actually forms. In most centipedes, a type of cleavage occurs that is somewhat intermediate between total and superficial cleavage. After a few intralecithal nuclear divisions, the yolk breaks up into blocks called yolk pyramids. Gradually the yolk pyramids disappear, and development shifts to the superficial type.

Myriapod Phylogeny

Myriapoda and Hexapoda had long been considered sister groups, together forming a clade called Atelocerata, in turn regarded as sister group to the Crustacea within Mandibulata. The sister-group relationship between myriapods and hexapods was based upon

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several seemingly strong synapomorphies, including proctodeal Malpighian tubules, lack of the second pair of antennae, uniramous legs, and tracheal respiratory systems. However, there is now strong evidence that hexapods arose from within Crustacea, and thus the putative synapomorphies linking Hexapoda to Myriapoda must have evolved through convergent or parallel evolution. Some molecular phylogenies suggested that Myriapoda is sister group to Chelicerata (within a clade called Myriochelata or Paradoxopoda), but most recent studies agree that Myriapoda is a sister group to the Pancrustacea (Hexapoda plus a paraphyletic Crustacea).

The monophyly of the four myriapod classes is supported by the following traits:

- **Chilopoda** Appendages of first trunk segment housing a poison gland; 15 pairs (secondarily more) of walking legs; alternation of long and short tergites, with reversal on segments 7–8, and spiracles associated with the segments bearing long tergites
- **Diplopoda** Trunk formed by diplosegments; antenna with eight articles, the distal article bearing apical sensory cones; spermatozoon without flagellum
- **Pauropoda** Antennae branching, with a special sensory organ (globulus); paired pseudoculi on lateral sides of head capsule
- **Symphyla** Single pair of tracheal stigmata on sides of head capsule; eyes absent; paired lateral pockets in mouth cavity of female functioning as spermathecae; 12 pairs of trunk legs; unpaired genital opening; paired terminal spinnerets

Chilopoda is probably sister group to the remaining myriapod classes, which are collectively classified as the Progoneata, meaning that their genital opening is anterior (in the region of the third body segment) rather than posterior as in the centipedes (Opisthogoneata). Within the Progoneata, Pauropoda and Diplopoda probably form a clade (Dignatha) defined by the lack of limbs on the postmaxillary segment, spiracles opening at the bases of the walking legs, a motionless pupoid stage after hatching, and the first free-living juvenile having three pairs of legs.

Myriapods with calcified exoskeletons are reasonably well preserved in the fossil records, the oldest specimens being from the middle Silurian (425 Ma), although older trace fossils from the Late Ordovician (some 450 Ma) have also been attributed to them. Both modern clades of chilognathan millipedes (Pentazonia and Helminthomorpha) are documented since the Pennsylvanian, in the Carboniferous. Extinct myriapod taxa are the Arthropleurida (which includes the giant *Arthropleura*, up to 2.6 m long), Eoarthropleurida, and Microdecemplicida, all Paleozoic. From middle Silurian to late Carboniferous are documented the Archypolypoda, a group of millipedes with the trunk composed of alternating smaller and larger units with one leg pair each. Myriapods with uncalcified cuticle such as centipedes and penicillate millipedes are fairly common in amber and are extensively documented since the Cretaceous, but the oldest centipedes—*Crussolum crusserratum*, a notostigmophoran, and *Devonobius delta*, a pleurostigmophoran of debated affinities—are known from the Silurian–Devonian and Middle Devonian (380 Ma), respectively.

Chapter Summary

This chapter introduced you to one of the four subphyla of Arthropoda, the Myriapoda—centipedes, millipedes, and two very small groups called Pauropoda and Symphyla. All of the 16,000 known species of living myriapods are terrestrial, but the lineage probably had its origin in the aquatic realm. Myriapods are familiar arthropods, easily distinguished from most other terrestrial invertebrates by a body divided into just two tagmata: the head and the long, homonomous, and many-segmented trunk bearing many pairs of jointed legs. As in the subphylum Hexapoda, myriapods have an aerial gas exchange system composed of tracheae and spiracles (convergent with those in Hexapoda). Also as in the Hexapoda, the head is equipped with a single pair of antennae. The mouthparts are represented by the mandibles and the first maxillae; a second pair of maxillae is present in the centipedes and symphylans, but in millipedes and pauropods the corresponding segment bears no appendages. Millipedes are slow-moving detritus feeders that generally spend their time burrowing through soil and litter. Uniquely among the arthropods, most millipede trunk segmental units bear two pairs of legs each and are described as diplosegments. In contrast to millipedes, most centipedes are fast-running predators, with one pair of legs per segment and with poison claws at the tips of the first pair of trunk legs (thus turned into peculiar maxillipeds called forcipules or prehensors). When threatened, centipedes usually strike out with the poison claws, with which they can inflict a painful bite. Important future research on the Myriapoda will include a better understanding of centipede venoms and millipede defensive secretions as well as the genomic and physiological adaptations they acquired in adapting to terrestrial environments.

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Courtesy of G. Giribet

CHAPTER 24

Phylum Arthropoda
Subphylum Chelicerata

The arthropod subphylum Chelicerata includes Xiphosura (horseshoe crabs), Arachnida (spiders, scorpions, mites, ticks, daddy longlegs, and several less familiar groups), and Pycnogonida (sea spiders); the first two taxa together have been traditionally referred to as Euchelicerata, but recent phylogenomic work has questioned this separation, as it finds that horseshoe crabs often nest within Arachnida (a classificatory change that we do not make in this edition as we await further studies and possible confirmation). In addition to the 113,000 or so described living species, there is an impressive array of fossil forms (about 2,000 species), such as the Paleozoic giant water scorpions (Eurypterida; nearly 250 described species), some of which were nearly 3 m long, that lived from the Ordovician to the Permian. Chelicerata had their origin in ancient Cambrian seas. Pycnogonida and Xiphosura remain entirely marine, but Arachnida invaded land long ago and today are mostly terrestrial, with notable exceptions among the mites. If the new position of horseshoe crabs is correct, this implies a recolonization of the sea. When compared with other Metazoa, Chelicerata are second only to the insects in species diversity, having adapted to virtually every imaginable situation and lifestyle on land, with the mites having an enormous diversity of life cycles.

In addition to the basic characteristics common to all arthropods, chelicerates are distinguished by several unique features (Box 24A). The body is typically divided into two main regions—the prosoma and opisthosoma (Figures 24.1–24.3), although this is different in mites and ticks.[1]

This chapter has been revised by Gonzalo Giribet and Gustavo Hormiga.

[1]These two body regions are sometimes also referred to as the cephalothorax and abdomen, but they are not homologous with those regions in other arthropods.

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

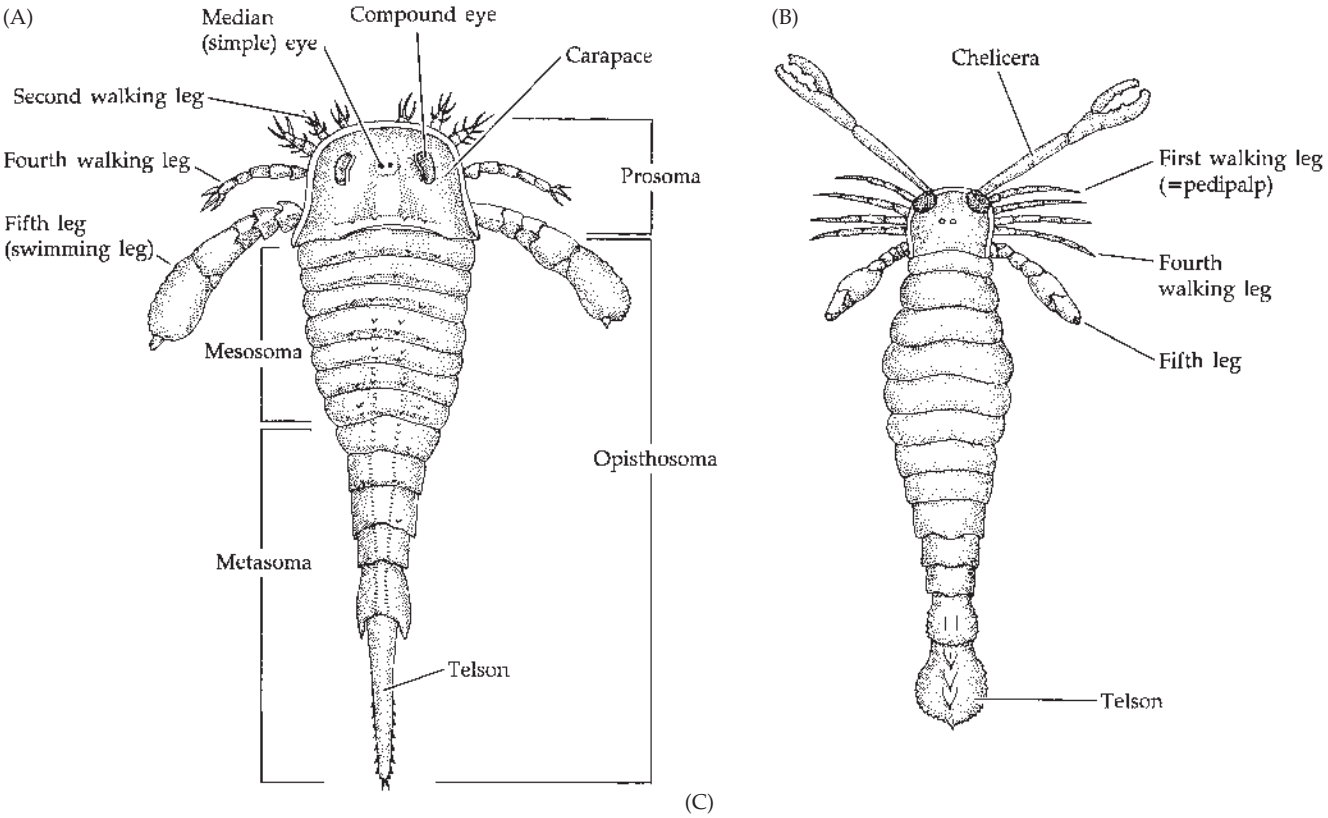

FIGURE 24.1 Water scorpions (subclass Merostomata, order Eurypterida), an extinct group of chelicerates. (A) *Eurypterus* (dorsal view). (B) *Pterygotus bohemicus*, which reached lengths of nearly 3 meters. (C) *Eurypterus remipes*, a species from the Silurian Period of the Paleozoic. Eurypterids flourished in Paleozoic seas; some probably invaded fresh water and perhaps even land.

Millard H. Sharp/Science Source

BOX 24A Characteristics of the Subphylum Chelicerata

1. Body of two tagmata—prosoma and opisthosoma. Prosoma composed of 7 somites, often covered by carapace-like dorsal shield. Opisthosoma composed of up to 12 somites and a postsegmental telson; subdivided into two parts in some groups.
2. Appendages of prosoma are chelicerae/chelifores, pedipalps/palps, and typically four pairs of walking legs; antennae absent. All appendages multiarticulate.
3. Gas exchange by book gills, book lungs, or tracheae; or through cuticle and gut.
4. Excretion typically by coxal glands and/or Malpighian tubules. Chelicerate Malpighian tubules are probably not homologous with those of insects, terrestrial isopods, or tardigrades.
5. With simple median and lateral (compound in xiphosurans) eyes
6. Gut with two to six pairs of digestive ceca.
7. Most are gonochoristic.

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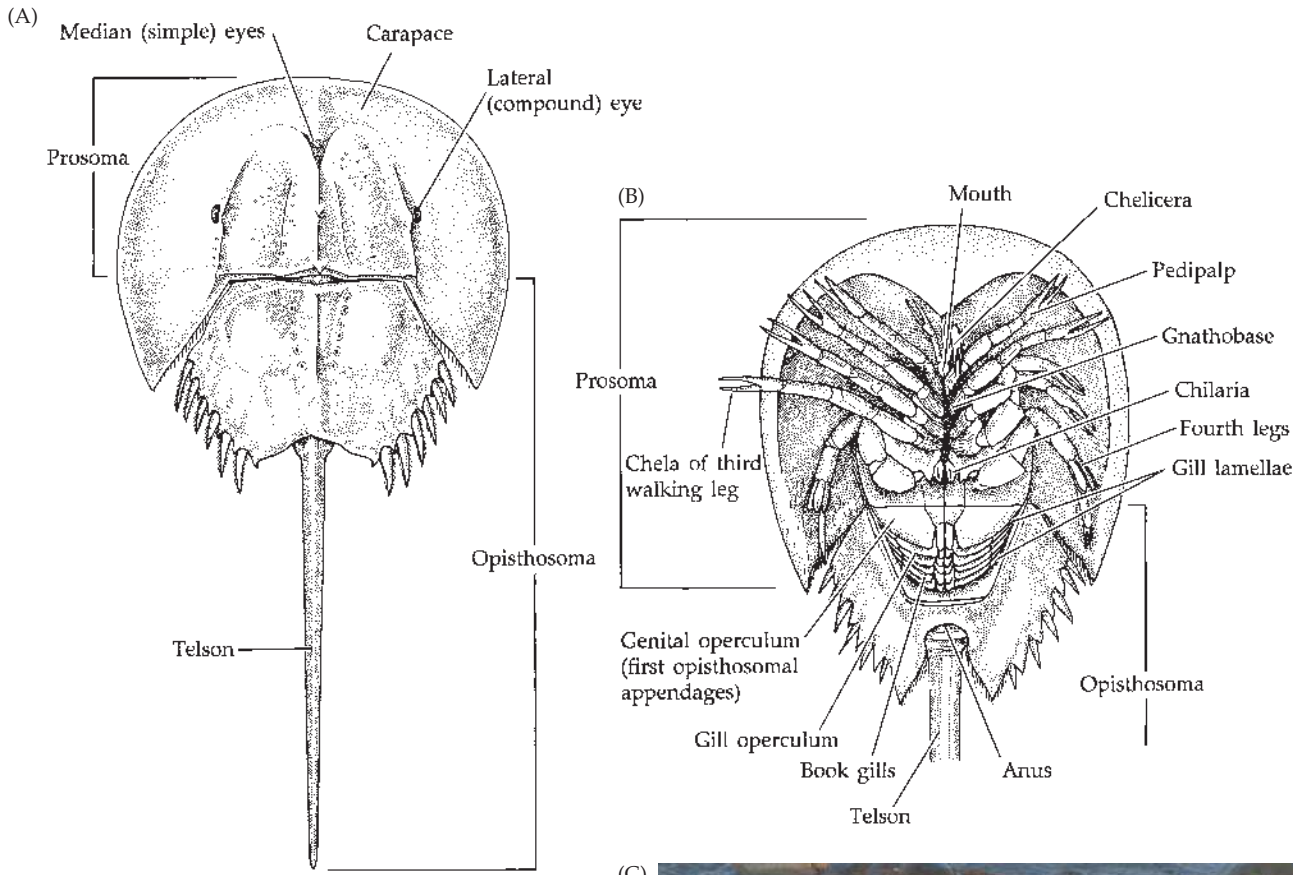

FIGURE 24.2 The American horseshoe crab, *Limulus polyphemus* (subclass Merostomata, order Xiphosura). (A) Dorsal view. (B) Ventral view. (C) A congregation of *L. polyphemus* on an Atlantic beach.

Joe McDonald/Getty Images

In contrast to most other arthropods, it is not possible to delineate a discrete "head" in chelicerates. There are no antennae, but generally six of the seven prosomal segments bear appendages. The first pair of appendages, corresponding to the second prosomal segment, is the chelicerae (called chelifores in pycnogonids), followed by the pedipalps, and then four pairs of walking legs. In the pycnogonids there may exist an additional pair of appendages, the ovigers, between the pedipalps and first walking legs, and the number of walking legs can be greater than four pairs. The chelicerae and pedipalps are specialized for an enormous variety of roles in the various chelicerate groups, including prey capture, sensation, locomotion, and copulation; some of the walking legs also may assume some of these functions, especially tactile (e.g., the first or second legs of some arachnid orders) or copulatory (e.g., the third leg of the male ricinuleids). The opisthosoma usually bears a terminal postsegmental telson. In Xiphosura, and in some arachnid orders, the opisthosoma may be subdivided into two regions, a mesosoma and a metasoma (Figure 24.1). A detailed discussion of chelicerate anatomy is provided in The Euchelicerate Body Plan section.

Chelicerata is a large and diverse taxon comprising three rather different groups: Xiphosura, which includes the horseshoe crabs; Arachnida, including the terrestrial spiders, scorpions, and mites, among others; and Pycnogonida, the sea spiders. To assist readers in gaining a grasp of this large and diverse subphylum, we treat the Euchelicerata and Pycnogonida separately in this chapter.

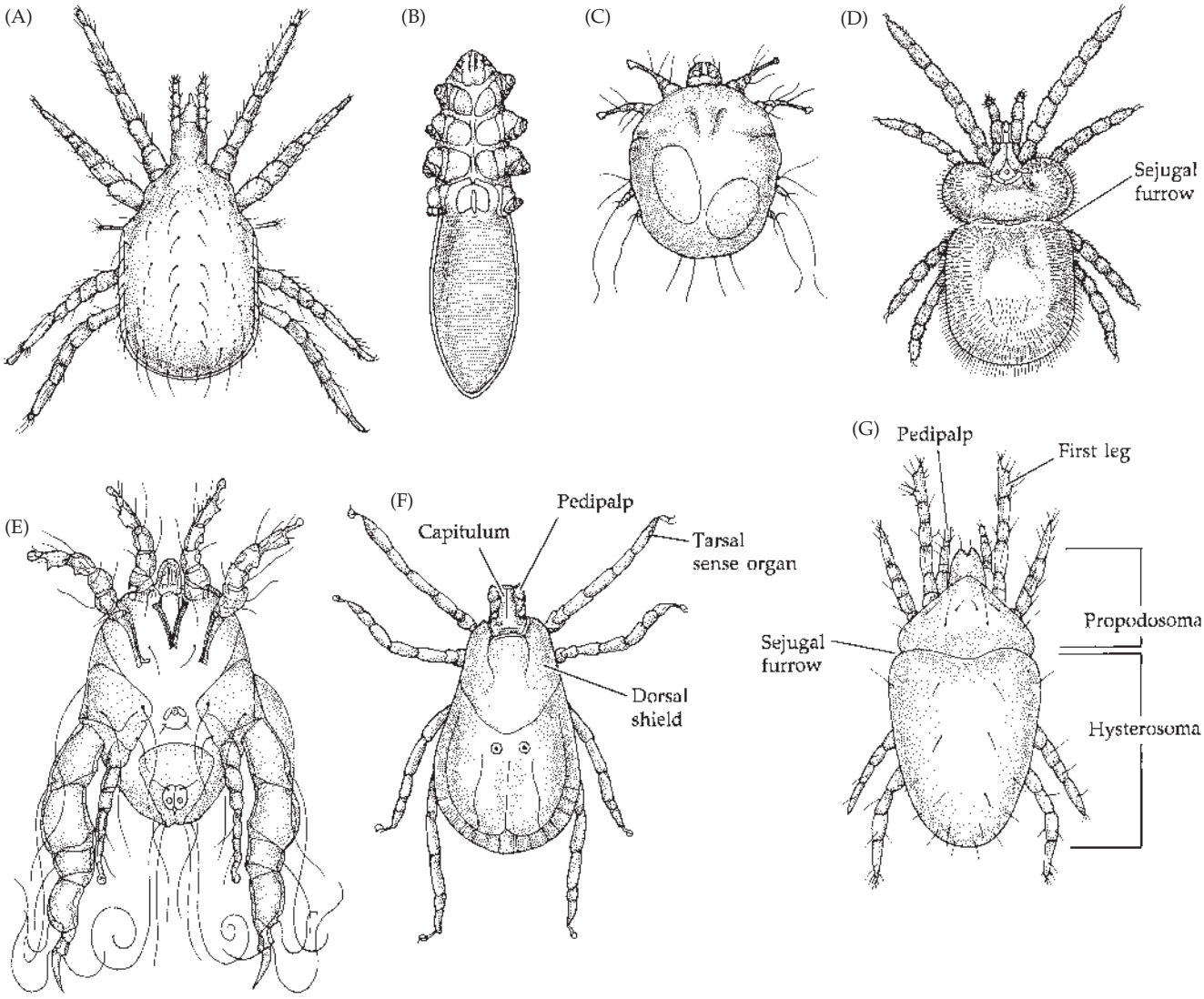

FIGURE 24.3 Members of the acarine orders. (A) The mite *Lasioseius ometes* (Parasitiformes, Mesostigmata). (B) A skin mite, *Demodex* (Acariformes, Trombidiformes), with very short legs. (C) A mange mite, *Sarcoptes scabiei* (Acariformes, Sarcoptiformes). (D) An adult chigger mite, *Trombicula* (Acariformes, Trombidiformes). Note the sejugal furrow between the second and third legs. (E) One of the feather mites, *Analges* (Acariformes, Sarcoptiformes). (F) A tick, *Dermacentor* (Parasitiformes, Ixodida). (G) *Tydeus starri* (Acariformes, Trombidiformes), with a deep sejugal furrow.

CLASSIFICATION OF CHELICERATA

CLASS PYCNOGONIDA The sea spiders, 1,368 extant species.

FAMILY AUSTRODECIDAE (e.g., *Austrodecus*)

FAMILY RHYNCHOTHORACIDAE (*Rhynchothorax*)

FAMILY PYCNOGONIDAE (*Pentapycnon, Pycnogonum*)

FAMILY COLOSSENDEIDAE (e.g., *Colossendeis, Decolopoda, Dodecolopoda, Pentacolossendeis, Hedgpethia*)

FAMILY ENDEIDAE (*Endeis*)

FAMILY PHOXICHILIDIIDAE (e.g., *Anoplodactylus, Phoxichilidium*)

FAMILY PALLENOPSIDAE (*Bathypallenopsis, Pallenopsis*)

FAMILY AMMOTHEIDAE (e.g., *Achelia, Ammothella, Nymphopsis, Tanystylum*)

FAMILY "ASCORHYNCHIDAE" (e.g., *Ascorhynchus, Nymphonella*)

FAMILY "CALLIPALLENIDAE" (e.g., *Austropallene, Callipallene, Pseudopallene*)

FAMILY NYMPHONIDAE (e.g., *Nymphon, Pentanymphon, Sexanymphon*)

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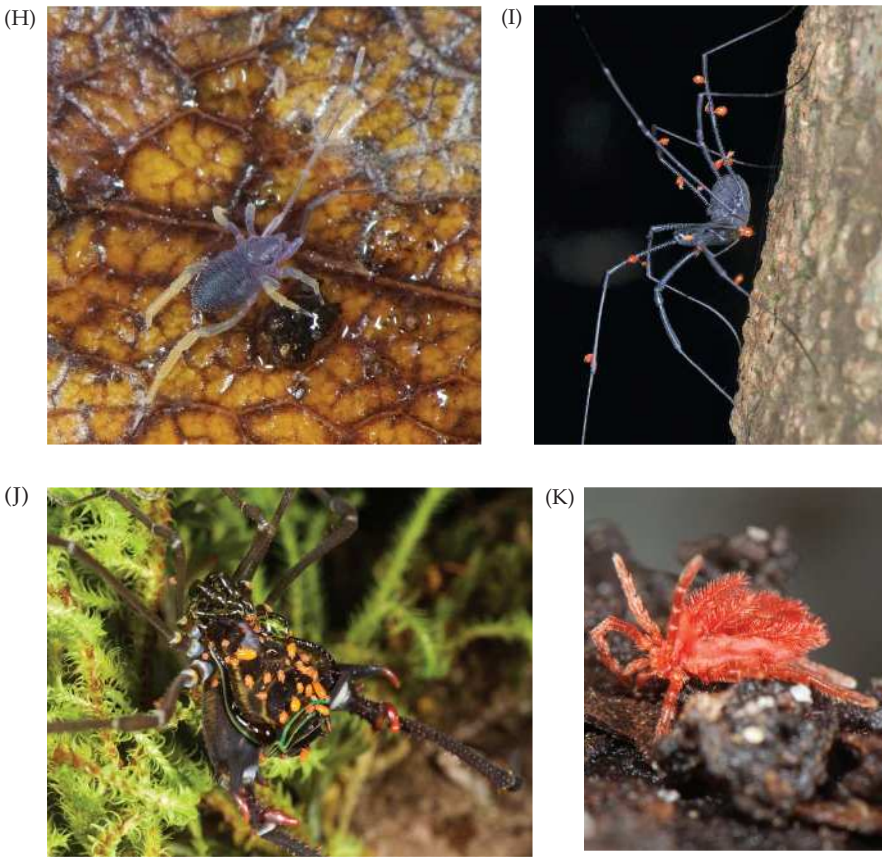

H–L courtesy of G. Giribet

FIGURE 24.3 (*continued*)
Members of the acarine orders. (H) An opilioacarid mite, *Neoacarus* sp. (Opilioacariformes) from South Africa. (I) Phoretic mites on the harvestman *Rhampsinitus transvaalicus*. (J) Phoretic mites on the harvestman *Sadocus polyacanthus*. (K) A Chyzeriidae mite (Acariformes, Trombidiformes). (L) Injured boa constrictor from Tobago with large tick infestation; look closely and you'll see numerous recently attached ticks, in addition to the engorged ones. (A after T. H. Savory. 1964. *Arachnida*. Academic Press, New York; B,D after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

CLASS EUCHELICERATA The eucheliceratas.

SUBCLASS MEROSTOMATA

ORDER XIPHOSURA Horseshoe crabs. (*Limulus*, *Carcinoscorpius*, *Tachypleus*)

SUBCLASS ARACHNIDA Spiders, scorpions, mites, ticks, and their kin; 16 extant orders.

ORDER AMBLYPYGI Whip spiders, tailless whip scorpions. (e.g., *Acanthophrynus*, *Damon*, *Heterophrynus*, *Stegophrynus*, *Tarantula*)

ORDER ARANEAE True spiders.

SUBORDER MESOTHELAE Segmented spiders; 1 family, Liphistiidae. (e.g., *Heptathela*, *Liphistius*)

SUBORDER OPISTHOTHELAE
Unsegmented spiders.

INFRAORDER MYGALOMORPHAE
Tarantula-like spiders; orthognathous chelicerae. About 27 families, including the following:

FAMILY CTENIZIDAE Trapdoor spiders. (e.g., *Cteniza*, *Cyrtocarenum*)

FAMILY EUCTENIZIDAE (e.g., *Eucteniza*, *Aptostichus*)

FAMILY ATYPIDAE Purse-web spiders. (e.g., *Atypus, Sphodros*)

FAMILY THERAPHOSIDAE Tarantulas and bird spiders. (e.g., *Acanthoscurria*, *Aphonopelma, Theraphosa*)

FAMILY DIPLURIDAE Diplurid funnel-web spiders. (e.g., *Diplura, Linothele*)

FAMILY ATRACIDAE Australian funnel-web spiders. (e.g., *Atrax*, *Hadronyche*)

INFRAORDER ARANEOMORPHAE
Araneomorph spiders; labidognathous chelicerae. About 75 families, including the following:

FAMILY HYPOCHILIDAE Lampshade weavers. (e.g., *Hypochilus, Ectatosticta*)

FAMILY GRADUNGULIDAE Long-claw spiders. (e.g., *Gradungula, Progradungula, Hickmania*)

FAMILY AUSTROCHILIDAE Missing-link spiders. (e.g., *Austrochilus, Thaida*)

FAMILY FILISTATIDAE Crevice weavers. (e.g., *Filistata, Kukulcania*)

FAMILY OONOPIDAE Goblin spiders. (e.g., *Costarina, Oonops, Opopaea, Orchestina*)

FAMILY DYSDERIDAE Woodlouse hunters. (e.g., *Dysdera*, *Harpactocrates, Rhode*)

FAMILY PHOLCIDAE Cellar spiders, daddy longleg spiders. (e.g., *Modisimus*, *Pholcus*, *Spermophora*)

FAMILY SCYTODIDAE Spitting spiders. (e.g., *Scytodes*)

FAMILY SICARIIDAE Brown recluse spiders. (e.g., *Loxosceles*, *Sicarius*)

FAMILY ARCHAEIDAE Assassin spiders. (e.g., *Austrarchaea, Eriauchenus*)

FAMILY ERESIDAE Velvet spiders. (e.g., *Eresus, Stegodyphus*)

FAMILY THERIDIIDAE Cobweb and widow spiders. (e.g., *Anelosimus*, *Argyrodes*, *Episinus*, *Latrodectus*, *Parasteatoda*, *Steatoda*)

FAMILY ULOBORIDAE Cribellate orb-weavers. (e.g., *Hyptiotes*, *Miagrammopes*, *Uloborus*)

FAMILY DEINOPIDAE Ogre-faced spiders. (e.g., *Deinopis, Menneus*)

FAMILY ARANEIDAE Ecribellate orb-weavers. (e.g., *Araneus*, *Argiope*, *Cyrtophora*, *Gasteracantha*, *Mastophora*, *Nephila*, *Neoscona*, *Zygiella*)

FAMILY TETRAGNATHIDAE Long-jawed orb-weavers. (e.g., *Dolichognatha*, *Leucauge*, *Meta*, *Pachygnatha, Tetragnatha*)

FAMILY MIMETIDAE Pirate spiders. (e.g., *Australomimetus*, *Ero, Mimetus*)

FAMILY LINYPHIIDAE Sheet-web spinners, dwarf spiders. (e.g., *Agyneta*, *Dubiaranea, Erigone*, *Haplinis*, *Oedothorax*, *Linyphia, Neriene*)

FAMILY ANAPIDAE Ground orb-weavers. (e.g., *Acrobleps, Anapis, Comaroma, Micropholcomma*)

FAMILY CLUBIONIDAE Sack-spiders. (e.g., *Clubiona, Elaver*)

FAMILY AGELENIDAE Funnel-weavers. (e.g., *Agelena, Coelotes, Tegenaria*)

FAMILY LYCOSIDAE Wolf spiders. (e.g., *Lycosa, Pardosa, Pirata, Schizocosa*)

FAMILY CTENIDAE Wandering spiders. (e.g., *Acanthoctenus*, *Anahita, Ctenus, Phoneutria*)

FAMILY TRECHALEIDAE Longlegged water spiders. (e.g., *Barrisca, Cupiennius, Trechalea*)

FAMILY PISAURIDAE Nursery-web spiders. (e.g., *Architis, Dolomedes, Pisaura*)

FAMILY OXYOPIDAE Lynx spiders. (e.g., *Oxyopes, Peucetia*)

FAMILY THOMISIDAE Crab spiders. (e.g., *Diaea, Misumena, Thomisus, Xysticus*)

FAMILY SPARASSIDAE Huntsman spiders. (e.g., *Delena, Heteropoda, Micrommata, Olios, Pandercetes*)

FAMILY GNAPHOSIDAE Ground spiders. (e.g., *Drassodes, Eilica, Gnaphosa, Micaria, Zelotes*)

FAMILY SALTICIDAE Jumping spiders. (e.g., *Habronattus, Lyssomanes, Maratus, Phidippus, Portia, Salticus, Spartaeus*)

ORDER OPILIONES Harvestmen, daddy longlegs.

SUBORDER CYPHOPHTHALMI Mite harvestmen; 6 families. (e.g., *Cyphophthalmus, Siro, Pettalus, Neogovea, Stylocellus, Troglosiro*)

SUBORDER EUPNOI Daddy longlegs; 7 families. (e.g., *Caddo, Leiobunum, Neopilio, Phalangium*)

SUBORDER DYSPNOI Daddy longlegs, hard-bodied daddy longlegs; 8 extant families. (e.g., *Acropsopilio, Ischyropsalis, Nemastoma, Ortholasma, Sabacon, Trogulus*)

SUBORDER LANIATORES Armored harvestmen; 29 families. (e.g., *Algidia, Fumontana, Sitalcina, Sandokan, Stygnomma, Zalmoxis, Vonones*)

ORDER PALPIGRADI Palpigrades, micro-whip scorpions; 2 families with 6 extant genera. (e.g., *Allokoenenia, Eukoenenia, Koenenia, Leptokoenenia, Prokoenenia*)

ORDER PSEUDOSCORPIONES Pseudoscorpions, false scorpions; 25 families. (e.g., *Chelifer, Chitrella, Chthonius, Dinocheirus, Garypus, Menthus, Pseudogarypus*)

ORDER RICINULEI Ricinuleids or hooded-tick spiders; 3 genera: *Cryptocellus, Pseudocellus, Ricinoides*

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ORDER SCHIZOMIDA Schizomids; 2 families. (e.g., *Agastoschizomus, Megaschizomus, Nyctalops, Protoschizomus, Schizomus*)

ORDER SCORPIONES Scorpions; 20 families.

PARVORDER BUTHIDA

SUPERFAMILY BUTHOIDEA (e.g., *Androctonus, Buthus, Centruroides, Tityus*)

SUPERFAMILY CHAERILOIDEA (e.g., *Chaerilus*)

SUPERFAMILY PSEUDOCHACTOIDEA (e.g., *Troglokhammouanus*)

PARVORDER IURIDA

SUPERFAMILY IUROIDEA (e.g., *Iurus*)

SUPERFAMILY BOTHRIUROIDEA (e.g., *Bothriurus*)

SUPERFAMILY SUPERSTITIONOIDEA (e.g., *Superstitionia*)

SUPERFAMILY CHACTOIDEA (e.g., *Euscorpius*)

SUPERFAMILY SCORPIONOIDEA (e.g., *Diplocentrus*, *Urodacus*)

SUPERFAMILY VAEJOVOIDEA (e.g., *Vaejovis*)

INCERTAE SEDIS (e.g., *Belisarius*, *Hadrurus*, *Uroctonus*)

ORDER SOLIFUGAE Sun spiders, wind spiders, camel spiders; 13 families. (e.g., *Biton*, *Branchia*, *Dinorhax*, *Galeodes*, *Solpuga*)

ORDER UROPYGI Whip scorpions or vinegaroons; 1 family with 16 genera. (e.g., *Albaliella*, *Chajnus*, *Mastigoproctus*)

SUPERORDER PARASITIFORMES Mites and ticks.

ORDER HOLOTHYRIDA About 25 species, mainly feeding on the fluids of dead arthropods. (e.g., *Allothyrus, Neothyrus*)

ORDER IXODIDA Hard ticks and soft ticks. (e.g., *Amblyomma, Dermacentor, Ixodes, Rhipicephalus, Argas, Nuttalliella*)

ORDER MESOSTIGMATA Free-living predatory mites. (e.g., *Uropoda, Lasioseius*)

SUPERORDER OPILIOACARIFORMES

ORDER OPILOACARIDA Primitive mites. (e.g., *Opilioacarus, Neocarus*)

SUPERORDER ACARIFORMES Mites, dust mites, and "chiggers."

ORDER TROMBIDIFORMES A large, diverse order of mites, comprising more than 25,000 described species in 151 families. (e.g., *Trombidium, Scirus, Demodex, Tydeus*)

SUBORDER PROSTIGMATA (e.g., *Halotydeus, Penthaleus*)

SUBORDER SPHAEROLICHIDA

ORDER SARCOPTIFORMES Large order of mites, comprising around 230 families and 15,000 described species.

SUBORDER ORIBATIDA "Chewing" mites, moss mites, or beetle mites. (e.g., *Archegozetes, Conoppia*)

SUBORDER ASTIGMATA "Biting mites," dust mites, many parasites of vertebrates. (e.g., *Acarus, Dermatophagoides*)

Synopses of Living Chelicerate Groups

Class Eucheliceratа

Body composed of 2 tagmata: prosoma and opisthosoma. Prosoma composed of 7 segments, often covered by a carapace-like dorsal shield; with simple median eyes and compound or simple lateral eyes. Opisthosoma of up to 12 segments (subdivided into 2 parts in some groups) and a postsegmental telson. Prosomal appendages are chelicerae, pedipalps, and 4 pairs of walking legs; antennae absent; all appendages uniramous and multiarticulated.

Subclass Merostomata

Prosoma covered by a large, hardened, carapace-like shield; pedipalps similar to walking legs; opisthosoma undivided or divided into mesosoma and metasoma; with flaplike appendages as book gills; telson long and spiked. The merostomates diversified during the great Cambrian invertebrate radiation. Fossil eurypterids and xiphosurans are known from the Ordovician, and they flourished in the Silurian and Devonian. Alas, only 4 species of merostomates have survived to modern times, all xiphosurans—the horseshoe crabs.

Order Xiphosura Certain extinct forms and the living horseshoe crabs (Figure 24.2). Opisthosoma unsegmented and undivided, but with 6 pairs of flaplike appendages, the first pair fused medially as a genital operculum over the gonopores, the last 5 pairs modified as book gills. Pedipalps and walking legs chelate; last (fourth) pair of legs splayed distally for support on soft sediments (*Carcinoscorpius, Limulus, Tachypleus*).

Extant members of the order Xiphosura (the horseshoe crabs) are regarded as "living fossils" and are, of course, far better known than their extinct relatives. Especially well studied is *Limulus polyphemus* (Figure

The class Pycnogonida (sea spiders) is treated separately at the end of this chapter.

24.2C), the common horseshoe crab of the Atlantic and Gulf coasts of North America and a favorite laboratory animal of physiologists. Living xiphosurans inhabit shallow marine waters, generally on clean sandy bottoms, where they crawl about or burrow just beneath the surface, preying on other animals or scavenging. The chelicerae are smaller than the other appendages, being composed of only three articles. Each walking leg is formed of seven articles (coxa, trochanter, femur, patella, tibia, tarsus, pretarsus), the last two of which form the chelae (Figure 24.2B). The coxal endites of the pedipalps and first three walking legs are modified as gnathobases for mastication. Arising from the coxae of the fourth walking legs are tiny appendage-like processes called flabella. In addition, just posterior and medial to the last walking legs is a pair of reduced appendages called chilaria. Their function is unknown, and there is some controversy about their evolutionary significance—some specialists believe that they may reflect an additional opisthosomal segment.

The four living species of Xiphosura belong to three geographically distinct genera in the family Limulidae. *Limulus* (*L. polyphemus*) is restricted to eastern North America, ranging from Nova Scotia to the Yucatán region of Mexico; *Tachypleus* (*T. gigas* and *T. tridendatus*) occurs in Southeast Asia; *Carcinoscorpius* (*C. rotundicauda*) has been collected only from Malaysia, Thailand, and the Philippines and is capable of migrating upriver into fresh water. Another 100 or so extinct species have been described, the oldest being a species of *Lunataspis* from deposits in Manitoba (Canada) that are 445 million years old.

Subclass Arachnida

Prosoma wholly or partly covered by a carapace-like shield; opisthosoma segmented or unsegmented, divided (in scorpions) or undivided; opisthosomal appendages absent or modified as spinnerets (spiders) or pectines (scorpions); penes absent (except in most Opiliones and some mites); gas exchange by tracheae, book lungs, or both but also through the cuticle; nearly all terrestrial; over 110,000 species, in 16 orders.

"Acari" The term "Acari" has been traditionally used for several lineages of mites, ticks, and chiggers (Figure 24.3) that are now thought to be nonmonophyletic and that are currently classified in at least six orders in two main clades of uncertain phylogenetic position within the arachnid tree of life. The first clade is Parasitiformes (encompassing the orders Holothyrida, Ixodida, Mesostigmata) and Opilioacariformes (order Opilioacarida). The second clade is Acariformes (encompassing the orders Trombidiformes and Sarcoptiformes). These two lineages include a huge morphological disparity and a large diversity of ecological and reproductive strategies. For convenience, the six acarine orders (in three superorders) are discussed together below.

In mites (Acariformes) the prosoma and opisthosoma are fused, and a region of flexible cuticle (the **cirumcapitular furrow**) separates the chelicerae and pedipalps from the rest of the body. This anterior body region is called the **capitulum** or gnathosoma, and the remainder of the body is called the **idiosoma**, which is in turn divided into **podosoma** and **opisthosoma**. Another nomenclature divides the body into proterosoma and hysterosoma: the proterosoma includes the gnathosoma and the first two pedigerous segments, and the hysterosoma includes the last two pedigerous segments and the opisthosoma. The old junction between prosoma and opisthosoma is usually visible as the **disjugal furrow**, but more often these are indistinguishably fused. Further, in Acariformes a secondary sejugal furrow sometimes exists between the second and third walking legs, the chelicerae are pincer-like or styliform, the pedipalpal coxae are uniquely fused with head elements, the opisthosoma is unsegmented except in a few primitive forms, gas exchange is cutaneous or by tracheae, the eyes are present or absent, and males of some species have a penis.

Mites and ticks comprise the largest group of arachnids. There are approximately 54,600 described species, and some experts suggest that there may be as many as one million or more yet to be described! Because of the size and diversity of these orders, we give a somewhat extended account. Even so, it is not possible to do justice here to the vast range of forms and lifestyles represented by the mites and ticks.

Mites and ticks occur worldwide. Most are terrestrial, many are parasitic, and some have invaded aquatic environments, both freshwater and marine. Their tremendous evolutionary success, especially of the Acariformes, is reflected in their species diversity and in their extremely varied lifestyles. This success is probably due, at least in part, to a compact body and reduced size. By coupling small size with the inherent arthropod quality of segment and appendage specialization, mites have exploited myriad microhabitats unavailable to larger animals. If the group is polyphyletic, then several ancestral arachnid lineages evolved convergently to capitalize on miniaturization.

Recent classification schemes divide the members of the old "Acari" into two or three groups. One of these is a group of omnivorous and predatory forms named Opilioacariformes with the single order Opilioacarida (Figure 24.3H), which constitutes the sister group of Parasitiformes (some authors group both into Parasitiformes). Opilioacarida are characterized by the retention of opisthosomal segmentation (at least ventrally) and the presence of a transverse groove (the disjugal furrow) separating the prosoma from the opisthosoma. These mites are found on tropical forest floors and in arid temperate habitats.

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The remainder of the thousands of mites and ticks are placed in Parasitiformes and Acariformes, the latter housing most of the species. The body of parasitiform mites is undivided dorsally, there being no clear transverse groove (Figure 24.3A). Parasitiformes includes free-living and symbiotic forms in all parts of the world. The free-living species inhabit various terrestrial habitats, including leaf litter, decaying wood and other organic debris, mosses, insect and small mammal nests, and soil. Most of these mites are predators on small invertebrates. Many species are full-time or part-time symbionts with other animals, either as immatures or as adults. Their hosts are frequently other arthropods, such as centipedes, millipedes, ants, and especially beetles. In some cases the relationship is truly parasitic, in others it is phoretic (Figure 24.3I,J,L), and in many instances the nature of the association is unknown.

The most familiar members of the Parasitiformes are the ticks (families Argasidae and Ixodidae; Figure 24.3F,L). Ticks are blood-sucking ectoparasites on vertebrates (one species, *Aponomma ecinctum*, lives on beetles). They are the largest-bodied members of the entire order, and some swell to 2 to 3 cm in length during a blood meal. The chelicerae are smooth and adapted for slicing skin, and together with the pedipalp coxae they form a structure called the capitulum. The ixodids are called the hard ticks because of a sclerotized shield covering the entire dorsum. They parasitize reptiles, birds, and mammals. They generally remain attached to their hosts for days or even weeks, feeding on blood. Some are vectors of important diseases, including *Dermacentor andersoni* (the vector of Rocky Mountain spotted fever) and *Rhipicephalus annulatus* (the vector of Texas cattle fever). Lyme disease (first described in Old Lyme, Connecticut, in 1975) is a bacterial disease that is harbored in deer and certain rodents and is transmitted by several tick species in North America, including the deer tick *Ixodes scapularis* and the western black-legged tick *Ixodes pacificus*.

Soft ticks (Argasidae) lack the heavily sclerotized dorsal shield of hard ticks. They are usually rather transient parasites on avian and mammalian hosts (particularly bats), typically feeding for less than an hour at a time. When not attached to a host, these ticks remain hidden in cracks and crevices or buried in soil. Disease-carrying soft ticks include *Argas persicus* (the vector of fowl spirochetosis) and *Ornithodoros moubata* (the vector of African relapsing fever, or "tick fever").

The vast and diverse Acariformes, once considered to be polyphyletic, are now recognized as a well-supported clade. These mites usually have bodies divided into two regions, but not as the normal prosoma and opisthosoma, which are fused. Rather, the disjugal furrow is lost, and a secondarily evolved sejugal furrow partly or wholly traverses the dorsum between the origins of the second and third pairs of walking legs (Figures 24.3D,G). In some acariform mites this division is secondarily lost.

Free-living acariform mites are found in virtually every conceivable situation: in soil, leaf litter, decaying organic matter, mosses, lichens, fungi, under bark, on freshwater algae, in sands, on seaweed, and at all altitudes and at most ocean depths. "Chiggers" is a name given to the larvae of acariform mites of several genera, notably *Trombicula*. They include both herbivores (some fungivores) and predators, and their feeding methods are diverse. Many ingest solid as well as liquid food, and a few aquatic forms actually suspension feed. One species, *Halacarellus auzendei*, is known from hydrothermal vent environments. Certain groups are serious pests that destroy stored grain crops and other food products. On the other hand, some predatory acariform mites have been used for biological pest control of other arthropods—even other mites! Bites from mites in the wild can be an annoyance to humans.

Most of the symbiotic acariform mites are parasites on vertebrate and invertebrate hosts. Various species parasitize marine and freshwater crustaceans, freshwater insects, marine molluscs, terrestrial arthropods, the pulmonary chambers of terrestrial snails and slugs, the outer surfaces of all groups of terrestrial vertebrates, and the nasal passages of amphibians, birds, and mammals. In addition to direct parasitism, many mites are phoretic, using their hosts for dispersal. There are also many plant-eating mites that are considered parasitic.

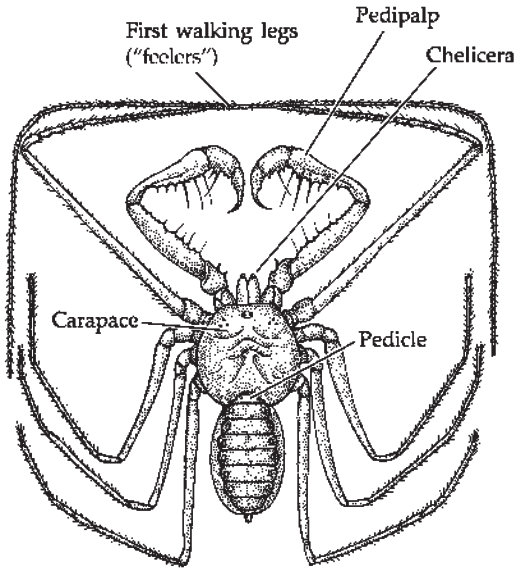
A great many acariform mites cause economic or medical problems by direct predation and parasitism, by acting as disease vectors, or by feeding on stored food products. The family Penthaleidae includes the red-legged earth mite (*Halotydeus destructor*) and the winter grain mite (*Penthaleus major*), both of which are serious pests of many important crops. Members of the superfamily Eriophyoidea are vermiform mites adapted to feeding on various plants. This group includes the gall and leaf-curl mites, as well as a number of others that serve as vectors for certain disease-causing viruses (e.g., wheat and rye mosaic viruses). Another family of mites (Demodicidae) includes parasites of hair follicles and sebaceous glands of mammals. Two species, *Demodex folliculorum* and *D. brevis*, occur specifically in the hair follicles and sebaceous glands, respectively, of the human forehead. Another, *D. canis*, causes mange in dogs. Some other problems caused by acariform mites include subcutaneous tumorlike growths in humans, various sorts of skin irritations, mange in many domestic animals, reduced wool production in sheep, and feather loss in birds.

With a mixture of reluctance and relief, we leave the mites; interested readers should consult the references at the end of this book for sources of additional information.

(A)

Courtesy of G. Giribet

(B)



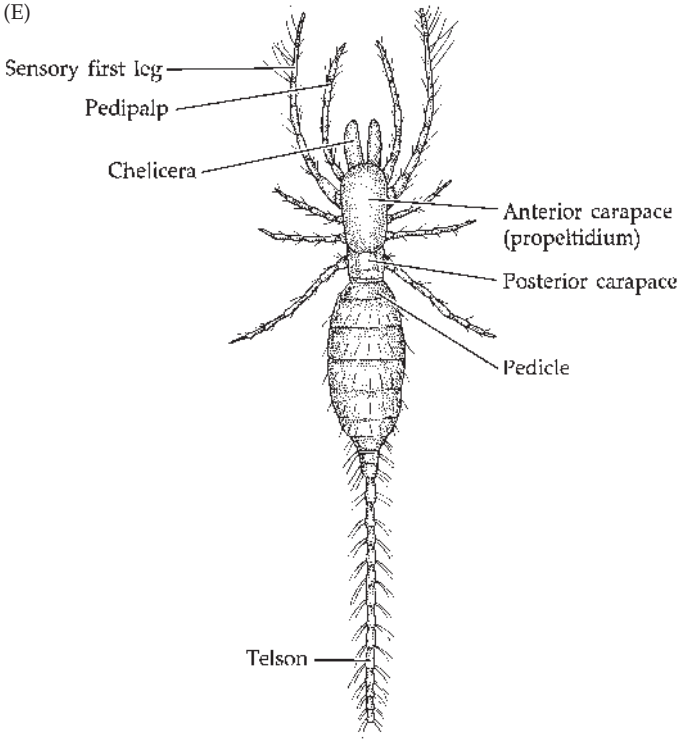
(C)

Bruce Marlin/Wikipedia/CC BY-SA 2.5

(D)

Courtesy G. Giribet

(E)



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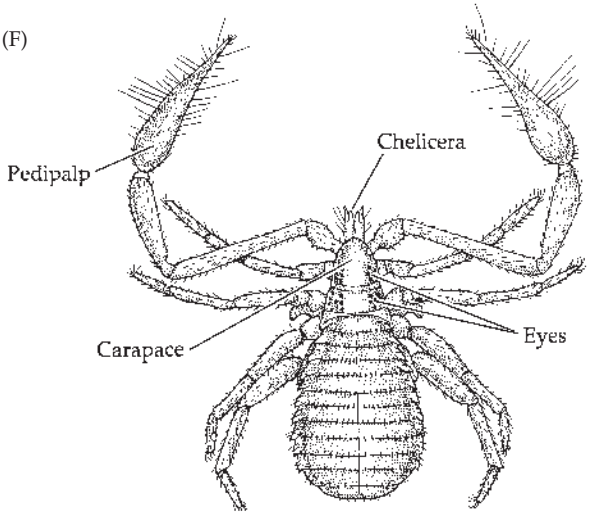

(G)

Courtesy of G. Giribet

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Order Amblypygi Whip spiders (Figure 24.4A,B). Prosoma undivided, covered by a carapace-like shield and connected to opisthosoma by narrow pedicel; opisthosoma segmented but undivided; with two pairs of book lungs; telson absent; chelicerae biarticulated, modified as spiderlike fangs; pedipalps raptorial; first pair of legs are greatly elongate as antenniform sensory appendages. With 8 eyes, except in some cave-dwelling species. Molting occurs throughout life as the animals keep growing in size.

The 160 or so extant species of amblypygids (there are 9 described fossil species) are commonly known as whip spiders or tailless whip scorpions, reflecting their similarities to both spiders and uropygids (whip scorpions).

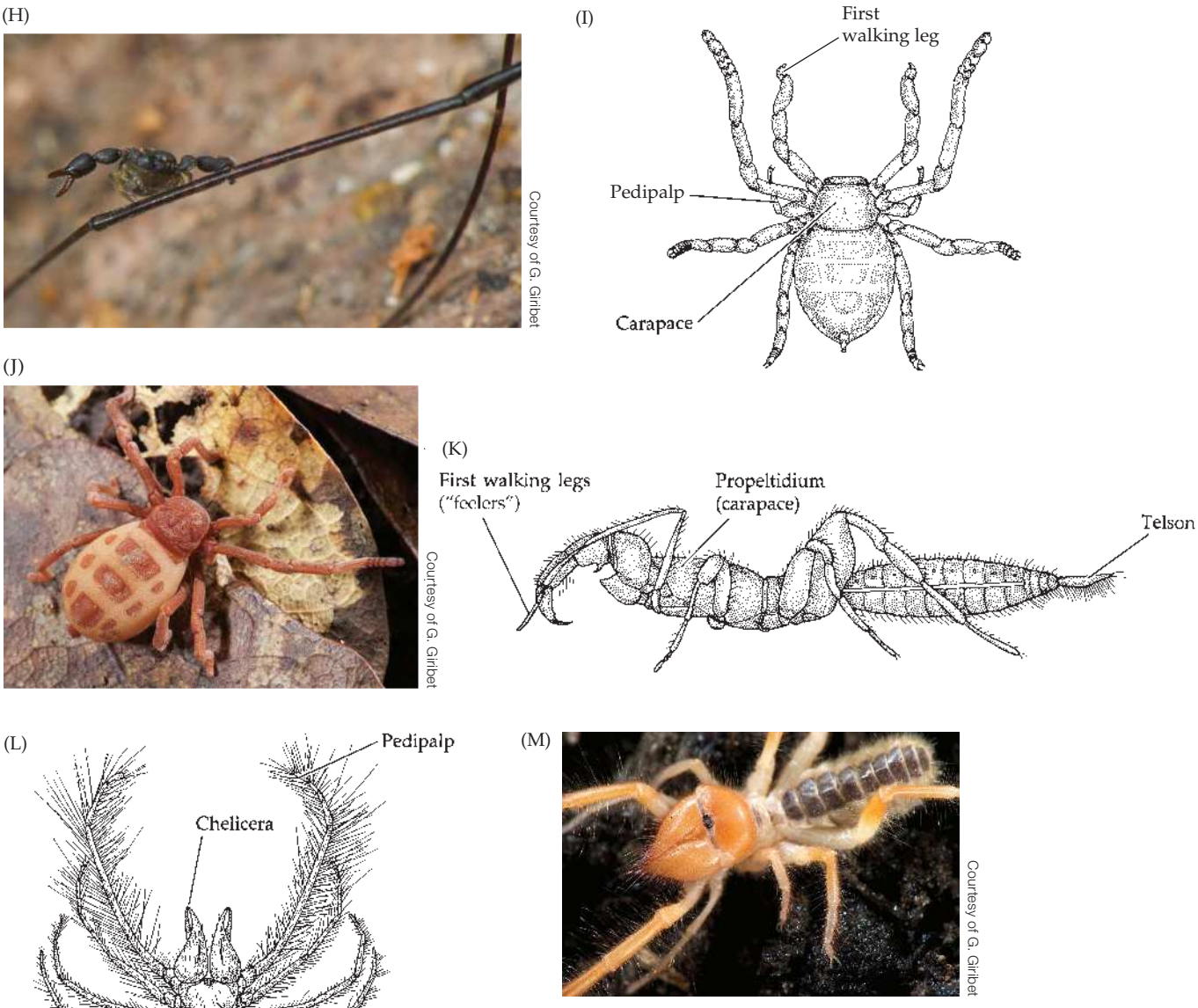
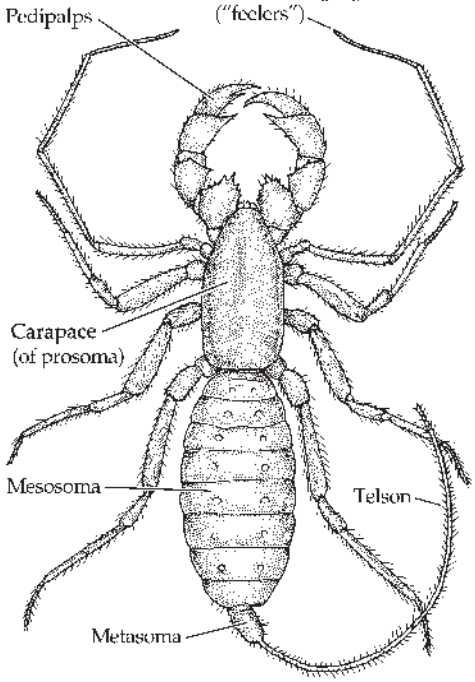


FIGURE 24.4 Some examples of arachnids other than spiders and scorpions. (A,B) Whip spiders (order Amblypygida). (A) *Heterophrynus batesii* (from the Amazon region). (B) *Stegophrynus dammermani*. (C,D) Daddy longlegs, or harvestmen (order Opiliones). (C) A daddy longlegs. (D) An armored harvestman (Laniatores), *Phareicranaus manauara*. (E) *Koenenia* (Palpigradi). (F–H) Pseudoscorpions (order Pseudoscorpiones). (F) *Chelifer cancroides*, a frequent hitchhiker on houseflies. (G) An unidentified female pseudoscorpion from New Zealand carrying its eggs. (H) A pseudoscorpion grabbing onto a harvestman's leg as a form of phoresy. (I,J) Ricinuleids (order Ricinulei). (I) *Ricinoides crassipalpe*, dorsal view. (J) A nymph of *Ricinoides atewa*. (K) A schizomid (order Schizomida), *Schizomus crassicaudatus*. (L,M) Sun spiders (order Solifugae). (L) *Galeodes arabs*. (M) *Eremobates*.

(*Continued on next page*)

(N)



(O)

Courtesy of G. Giribet

(P)

Courtesy of L. Kováč

(Q)

Courtesy of G. Giribet

FIGURE 24.4 (*continued*) Some examples of arachnids other than spiders and scorpions. (N,O) Whip scorpions (order Uropygi). (N) *Mastigoproctus*. (O) *Thelyphonellus amazonicus*. (P) The cave palpigrade *Eukoenenia spelaea*. (Q) An unidentified schizomid from Panama. (B,F,L after T. H. Savory. 1964. *Arachnida*. Academic Press, New York.)

Externally they resemble whip scorpions, they have some internal characters related to spiders, but they lack spinnerets and poison glands. Amblypygids are widely distributed in warm humid areas, where they are found under bark or logs or in leaf litter and in similar protected habitats; several species are cave dwellers. Some species are able to stay underwater hours at a time or live in beaches; others live in extremely dry environments, including deserts. One western African small blind species inhabits termite nests.

Most species are less than 5 cm in length, but the first pair of legs may be as long as 25 cm! These limbs are used as touch receptors and chemoreceptors (like antennae in nonchelicerate arthropods) and are important in prey location because these animals hunt at night. Amblypygids walk sideways with these long "feelers" extended, sensing for potential prey. Once located, the prey is grasped by the enlarged spiny pedipalps and torn open by the chelicerae. The body fluids are then sucked from the victim and ingested. Many species of amblypygid have complex mating behaviors.

Order Araneae Spiders (Figure 24.5). Spiders, of course, are the most familiar of all chelicerates, and they are one of the most abundant groups of land animals. In fact, they might be the most commonly encountered macroscopic terrestrial invertebrates (along with isopods, ants, and flies) in the world! They have successfully exploited nearly every terrestrial environment, and many freshwater and intertidal habitats as well. Spiders display a truly staggering array of lifestyles—yet they all utilize a fairly uniform body plan, and the vast majority are generalist predators. Prosoma undivided, covered by a carapace-like shield and attached to opisthosoma by narrow pedicel; opisthosoma undivided and unsegmented except in liphistiids and some mygalomorph families, which have discrete tergites (i.e., "segmented abdomens"); chelicerae modified as fangs, served by venom glands located in the prosoma (absent in the families Uloboridae and in the Anapidae genus *Holarchaea*); pedipalps modified in the adult males as copulatory organs; opisthosoma bears book lungs and/or tracheae, silk-producing glands, and spinnerets, the last being highly modified appendages that serve to spin the silk produced by the silk glands; most with 8 eyes. Most araneomorphs cease to molt

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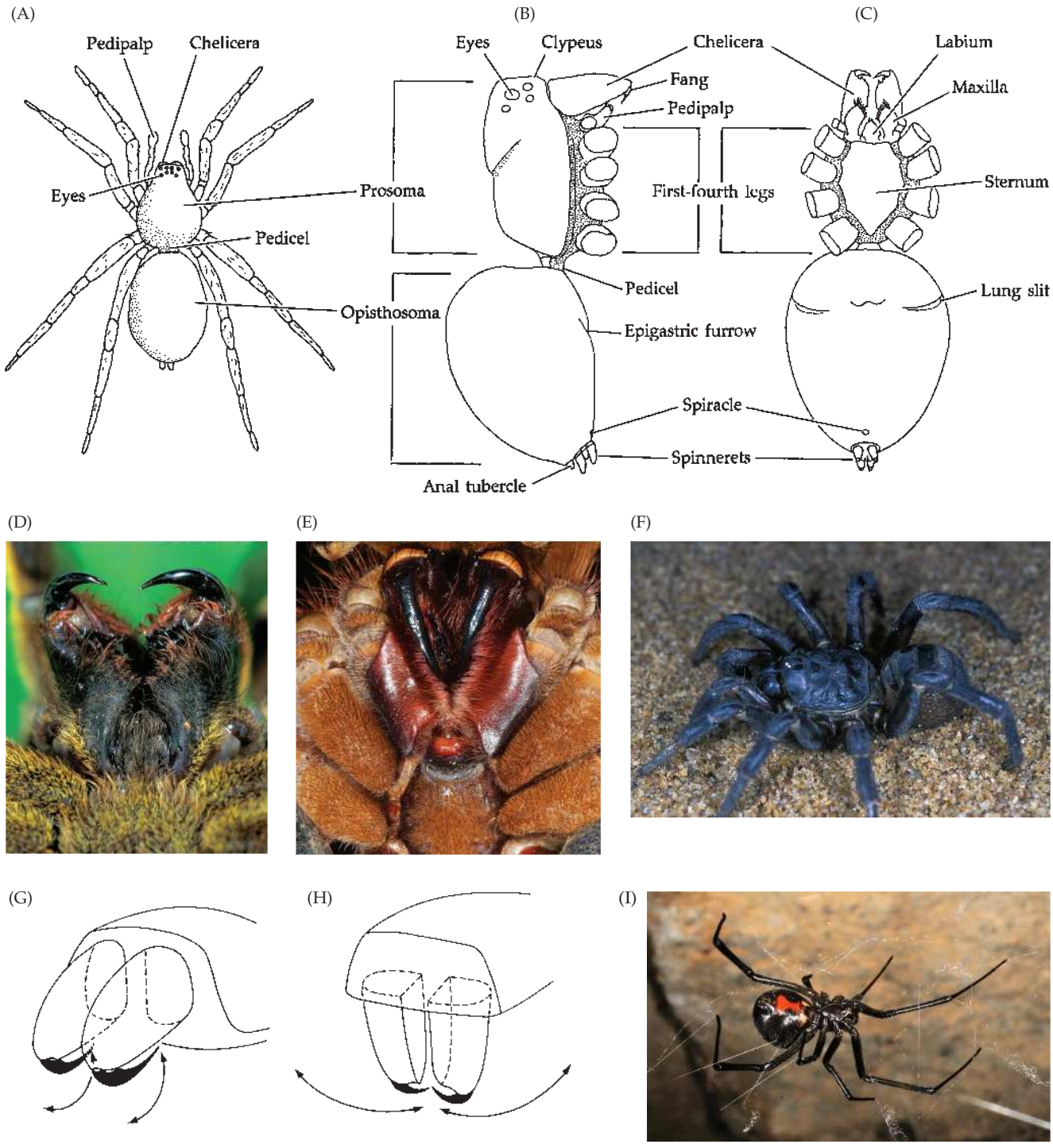

FIGURE 24.5 Spiders. (A–C) A generalized spider. (A) Dorsal view. In (B) (lateral view) and (C) (ventral view) the legs have been omitted, except the coxae. (D) The cheliceral fangs of *Phoneutria*, a ctenid spider (Ctenidae) from Ecuador with a highly toxic venom (the poison pores are visible at the end of the fangs). (E) Fangs of *Theraphosa blondi* (Theraphosidae) from Brazil. (F) A liphistiid (suborder Mesothelae) from Thailand. Note the evidence of opisthosomal segmentation. (G,H) The orientation and plane of motion of the chelicerae of an orthognathous (G; see also D) and a labidognathous (H; see also E) spider. (I) The notorious black widow spider, *Latrodectus* (Theridiidae).

(*Continued on next page*)

once adulthood is achieved, but mygalomorphs molt through their life time.

The body is divided into a fused prosoma and a fleshy, less sclerotized, opisthosoma. The first opisthosomal segment forms a narrow pedicel, which joins the two body regions. Each chelicera has two segments; the basal segment is short and conical (the paturon), and the distal segment is a hard, curved fang, usually bearing a pore from the duct of the poison gland (Figures 24.5D,E and 24.16A). A medial flap (the labium)

FIGURE 24.5 (*continued*) Spiders. (J) An orb-weaving spider from Madagascar, *Caerostris* sp. (Araneidae). (K) *Theraphosa blondi* (Theraphosidae), the Goliath tarantula, from the Brazil Amazon region; this is the largest extant spider. (L) *Cupiennius coccineus* (Trechaleidae), from the rain forests of Costa Rica, a favorite study subject of neurobiologists. (M) A female of the Tasmanian cave spider *Hickmania troglodytes*, from Australia (Gradungulidae). (N) Liphistiid spider "trap door" from Thailand (closed and open). Note the silk trip lines radiating from the entrance. (O) *Myrmecotypus* sp. (Corinnidae), from the rain forests of Brazil, a spider that mimics ants; ant mimicry has evolved multiple times among spiders. (B,C,G,H after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

projects ventrally over the mouth. Each pedipalp is composed of six segments, and in most spiders the proximal segments are enlarged as lobes called endites, which bear gnathobases that flank the mouth and are used to handle and grind food (sometimes endites are also referred to as maxillae, although endites are not homologous with the maxillae of crustaceans and insects). Beyond the gnathobases, the pedipalps extend forward as tactile organs in females and juveniles, but they are highly modified as sperm transfer organs in

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mature males. In a few species of spiders (e.g., tarantulas) the pedipalps function as walking "legs." The ventral surface of the prosoma bears a cuticular plate, or sternum, around which arise the four pairs of walking legs, each composed of eight articles.

The opisthosoma bears openings for gas exchange, the gonads and associated structures, the spinnerets, and the anus. On the ventral surface posterior to the pedicel is a transverse **epigastric furrow** in which the gonopores are located. In most females, a slightly elevated plate, the **epigynum**, lies in front of the epigastric furrow and bears the openings to the seminal receptacles. Lateral to the furrow are spiracles that open to the book lungs, or anterior tracheae. The hind part of the opisthosoma bears the anus and the spinnerets (the latter are situated near the middle of the opisthosoma in the Mesothelae). The ability of spiders to produce silk and fashion it into a great variety of functional devices has been a major factor in their evolutionary success, as we will see below.

There are more than 50,000 described spider species, classified into about 129 extant families. The largest spiders by leg span are the giant huntsman spiders (Sparassidae), some of which reach 30 cm (12 in.) in diameter. The largest spider by weight is probably the goliath birdeater tarantula (*Theraphosa blondi*), which can weigh over 170 g (6.0 oz). The smallest adult spiders are found in the micro-orb-weaver genus *Patu* (Symphytognathidae), the males measuring under 0.4 mm. The order Araneae is divided into two suborders. The suborder Mesothelae includes the "segmented" spiders (family Liphistiidae, about 145 species), which are characterized by persisting segmentation of the opisthosoma (Figure 24.5F), with conspicuous tergites, and midabdominal location of the spinnerets. Most are 1–3 cm long and build burrows with a trapdoor over the entrance; some have silk trip lines that converge radially onto the entrance (Figure 24.5N). All are predators, feeding on animals that pass within striking distance of the burrow opening.

The other suborder, Opisthothelae (with more than 49,000 species), comprises two large groups: the infraorder Mygalomorphae (tarantula-like spiders) and the infraorder Araneomorphae ("typical" spiders). Almost all members of both infraorders have an unsegmented opisthosoma and posteriorly located spinnerets, but they can be differentiated by the nature of the chelicerae (Figures 24.5G,H). Mygalomorph spiders have chelicerae that articulate in a manner that enables movement of the appendages parallel to the body axis (**orthognathous**), whereas araneomorph spiders have chelicerae that move at right angles to the body axis (**labidognathous**). An intermediate condition, known as **plagiognath** chelicerae, can be found in liphistiids, some mygalomorphs (e.g., Hexathelidae), and some araneomorphs (e.g., Hypochilidae).

Order Opiliones Daddy longlegs, or harvestmen, including mite harvestmen (Figure 24.4C,D). Divided into 4 extant suborders (Cyphophthalmi, and the three Phalangida suborders: Eupnoi, Dyspnoi, and Laniatores) and an extinct one (Tetrophthalmi). With an important fossil record, including multiple Paleozoic species. Prosoma entire or divided (as it also is in schizomids, palpigrades, and solifuges), sometimes into a proterosoma and two free segments. The prosoma joins broadly to the often segmented opisthosoma, but prosoma and opisthosoma can fuse dorsally in what is known as a scutum completum. Chelicerae small, of 3 articles, pincerlike; pedipalps long and leglike or well developed into a prehensile appendage, especially in Laniatores. Blind or with 1 pair of median eyes; whether the eyes of some Cyphophthalmi have their origin in median or lateral eyes remains debated. One pair of tracheae on opisthosoma; male with spermatopositor organ (in Cyphophthalmi) or penis (in Phalangida); female with an ovipositor organ.

The order Opiliones is a large and diverse group of about 6,500 species of uncertain relationships to other arachnid orders. Opiliones are known from nearly all climatic regions of the world, including subarctic areas, but are most abundant in tropical and temperate regions of the Southern Hemisphere. Most species have small bodies, less than 2 cm in length, but many Phalangida have very long legs (up to 10 cm).

Opiliones prefer damp, shaded areas and are commonly found in leaf litter, on trees and logs in dense forests, and in caves. They feed on various small invertebrates and also scavenge on dead animal and plant matter, mostly at night. Food is grasped by the pedipalps and passed to the chelicerae for chewing. These animals are among the few arachnids capable of ingesting solid particles instead of the usual liquefied food. Opiliones possess a pair of defensive repugnatorial glands, which produce noxious secretions containing quinones and phenols. As discussed later, most arachnids mate by indirectly passing sperm from the male to the female. Phalangida (and some mites) are the only arachnids in which males use a penis for direct copulation, while in Cyphophthalmi the male uses a "penislike" spermatopositor organ to place a spermatophore near the female gonostome—the ventral opening where the spermatopositor, penis, or ovipositor organs protrude in Opiliones. Many Opiliones display parental care, including of the rarer exclusive paternal form, also known from pycnogonids.

Order Palpigradi Palpigrades or micro-whip scorpions (Figure 24.4E). Minute arachnids with the prosoma divided into proterosoma, covered by the carapace-like propeltidium, followed by 2 free segments and joined to opisthosoma by a narrow pedicel; opisthosoma segmented and divided into broad mesosoma and short narrow metasoma, the latter bearing a long multiarticulated telson; eyes absent.

Palpigrades are delicate animals that walk by sensing the substrate with what seems a nervous behavior of the first pair of walking legs and using their unmodified palps for walking (unlike all other arachnids). While moving, most palpigrades keep the first pair of legs held upwards, moving them laterally. It is possible that the uplifted flagellum is associated with perception of the environment. These small, often highly translucent arachnids range in size from 0.65 mm in *Eukoenenia grassii* to 2.8 mm in the "giant" *E. draco* from caves on the island of Mallorca, Spain. These tiny arachnids have undergone a great deal of evolutionary reduction in association with their small size and cryptic habits. They are colorless, have very thin cuticles, and lack circulatory and gas exchange organs. Most are found under rocks or in caves, in very humid environments, and a few species live on sandy beaches. One species has recently been reported to feed on heterotrophic Cyanobacteria. The mode of sperm transfer in these arachnids remains unknown.

These rare animals have been recorded from widely separated parts of the world, and their biology and biogeography remain poorly known. The phylogeny of palpigrades has been recently investigated. The living members of the order are currently divided into two families: Eukoeneniidae, with four genera and more than 100 species, and Prokoeneniidae, with two genera and seven species. However, the position of Palpigradi among the arachnid orders remains elusive.

Order Pseudoscorpiones False scorpions (Figure 24.4F–H). Prosoma covered by a dorsal carapace-like shield, but clearly segmented ventrally. Opisthosoma undivided but with 11–12 segments and broadly joined to prosoma. Chelicerae chelate bearing silk glands; pedipalps large and scorpion-like, with venom glands in most species (in the clade Iocheirata); eyes present or absent.

There are about 3,700 described species of false scorpions, with the body lengths of adults generally ranging from 0.7 to 5 mm, but the largest species, *Garypus titanius* from Ascension Island, reaches 12 mm in length. The group is cosmopolitan and found in a great variety of habitats—under stones, in litter, in soil, under bark, and in animal nests. The genus *Garypus* is found on sandy and cobble marine beaches, and one pseudoscorpion species, *Chelifer cancroides*, typically cohabits with humans and is found in homes worldwide.

These strange little creatures resemble scorpions—to which they are probably related—in general appearance, but they lack the elongation of the opisthosoma and telson and do not have a stinging apparatus. However, most species possess poison glands in the pedipalps with which they immobilize their prey, usually other tiny arthropods (e.g., mites). Once captured, the victim is torn open by the chelicerae and the body fluids are sucked out. Also, like spiders, false scorpions produce silk, but the silk glands open on the chelicerae, with the glands located in the prosoma. This silk is used to build silken chambers for hibernation, molting, and egg laying.

A number of false scorpions use larger arthropods as temporary "hosts" for purposes of dispersal. This phenomenon of "hitchhiking," known as phoresy, typically involves females that grab onto the larger host animal with their pedipalps. The host is often a flying insect or other arthropod (Figure 24.4H). The abovementioned cosmopolitan species, *Chelifer cancroides*, for example, is frequently encountered as a phoretic "guest" on houseflies.

Order Ricinulei Ricinuleids or hooded-tick spiders (Figure 24.4I,J). Prosoma fully covered by a carapace-like shield and broadly joined with opisthosoma. Opisthosoma unsegmented, with paired tracheae; with a prosomal-opisthosomal locking mechanism. Chelicerae pincerlike, covered with a flaplike hinged plate named the **cucullus**; pedipalps small, with coxae fused medially. Eyes absent in extant species, but some have a lighter patch in the side of the prosoma that is thought to be light sensitive; 2 pairs of lateral eyes present in some fossil species. Third leg pair of males modified for sperm transfer. Cuticle very thick and ornamented with numerous sensory structures and sensory setae (Figure 24.4I,J).

There are 98 extant described species of ricinuleids; they are small, the largest species reaching 11 mm long, and live in caves and leaf litter in tropical forest in western Africa (*Ricinoides*) and the Neotropics (*Cryptocellus* and *Pseudocellus*), but fossil species are known from Myanmar Cretaceous amber. All are slow-moving predators on other small invertebrates. Ricinuleids have a hexapod larva and three other developmental stages (protonymph, deutonymph, and tritonymph); they may take 1 to 2 years to reach maturity and live 5 to 10 years. In immatures, the tergites and sternites are more widely spaced, and there are fewer than in the adults, where they almost touch.

Order Schizomida Schizomids (Figure 24.4K,Q). Prosoma divided; first 5 segments (the proterosoma) covered by a short carapace-like shield (the propeltidium), followed by 2 free segments, the mesopeltidium and metapeltidium. Opisthosoma segmented and divided; mesosoma with 1 pair of book lungs; metasoma with short, thin telson. Eyes present or absent.

There are about 300 species of small (less than 1 cm) arachnids in this order. Although some authors classify them as a suborder of Uropygi, they are distinguished from true whip scorpions by the divisions of the prosoma and the shorter telson. Schizomids live in leaf litter, under stones, in caves, and in burrows and are most common in tropical and subtropical areas of Asia, Africa, and the Americas. A few temperate species are known.

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The first walking legs are sensorial and resemble those of the closely related uropygids; together, the two comprise a clade. Like the uropygids, schizomids are predators on small invertebrates, and they also possess opisthosomal repugnatorial glands.

Order Scorpiones True scorpions (Figure 24.6). Body clearly divided into 3 regions: prosoma, mesosoma, and metasoma. Prosomal segments fused and covered by a carapace-like shield. Opisthosoma elongate, segmented, and divided into mesosoma and metasoma of 7 and 5 segments, respectively; telson spinelike, with poison gland. Chelicerae of 3 articles; pedipalps large, chelate, of 6 articles. With a pair of median eyes and sometimes additional pairs of lateral eyes, but some species are blind. First mesosomal segment bears a gonopore covered by genital operculum; second mesosomal segment bears a pair of unique sensory appendages called pectines; third through sixth mesosomal segments each with a pair of book lungs. Metasoma without appendages.

Scorpions are among the oldest terrestrial arthropods, and some consider them the most primitive arachnids, although recent phylogenetic analyses suggest that they are related to the other arachnids with book lungs, or Tetrapulmonata (Araneae, Amblypygi, Uropygi, and Schizomida). Others believe that they evolved from aquatic ancestors, perhaps from the eurypterids or a common ancestor, and invaded land during the Carboniferous Period. All of the roughly 2,000 known species are terrestrial predators. They inhabit a variety of environments, ranging from deserts to tropical rain forests, where some arboreal species occur, and even deep caves. They are notably absent from colder regions of the world. Scorpions include the largest living arachnids, with some reaching lengths of 18 cm.

The chelicerae are short and bear gnathobases for grinding food. The pedipalps are large, with the last two articles forming grasping chelae. The walking legs each comprise eight articles (coxa, trochanter, femur, patella, tibia, metatarsus, tarsus, pretarsus). The ventral surface of the mesosoma bears the genital pore, a

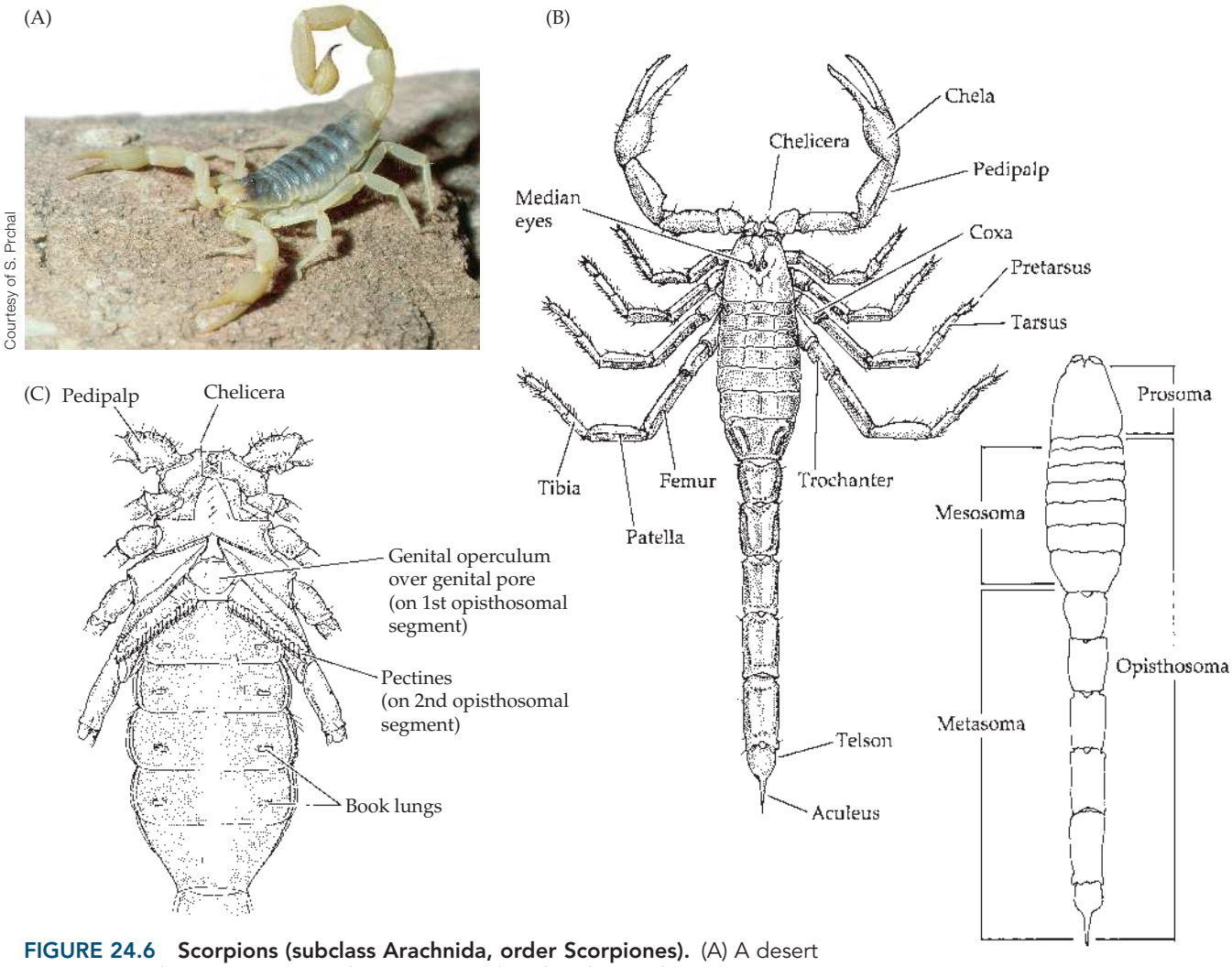

FIGURE 24.6 Scorpions (subclass Arachnida, order Scorpiones). (A) A desert scorpion, *Androctonus*. (B,C) *Buthus martensii* (dorsal and ventral views).

pair of pectines, and four pairs of spiracular openings to the book lungs. The anus is located on the last true segment of the metasoma and is followed by a stinging apparatus derived from the telson and bearing a sharp barb called the aculeus.

Scorpions are admired and feared in many cultures. They are well known for glowing in the dark under UV light; even the cast-off exuvium glows. Scorpions display complex mating behaviors and maternal care.

Order Solifugae Sun spiders, camel spiders, or wind spiders (Figure 24.4L,M). Prosoma divided into a proterosoma covered by a carapace-like shield and 2 free segments; opisthosoma undivided, but with 11 segments, bearing 3 pairs of tracheae; chelicerae huge and held forward, consisting of 2 articles; pedipalps long and leglike; propeltidium with 1 pair of eyes. On the ventral side of the fourth pair of legs, solifuges have up to 10 malleoli or racquet organs, unique sensory organs that occur in these animals.

Most of the 1,105 or so species of solifuges (or solpugids) live in tropical and subtropical desert environments of the Americas, Asia, and Africa. In contrast to many arachnids, they are often daytime hunters, hence the common name "sun spiders." They are also known as "wind spiders" because the males run at high speeds, "like the wind," or "camel spiders" because they are often found in deserts.

Some solifuges are only a few millimeters long, but many reach lengths of up to 7 cm. The feeding habits of many solifuges are unknown. Among those that have been studied, most are omnivorous, but they frequently show a preference for termites or other arthropods. Lacking poison, they rip their live prey apart with their strong chelicerae. They can also end up killing their partners during their aggressive copulation behavior.

Order Uropygi Whip scorpions and vinegaroons (Figure 24.4N,O). Prosoma elongated and covered by a carapace-like shield. Opisthosoma segmented and divided; mesosoma broad with 2 pairs of book lungs; metasoma short with long, whiplike telson; first walking legs elongated and multiarticulated distally. With 1 pair of median and 4 or 5 pairs of lateral eyes.

Whip scorpions are moderately large arachnids reaching lengths of up to 8 cm. There are 124 known species of living Uropygi (or Thelyphonida), most of which occur in Southeast Asia; a few are known from the southern United States, Mexico, and parts of Central and South America; and some species in Africa have probably been introduced. With the exception of a few desert species, whip scorpions live under rocks, in leaf litter, or in burrows in relatively humid tropical and subtropical habitats. The telson is sensitive to light, and most uropygids are negatively phototactic and active only at night.

The elongate first walking legs are held forward as "feelers," aiding the animals in their nocturnal hunting excursions. They feed on various small invertebrates by grasping prey with the pedipalps and grinding it with the chelicerae. The long telson is constantly moving about, probably serving as a sensory structure in case a predator moves in from behind.

Whip scorpions possess a pair of repugnatorial glands that open near the anus. When a uropygid is threatened by a potential predator, it raises the opisthosoma and sprays an acidic liquid from these glands on the would-be attacker. Some forms (e.g., *Mastigoproctus*) produce a secretion high in acetic acid, earning them the common name "vinegaroons." The spray nozzle of vinegaroons is like a turret, such that they can spray in almost any direction, even in front of them. Most live in self-made burrows.

Uropygi are closely related to Schizomida. In fact, some authors use the name Thelyphonida for the whip scorpions and the term Uropygi to refer to Schizomida + Thelyphonida as a clade. This clade is, in turn, closely related to Amblypygi and Araneae, constituting the group Tetrapulmonata, or the lung-bearing arachnids.

The Eucheliceratе Body Plan

Looking over the taxonomic summaries in the Synopses of Living Chelicerate Groups section will give you a good sense of diversity within Eucheliceratа. This section covers the general biology and structure of members of this large class, with an emphasis on the xiphosurans, spiders, and scorpions. We hope to convey an impression not only of diversity but also of unity within this group and to reinforce the concept of the evolutionary plasticity of the arthropod body plan in general.

As noted earlier, the body of chelicerates is typically divided into two main regions, the **prosoma** and the **opisthosoma** (Figures 24.1, 24.2, 24.5, and 24.6); a discrete head is not recognizable. The prosoma includes 7 segments; the opisthosoma includes up to 12 segments and a postsegmental, postanal telson. As in other arthropod groups, these basic body regions have undergone various degrees of specialization and tagmosis. In most eucheliceratеs the entire prosoma is fused and covered by a carapace-like shield. However, in certain groups (e.g., schizomids, palpigrades, solifuges, and some harvestmen) the prosoma is divided into three parts: a **proterosoma**, comprising the first five segments, all fused and covered by a carapace-like shield (often called the propeltidium), and two free segments (often called the **mesopeltidium** and **metapeltidium**). The opisthosoma may be undivided, as it is in most spiders, ricinuleids and harvestmen or divided into an anterior **mesosoma** and posterior **metasoma**, as it is in scorpions and in eurypterids.

The appendages further distinguish the eucheliceratеs from other arthropods. There are no antennae, and the first segment bears the eyes, with all six following segments of the prosoma bearing appendages. The

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first pair of appendages is embryologically postoral, often pincerlike, **chelicerae**. During embryogeny, the chelicerae migrate to a position lateral to the mouth, or even preoral, as compared with adults of most groups; here they serve as fangs or grasping structures during feeding. The chelicerae can be formed of two or three articles and are followed by a pair of postoral **pedipalps**, which are usually elongate or, more rarely, chelate. The pedipalps are usually sensory in function, but in some groups (e.g., scorpions) they aid in feeding and defense. The remaining four segments of the prosoma typically bear four pairs of walking legs.

The number of segments and appendages on the opisthosoma varies. In general, appendages are absent or very reduced, although in the horseshoe crabs they persist as large platelike limbs, called **book gills**, that function in locomotion and gas exchange. In most chelicerates, the opisthosomal limbs are greatly reduced and persist only as specialized structures, such as the silk-producing spinnerets of spiders or the pectines of scorpions.

In summary, we may define the Eucheliceratа as arthropods in which the body is divided into two regions (or two tagmata): a prosoma and an opisthosoma (with modifications of this body plan in mites, as discussed earlier). Additionally, the first two pairs of appendages are chelicerae (deutocerebral) and pedipalps (tritocerebral), and the remaining four pairs of prosomal appendages are walking legs and innervated by subesophageal ganglia. Evolutionarily, this body plan has been a highly successful one.

As mentioned earlier, the great success of spiders seems to have been due in large part to the evolution of complex behaviors associated with silk and web production, particularly among araneomorph spiders, whose silk fibers are stronger than those of mygalomorphs and liphistiids. Because we are paying special attention to members of the order Araneae in this chapter, and because silk production is so important to nearly all facets of their lives, we present a special section on spider silk and its uses.

Spinnerets, Spider Silk, and Spider Webs

Spider silk is a complex fibrous protein composed mostly of the amino acids glycine, alanine, and serine. Spider silk proteins are known as **spidroins**. The silk is produced in a liquid, water-soluble form that transforms into an insoluble thread after it is extruded from the body. This near instantaneous transformation involves as much as a tenfold increase in the molecular weight of the silk protein, which is enhanced by the formation of intermolecular bonds.

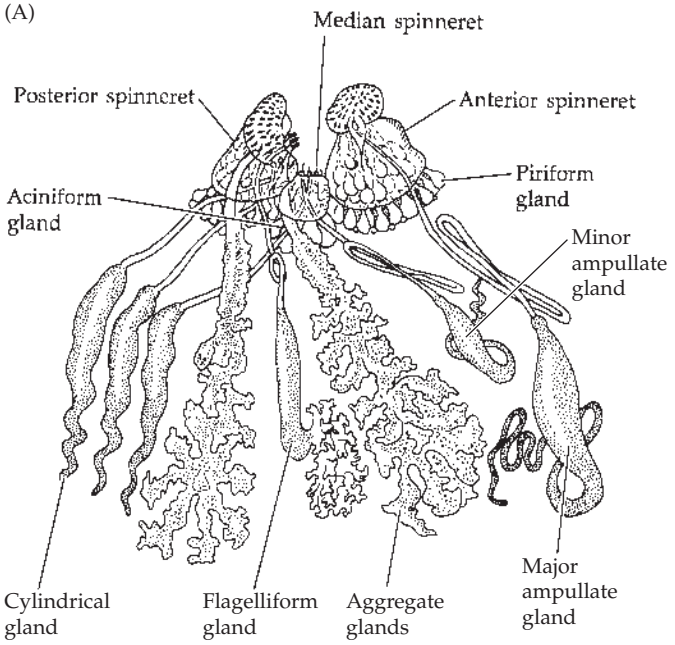
Spider silks are among the toughest energy-absorbing materials known. Some types of silk require up to ten times more energy to fracture than an equivalent volume of the synthetic fiber Kevlar (Kevlar is five times stronger than steel in terms of tensile-strength-to-weight ratio). Some spider silks can stretch as much as rubber. Spider silk is so strong that in some parts of the world (the Solomon Islands, for example) people actually use it as fishing nets by stacking numerous webs on top of one another.

The spider silk-producing organs are located in the opisthosoma and comprise several types of **silk glands**, depending on the taxonomic group. For example, an adult female orb-weaver (e.g., *Araneus*) has seven gland types, each producing silks with different physicochemical properties and functions. The liquid silk produced by these glands (also called "dope") is secreted into ducts that open to the outside through spigots located on the spinnerets (Figure 24.7). As the liquid silk travels along this duct, ionic exchanges occur and water is removed. A muscle-controlled valve toward the distal end of the duct is also involved in the process that causes a phase shift from liquid to a solid fiber. The apparatus spins the silk into threads of different thicknesses and properties. By spinning various kinds of silks in different diameters, spiders produce a variety of threads with unique properties for specific functions and at particular times. The **spinnerets** are highly modified opisthosomal appendages, and they retain some musculature that allows for their movement during spinning (Figure 24.7C). The spinnerets are located in body segments 11 and 12 (opisthosomal segments 4 and 5).

The numbers and kinds of glands and spinnerets vary. Ancestrally, spiders had four pairs of spinnerets (two pairs per segment): anterior lateral, anterior median, posterior lateral, and posterior median. Mesothelae spiders retain the four pairs of spinnerets (although in some species the anterior median pair is reduced to nonfunctional knobs). The recently described uraraneid fossil *Chimerarachne*, from the mid-Cretaceous, has two long pairs of lateral, multiarticulated, spinnerets and two pairs of median spinnerets that are very small in comparison and not articulated. Most extant spiders have three pairs (by the loss or modification of the anterior median spinnerets), although some have only one or two pairs of spinnerets. In many spiders there is a nonfunctional remnant of the anterior median spinnerets known as the **colulus**.

Another spinning organ, the **cribellum** (Figure 24.7D), occurs in several families of araneomorph spiders. Although the cribellum is a synapomorphy of Araneomorphae, it has been independently lost multiple times in this large clade. Like the colulus, the cribellum is a homologue of the anterior median spinnerets. This spinning organ is a platelike structure, anterior to the spinnerets, that bears many small spigots (up to 40,000 in some species). Cribellate silk is emitted in many extremely fine threads and then combed into a delicate mesh (Figure 24.7E) over a pair of axial fibers from the spinnerets by a row of special macrosetae (the calamistrum) on the metatarsus of the fourth legs (Figure 24.7F). In some species the calamistrum consists of two rows of macrosetae. Cribellate orb-weavers (e.g., the Uloboridae) use the resulting mesh, known as a "hackle band," to build the

(A)



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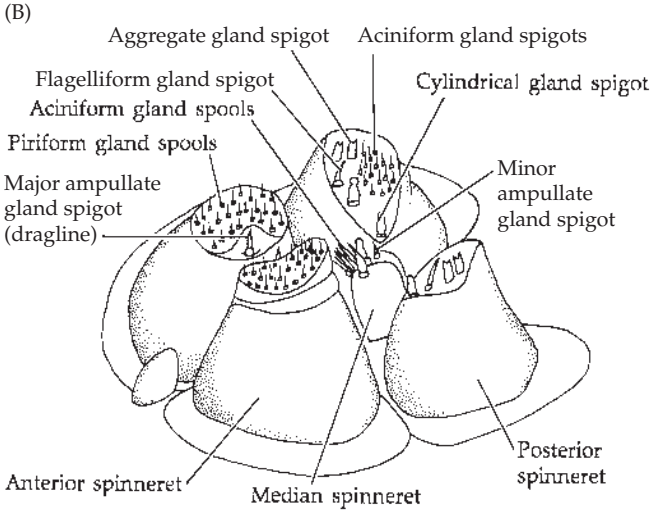

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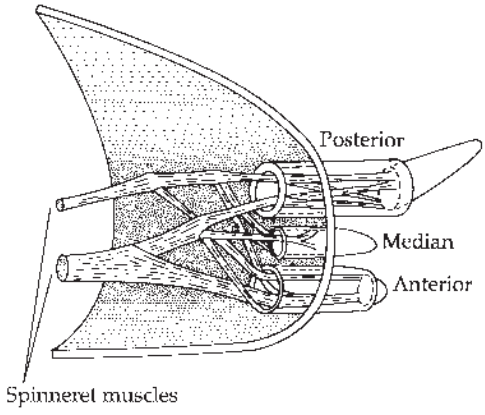

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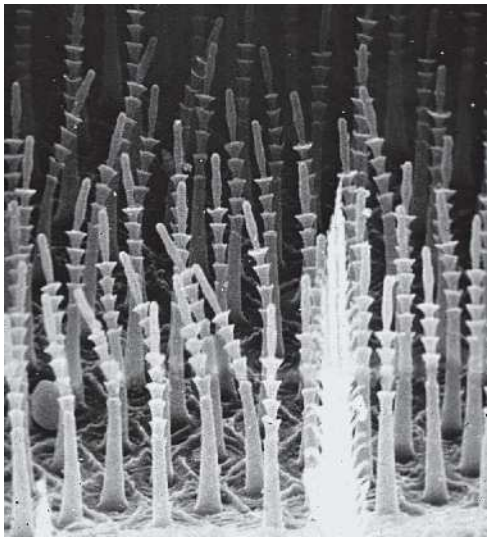

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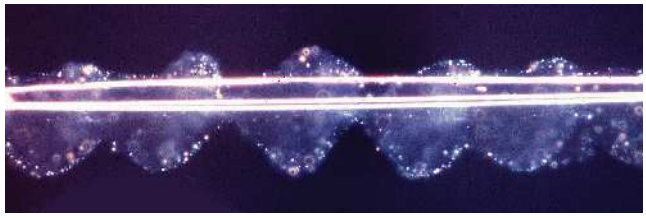

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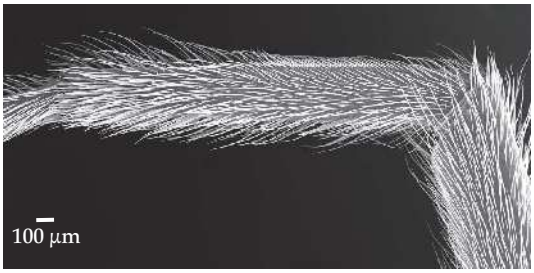

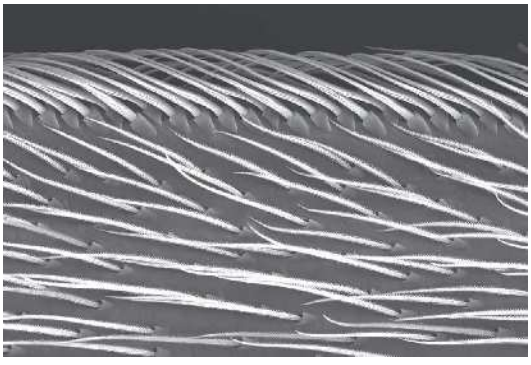

Courtesy of G. Hormiga

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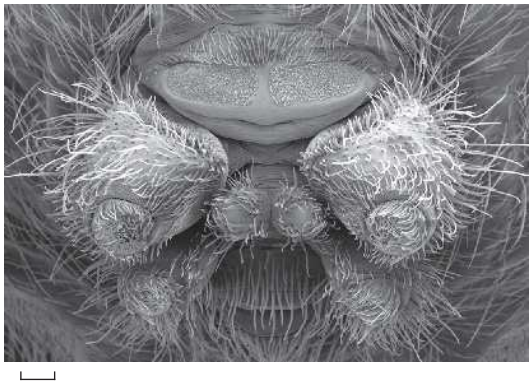

Courtesy of G. Hormiga

100 μm

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FIGURE 24.7 Silk glands and spinnerets in spiders. (A) The silk glands and spinnerets of *Nephila* (Araneidae), the golden silk spider. Only one member of each pair of glands is shown. (B) The spinnerets of the orb-weaver *Araneus* (external view). (C) Cutaway view of the posterior end of the opisthosoma (*Tegenaria*, Agelenidae). Note the spinneret muscles. (D) The cribellar spigots of *Hypochilus* (Hypochilidae) (SEM, 1,600×). (E) The cribellate silk of *Uloborus* (Uloboridae). (F) SEMs of the comblike calamistrum on the metatarsus of each fourth walking leg of *Amaurobius similis* (Amaurobiidae), used to brush the silk threads as they emerge from the cribellum. (G) An SEM (237×) of the spinning apparatus of *A. similis*. The platelike structure anterior to the three pairs of spinnerets is the cribellum. (B after R. S. Wilson. 1969. *Amer Zool* 9: 103–111.)

sticky spiral of their orbs. The cribellum and the calamistrum appear after the third molt, and in males both structures disappear with the final molt, although nonfunctional remnants can be found in the adult males of some species. Similarly, the spigots involved in the spinning of the viscid sticky silk of ecribellate orb-weavers disappear in the final molt of males (there are exceptions, such as the adult males of many erigonine linyphiids, which retain this triplet of spigots).

The varied uses of silk are intimately associated with nearly every aspect of the lifestyle and habits of spiders, as explained more fully in following sections. Different types of silk are used as safety lines and climbing lines (drag lines), to anchor or cement drag lines to the substrate, for the construction of retreats and egg sacs, to wrap prey for brief storage, and to line burrows. In addition, several kinds of silks are used to build foraging webs. Adult males of many araneomorph spiders also use silk to build a sperm web, which is then used to deposit sperm (through the gonopore, in the abdomen) prior to charging their copulatory organs in the pedipalps (a process termed "sperm induction"). Sperm webs are built using special silk glands that open through a set of spigots along the anterior margin of the epigastric furrow (these male spigots are known as "epiandrous fusules"). The number and arrangement of spigots in the spinnerets and of epiandrous fusules varies taxonomically. Many newly hatched spiderlings spin long, thin threads to ride the wind for aerial dispersal ("ballooning").

Although all spiders can produce and use silk, not all of them build webs for prey capture (for example, jumping spiders do not build capture webs but often make silk retreats). In those spiders that use foraging webs, the diversity of web types and architectures is extraordinary, ranging from the highly geometrical, densely woven, micro-orb webs of symphytognathids to the deceivingly simple single line snares of mastophorine araneids whose bodies mimic the pheromones of the preys they feed on. Almost everything in between these extremes of web types seems to exist or be possible, and much of spider web architecture and natural history remains to be discovered and/or described, particularly in the tropical regions. The construction and use of prey-capture webs are discussed in more detail in the Feeding and Digestion section. In general, capture webs serve both to trap and retain prey long enough for it to be subdued and, through vibrations, to signal the spider of its presence. Indeed, most spiders live in a world dominated by vibrations, a world where a potential meal, predator, or mate reveals itself with characteristic resonance patterns. We present here a brief description of the construction of a familiar orb web, as commonly built by members of the families Araneidae and Tetragnathidae.

The spinning of an orb web takes place in three stereotypical phases, which are apparently genetically programmed (Figure 24.8). The first phase is the construction of a supportive Y-shaped framework and a series of radiating threads. The upper branches of the Y are initially laid down as a horizontal thread between two objects in the spider's environment. The spider sits in one spot and secretes the thread into the air; the loose end is then carried by air movements and flutters about until it contacts and sticks to an object. The spider then tacks down its end of the thread, moves to the center of the horizontal line, and drops itself on a vertical thread. The vertical thread is pulled taut and attached, thereby producing the Y-shaped frame. The intersection of the three branches of the Y becomes the hub of the final web, and it is from this point that the radii are extended. Radial threads are then attached to the frame threads. Once this initial phase is complete, the spider quickly lays down a nonsticky temporary spiral thread, starting from the hub, as the second phase of construction (the temporary spiral is left in the finished orb web of some species, such as those in the genera *Nephila* and *Phonognatha*). This spiral thread, along with the initial framework of threads, serves as a working platform during the third and final phase of web building—the production of the sticky spiral or prey trap. In ecribellate orb-weavers this final thread, the sticky spiral, is always coated with a gluey glycoprotein that automatically assumes a beaded distribution after it is deposited (Figure 24.9A). As the sticky spiral is laid down, the temporary spiral is removed or eaten.

Some orb-weavers (e.g., many species of *Argiope* and *Cyclosa*) produce a dense mesh of silk, called a **stabilimentum**, across the hub of their webs (Figure 24.9B). The form and materials used for stabilimenta vary widely taxonomically, and their phylogenetic distribution implies that stabilimenta have evolved independently multiple times. Consequently, the function of the stabilimentum also may vary across groups. Stabilimenta have been hypothesized to serve as a camouflaging device, to aid in thermoregulation, to have a defensive function, to warn large flying animals such

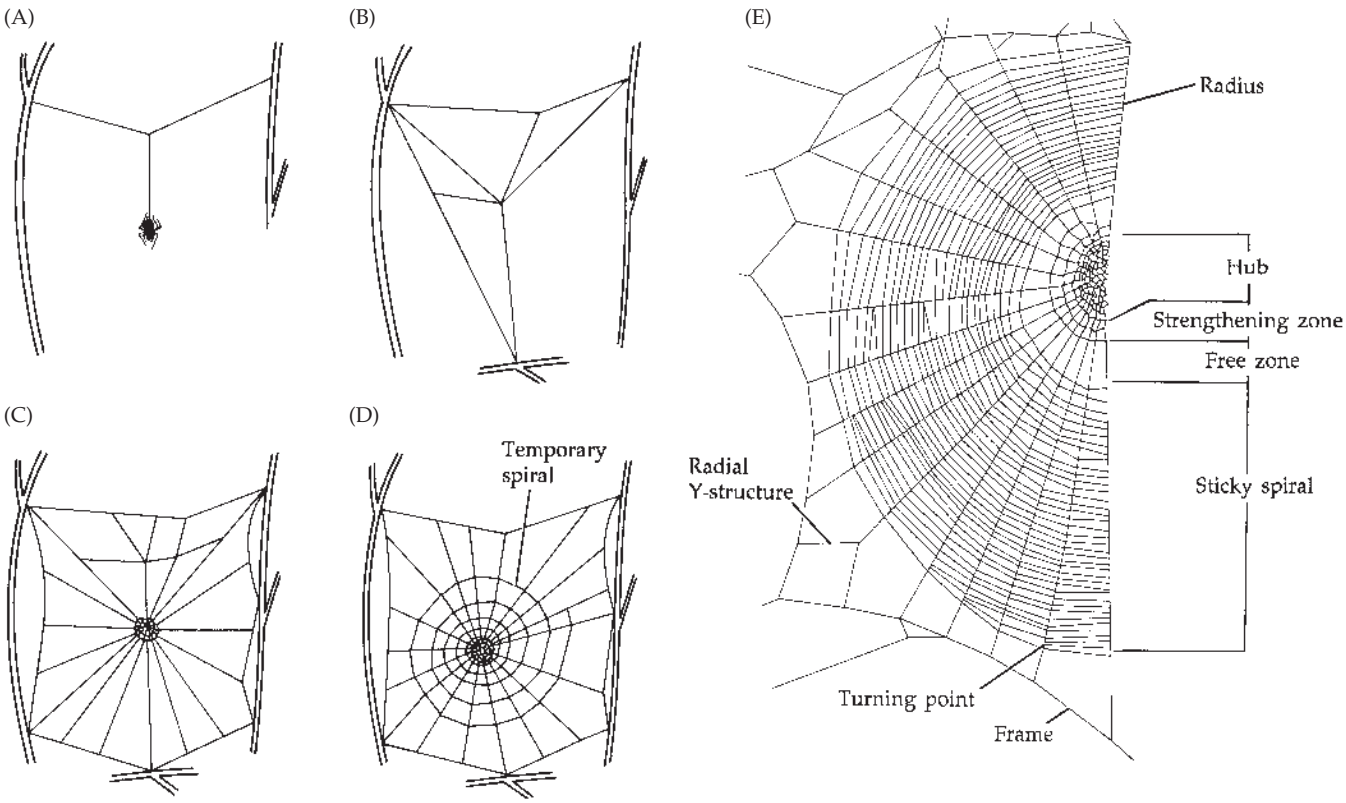

FIGURE 24.8 Construction of an orb web. (A) Formation of the Y-shaped frame. (B,C) Addition of radial threads. (D) Addition of the temporary spiral or working platform. (E) A portion of the completed orb web, with the temporary spiral replaced by the sticky spiral. (E after R. Foelix. 2011. *Biology of Spiders*. Oxford Univeristy Press, Oxford.)

as birds of the otherwise difficult to see webs (and thus prevent web damage), and to act as a visual guide to lure prey towards the web (by reflecting UV light and imitating floral patterns). Many orb-weavers (e.g., *Araneus*) can spin an entire web in less than 30 minutes, and most build a new web every night, but some have long-lasting webs (e.g., species of the araneids *Nephila* and *Cyrtophora*). When building a new orb web, spiders do not "waste" the silk of the old web, but eat it before or during the production of the new one. Radioactive labeling experiments show that the silk proteins from eaten webs appear at the spigots in new threads soon after ingestion, often within a few minutes!

Orb web building behavior is highly stereotypical and programmed, although there is some plasticity in the process, as spiders can, to some extent, adapt their web building behavior to a specific situation. In general, web architecture is fairly constant within species, in the sense that under similar circumstances and physical conditions, different individuals of the same ontogenetic stage and sex will build very similar webs. Among orb-weavers of the same species, the number of radii and spiral turns varies little. Web building appears to depend entirely on tactile input—normal webs are produced at night and by experimentally blinded spiders. Even gravity does not seem to be necessary, as illustrated by two famous orb-weaver spiders sent into space aboard Skylab.

Orb-weavers are an ancient group, with the oldest fossils being of Jurassic age and the oldest fossilized orb web spiders from the Cretaceous. Three groups of spiders make similar orb webs using different types of silks but with presumably homologous stereotypical behaviors. These are the deinopids and uloborids (formerly grouped under the superfamily Deinopoidea, no longer recognized as a natural group), which use cribellate silk for the capture spiral, and the araneoids (Araneoidea, a lineage comprising 17 families), which use a novel type of sticky, viscid, and gluey silk. During the last few decades the dominant paradigm has been that deinopoids and araneoids are reciprocally monophyletic and that together they form a clade (known as Orbiculariae). In recent years, several molecular studies (including phylogenomic approaches using thousands of genes) have rejected the long-accepted monophyly of Orbiculariae and of Deinopoidea, by placing the cribellate orb-weavers (Deinopidae and Uloboridae) with other groups and not with the ecribellate orb-weavers (Araneoidea). Orb webs have a complex evolutionary history, and while some studies support a single origin of orb webs, more recent results suggest that orb webs have likely evolved several times independently.

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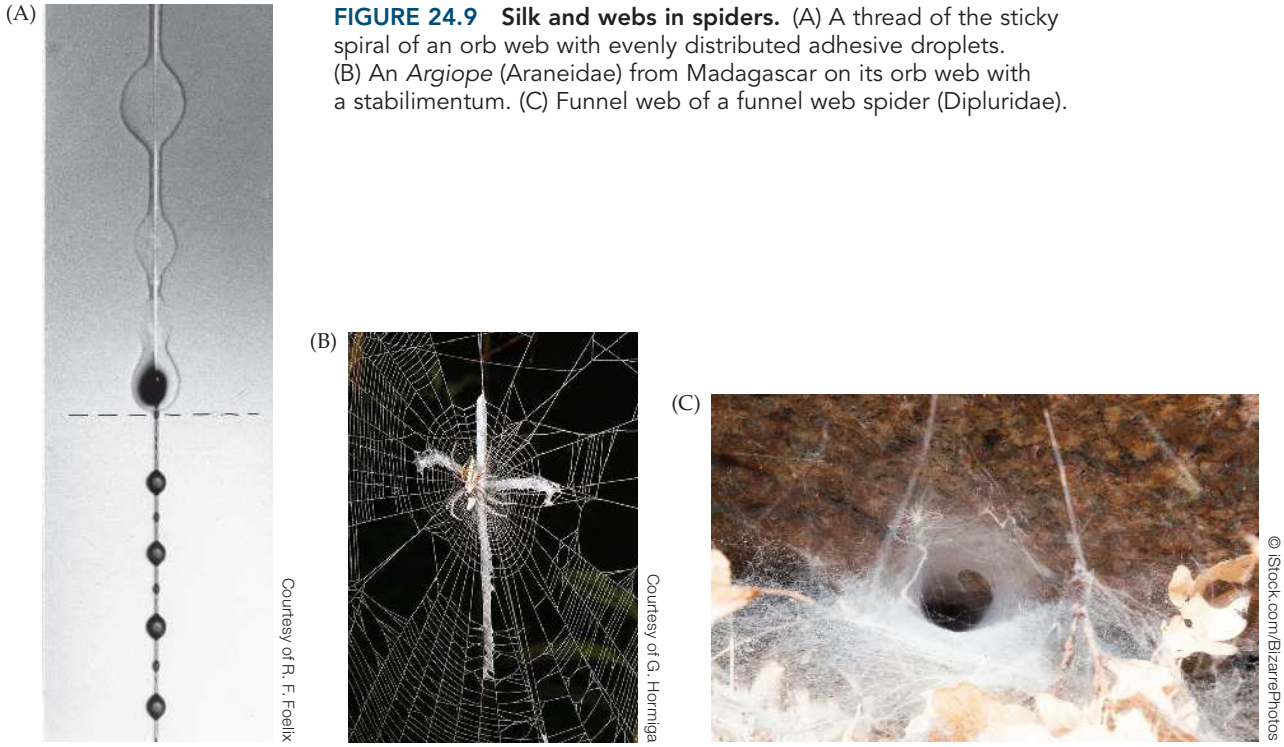

FIGURE 24.9 Silk and webs in spiders. (A) A thread of the sticky spiral of an orb web with evenly distributed adhesive droplets. (B) An *Argiope* (Araneidae) from Madagascar on its orb web with a stabilimentum. (C) Funnel web of a funnel web spider (Dipluridae).

For over a century specialists have debated about the origin and evolution of spider silk and webs. The silks and fibrous proteins found in many arthropod groups (e.g., in Lepidoptera and numerous other insect taxa, pseudoscorpions, tanaid crustaceans, and others) seem to have evolved independently of the silks of spiders. Silk production is ancestral in spiders, and all spiders retain both the ancestral and less complex silk types and the more recently evolved silk glands. This implies that silk gland evolution is correlated with selection for additional, not alternative, silk types and functions. It has been suggested that spider silk glands are derived from epidermal invaginations. In males, the epiandrous silk glands are derived from dermal glands. Silk gland spigots may have evolved from setae (cuticular "hairs") or from sensory setae (such as morphologically similar chemoreceptor setae of mygalomorphs). It is unclear why spider silk first evolved, but many researchers favor the idea that its origin was linked to wrapping and protecting eggs. The recent discovery of spinnerets with spigots in the mid-Cretaceous fossil arachnid *Chimerarachne yingi* allows for the possibility that spinnerets and the concomitant abdominal silk glands could have evolved before the most recent common ancestor of spiders. A recent book by Eberhard (2020) provides an encyclopedic treatment on the biology of spider webs and web building behaviors.

Some spider species cooperate in web building, prey capture, and even spiderling rearing. Such social activity has been reported for some 20 species in at least six families. In spiders, group living takes two different forms: cooperative (nonterritorial permanently social or quasi-social) and colonial (territorial permanently social or communal). Cooperative social species (e.g., several species in the theridiid genus *Anelosimus* and in the eresid *Stegodyphus*) have communal nests and communal capture webs that they inhabit throughout the entire lifetime of the individual, with colony members cooperating in prey capture and raising young. Colonial species (e.g., the uloborid *Philoponella republicana*) form aggregations, but individuals in the colony generally forage and feed alone, and there is no maternal care beyond the egg stage.

The theridiid *Anelosimus eximius* (Figure 24.15A), and some other species in this genus of cobweb weavers, exhibit the highest level of sociality known to spiders. These social species can form very large colonies, up to thousands of individuals, sometimes covering entire trees. These individuals live in a communal web and cooperate in brood care, prey capture, feeding, and web building.

Locomotion

Eucheliceratе locomotion follows the principles of arthropod joint articulation and leg movements discussed in Chapter 20. Except for the xiphosurans and a few aquatic arachnids, the legs must also be strong enough to support the body on land. Walking by terrestrial eucheliceratеs demands that the body be supported off the substratum and that the four pairs of legs move in sequences that maintain the animal's balance.

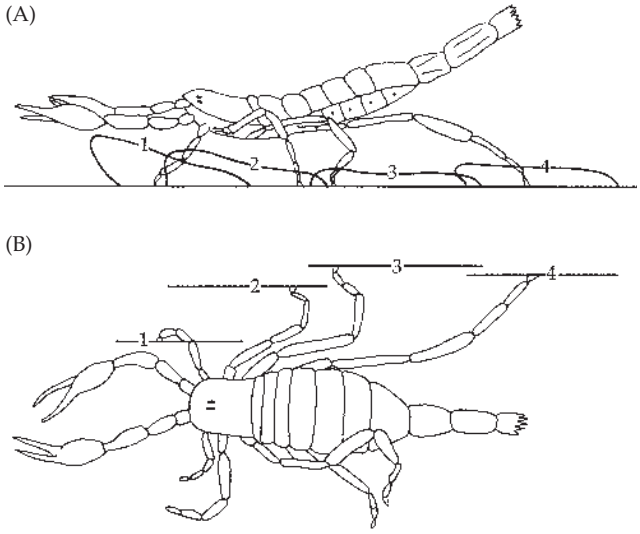

FIGURE 24.10 Walking in scorpions. Numbers denote legs 1–4. (A) The paths of the leg tips during their recovery strokes. Notice that the anterior legs are lifted higher off the ground than are the posterior legs. (B) Distance of each leg tip from the body.

The xiphosurans are slow benthic crawlers and shallow burrowers, utilizing their stout prosomal limbs to push their heavy bodies over and through the sand. The legs are close together (Figure 24.2B), and thus coordination of movement sequences is essential. Horseshoe crabs are also able to swim, upside down, by beating the opisthosomal appendages.

The details of scorpion walking patterns are fairly well understood. During simple forward walking, each of the eight limbs moves through the usual power and recovery strokes. In scorpions (and many other arthropods) the joints between the coxae and the body are virtually immovable and do not contribute to the overall motion of the limbs. Not all of the walking legs move in the same pattern. The tips of the anterior legs are brought quite high off the ground during their recovery strokes; they may be used to feel ahead as the animal moves (Figure 24.10A). Also, the tips of each pair of legs extend different distances from the body, allowing for stride overlap without contact between legs (Figure 24.10B). Leg movements in scorpions do not follow the usual metachronal model. Rather, the typical sequence of movement along one side of the body is leg 4, then 2, then 3, and finally 1, with the legs on the opposite side being generally, but not precisely, out of phase. The somewhat staggered overlap of the movement sequences produces a smooth gait during forward walking, unlike the jerky motion of an insect moving by the alternating tripod pattern described in Chapter 22. Like many arthropods, scorpions are also able to change speeds, turn abruptly, walk backward, and burrow in loose sand.

Spiders have evolved a number of methods of locomotion, all involving the usual leg motions inherent in jointed arthropod limbs, which involve flexors and extensor muscles. However, in spiders the femur-patella and the metatarsus-tarsus joints lack extensor muscles. In these latter joints, extension is accomplished by increasing hemolymph pressure through a hydraulic mechanism. During normal spider walking, the eight ambulatory limbs move in a so-called diagonal rhythm sequence (Figure 24.11). That is, legs 2 and 3 on one side of the body are moving simultaneously with legs 1 and 4 on the opposite side. This gait maintains a four-point stance while distributing the body weight more or less equally among those appendages in contact with the substratum. During very slow walking, however, posterior to

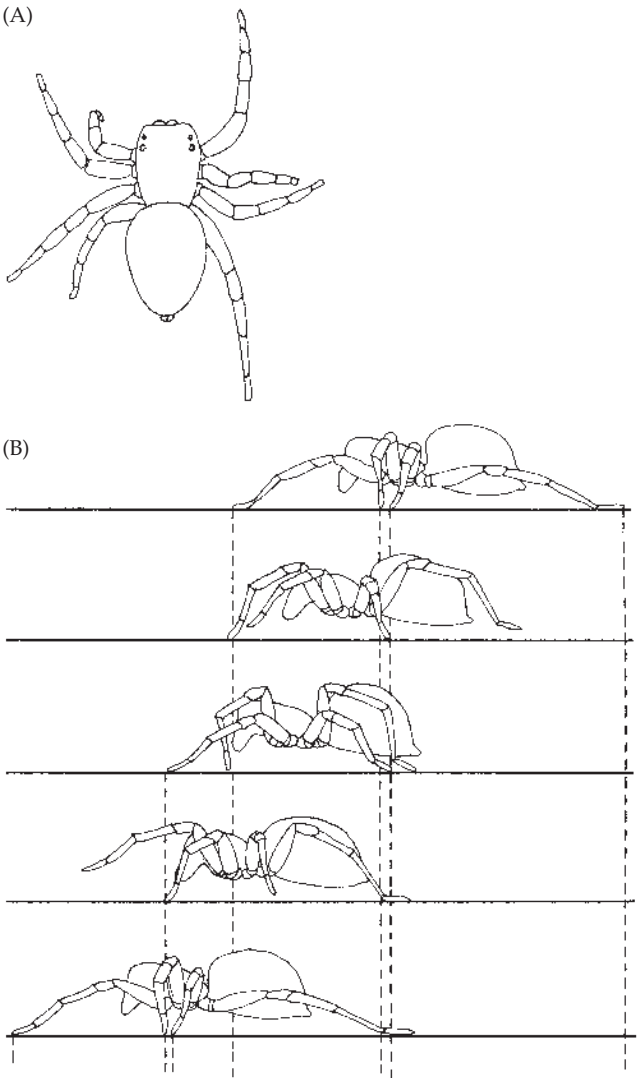

FIGURE 24.11 Walking in spiders. (A) A salticid with legs in walking positions (dorsal view). (B) A lycosid during slow walking (lateral view). Vertical dotted lines connect each leg through its power and recovery strokes relative to the forward progress of the body. Note the large degree of overlap in leg movements, particularly of the first two legs. Tangling is prevented in part by keeping the tips of adjacent legs at different distances from the body. (After R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

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anterior metachronal waves of limb motion are detectable. The stride lengths of the legs overlap somewhat and vary with speed and direction of movement. The placement of the legs on the body, and the arcs through which they swing, prevent contact between legs.

A number of spiders (e.g., members of the family Salticidae, or jumping spiders) are also capable of jumping (Figure 24.12A). Propulsion is achieved primarily by a rapid extension of the fourth pair of legs. Once the spider is airborne, the front legs are extended forward and used in landing. Salticids jump during normal locomotion and also when capturing prey and escaping from predators.

Silk plays an important role in various methods of spider locomotion. When walking or jumping, most spiders continually produce a strong thread behind them, called a dragline (Figure 24.12B), produced by the major ampullate silk glands. The dragline is periodically cemented to the substratum with silk from the **piriform glands**, providing a safety line for the wandering spider. Thus, a spider brushed from a surface does not fall to the ground; instead, it pays out dragline silk and dangles like a tethered mountaineer who has lost his/her footing. Silk is also used to provide a substratum on which spiders move. Web spinners crawl over (e.g., diplurids and agelenids) or under (e.g., linyphiids and cyatholipids) their sheet webs with limb movements more or less like those used in normal walking, except that stride lengths must correspond to the distances between threads in the web. Many spiders are able to move about on a single thread (Figure 24.12C). This may involve dropping vertically as a thread is paid out from the spinnerets, climbing up a vertical thread, or moving while hanging upside down on a horizontal thread (they do not walk atop single threads, tightrope fashion). Most spiders that are capable of these sorts of activities possess intricately fashioned "thread clamps" on some or all of the leg tips (Figure 24.12D,E).

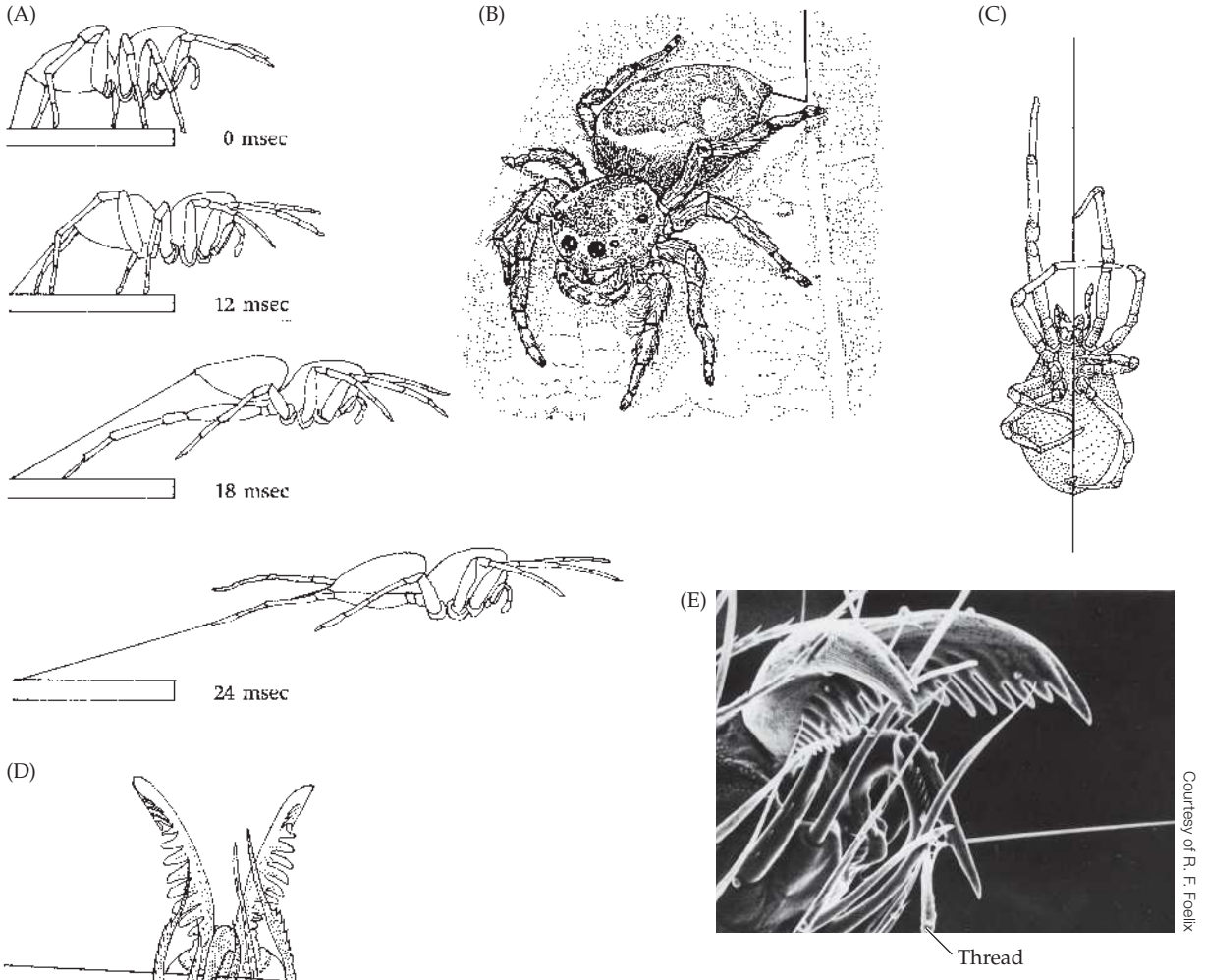

FIGURE 24.12 More aspects of spider locomotion. (A) A salticid jumping. Note the dragline of silk. (B) A salticid paying out its dragline while walking. (C) The orb-weaver *Zygiella* (Araneidae) climbing up a single thread. (D,E) The tarsal tip of *Araneus* (Araneidae) grasping a single thread. (A,C after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

(A)

Courtesy of David McIntyre

(B)

blickwinkel/Alamy Stock Photo

FIGURE 24.13 Aquatic spiders and their adaptations. (A) A wolf spider walking on the surface of water. (B) A diving spider (*Argyroneta*) with its "diving bell."

Many spiders also excavate burrows, and a few lycosoids (such as the fishing spiders of the genus *Dolomedes*) and some daddy longlegs can walk on water (Figure 24.13). One species, *Argyroneta aquatica* (family Dictynidae), actually lives underwater. *Argyroneta* can walk on submerged substrates and can build a "diving bell" that allows gas exchange to oxygenate the air trapped in it; they spend most of their time in this bell when not wandering around in search of prey. There are also several intertidal species (e.g., *Desis bobmarleyi* in the family Desidae) that can tolerate submergence at high tides, in some cases by utilizing the air bubbles trapped in empty barnacle shells or other such structures.

Some daddy longlegs with extreme long legs have the ability to break off legs to avoid enemies, and many function well missing one or several legs, which do not regenerate.

Feeding and Digestion

Feeding The basic chelicerate feeding strategy is one of prey capture followed by extensive external digestion and then ingestion of liquefied food or, more rarely, of small particulate material. There are exceptions to this pattern, of course, most of which involve drastic modifications of the mouthparts. For example, we have already mentioned the varied feeding habits among the mites and ticks, many of which are herbivores or parasites with piercing mouthparts. Whereas many chelicerates are highly specialized in terms of their feeding behavior, others are generalists. Horseshoe crabs, for example, commonly feed on a variety of invertebrates, including worms, molluscs (especially bivalves), crustaceans, and other infaunal and epibenthic creatures, but they also scavenge on almost any organic material. Food is gathered by any of the chelate appendages and passed to the gnathobases along the ventral midline, where it is ground to small bits and then moved forward to the mouth, as in many nonchelicerate arthropods. This mode of feeding by ingesting solid food is also found in Opiliones.

Scorpions feed mostly on insects, although some large species occasionally eat snakes and lizards. Most are nocturnal and detect prey mainly by highly sensitive mechanoreceptors. A fascinating method of prey location by the Mojave Desert sand scorpion, *Paruroctonus mesaensis*, has been described by Phillip Brownell and colleagues (see References). Brownell noticed that *Paruroctonus* ignores both airborne vibrations (e.g., wingbeats) and visual input but responds immediately to nearby prey that are in contact with the sand. This scorpion is even able to detect buried prey, which it immediately uncovers and attacks. Apparently the scorpion senses subtle mechanical waves set up in the loose sand by movements of the prey. Special mechanoreceptors in the walking legs are stimulated as the waves pass beneath the scorpion's limbs. The information is processed to determine the direction and approximate distance to the prey source.

Once a scorpion locates a victim, the prey is grasped by the chelate pedipalps. The opisthosoma is arched over the prosoma, bringing the telson and stinging apparatus into position to inject venom (Figure 24.14). Muscular contractions force the venom through a pore in the aculeus and into the prey. The venom is a neurotoxin that can quickly paralyze and kill most prey; in fact, some scorpion venoms can kill large animals, including humans. Perhaps the most familiar of these dangerous scorpions are two species that occur in the American Southwest: the bark scorpion (*Centruroides exilicauda*) and the stripe-tailed scorpion (*Vaejovis spinigerus*). A North African species, *Androctonus australis*, produces a venom considered to be as potent as that of cobras. Other genera of potentially dangerous scorpions include *Buthus* and *Parabuthus* (southern Europe, Africa, and the Middle East) and *Tityus* (South America). Small doses of venom can also be used to "tame" the mate during the precopulatory dance.

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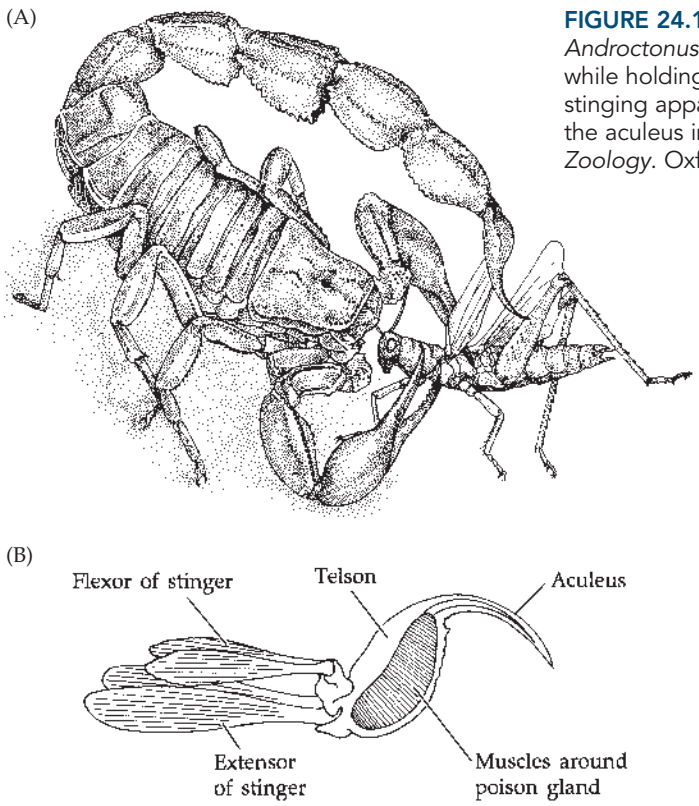

FIGURE 24.14 Stinging apparatus in scorpions. (A) The scorpion *Androctonus australis*, applying its stinging apparatus to a grasshopper while holding the prey with its pedipalps. (B) The scorpion's telson and stinging apparatus. The telson is normally held flexed; extension drives the aculeus into the prey. (B after P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

The sequence of events in the ingestion of food by scorpions is typical of many arachnids. Once it has been captured and stung, the prey is passed to the chelicerae, which tear it into small bits. The gnathobases grind and mash the food as digestive juices are released through the mouth; this process reduces the food to a semiliquid form. As this organic "soup" is ingested, the hard parts are discarded, and more bits of food are moved between the gnathobases for processing.

Virtually all spiders are predatory carnivores, although young spiderlings in certain families may consume pollen and fungal spores caught on web silk. In some rare cases, some species exploit other food sources, such as nectar, but the vast majority are generalist carnivores. With the exception of a few families (e.g., Salticidae, Oxyopidae, Thomisidae, and Lycosidae), spiders hunt or feed mainly at night. Most spiders can be separated into two broad categories based on prey-capture strategies. The first is the more sedentary spiders that use some sort of silken web, trap, or net to catch prey. The second is the "wandering" spiders that actively hunt or ambush prey without the direct use of silk (although many wrap their victims after capture).

Earlier, we described the construction of the familiar orb web (Figure 24.8). When a potential prey item, such as a flying insect, strikes and adheres to a web, its movements send out vibrations that alert the spider to the presence of food. The spider then moves rapidly to the victim and bites it. The immense majority of spiders are solitary, but as we have mentioned, a few live and feed communally, so in this case they tend to move in synchronized bursts—to distinguish vibrations of trapped prey from those of their moving mates (Figure 24.15A).

Another type of silken trap is the horizontal sheet web produced by members of several families, such as the Linyphiidae and Agelenidae. Sheet webs are often suspended by a network of supporting threads (Figure 24.15B). Insects become entangled in the sheet web, sometimes first getting caught in the supporting threads and then dropping to the sheet. Once on the sheet, the prey is captured.

Many theridiid spiders build vertical frame webs (Figure 24.15C). Near their attachment to the substratum, the vertical trap threads are beaded with a gluey, sticky coating from silk glands (aggregate glands). Walking prey contact these sticky droplets and become trapped, and if they are attached to multiple trap lines, the tension of these silk lines will pull the prey upward, off the ground. Upon sensing movement in the web, the spider rushes to the prey, wraps it in silk, and bites it.

Members of the genus *Hyptiotes* (family Uloboridae) spin modified orb webs consisting of only three sectors (Figure 24.15D). The spider produces a tension thread from the point of convergence of the radii and also a short attachment thread stuck to the substrate; the spider's body acts as a bridge between these two silk threads. When an insect strikes the web, the spider releases the tension thread, and the web, called a spring trap, collapses around the prey.

Although it is not known what the ancestral web architecture of spiders might have been, araneologists have traditionally looked at liphistiids (Mesothelae; Figure 24.5N), the sister group to the lineage that includes all other extant spiders (the Opisthothelae), to conjecture about the biology of primitive spiders. Many liphistiids build simple subterranean silken tubes with a single opening from which threads radiate outward (Figure 24.5N). The spider resides in the tube, and the threads serve as "fishing lines" or trip lines that allow the spider to detect passing prey, thus extending its sensory zone as far as these lines reach. An interesting modification of this system is seen in the purse web of some atypids (family Atypidae), such as *Atypus* and *Sphodros* (Figure 24.15F). Here the silken tube is mostly buried beneath the soil, with just a short portion of the blind end lying horizontally above the

FIGURE 24.15 The use of spider silk for prey capture. (A) Two *Anelosimus eximius* (Theridiidae) and their prey in Ecuador, an unusual case of communal prey capture. (B) The horizontal sheet web of *Frontinella* (Linyphiidae) in the Dominican Republic. (C) The delicate sheet web of a New Zealand Physoglenidae, *Runga*. (D) The web of an *Achaearanea* from Ecuador (Theridiidae). (E) The Australian gradungulid *Progradungula otwayensis* holding its cribellate silk catching ladder. (F) The purse web of the North American mygalomorph spider *Sphodros* (Atypidae). When the spider senses the presence of an insect on the tube, it stalks it through the silk with its formidable chelicerae. (G) The cribellate orb web of *Sybota*, an uloborid from Chile. (H) *Exechocentrus lancearius* (Araneidae), a bolas spider from Madagascar that presumably uses chemical mimicry to lure its prey. (I) The micro-orb web of *Patu* (Symphytognathidae) built on the forest leaf litter in the Dominican Republic. Symphytognathids include the smallest known adult spiders (less than half a millimeter). (J) The araneophagic pirate spider *Gelanor latus* (Mimetidae), from Brazil. Mimetids are members of the ecribellate orb-weaving clade and have abandoned building capture webs.

surface or vertical against a tree trunk or a rock. Insects crawling over the exposed tube are detected by the spider, and their large orthognathous chelicerae make two parallel slices in the tube wall near the prey. Their large cheliceral fangs are extended through the incisions to grab the victim and pull it through the tube wall. After the prey is killed, the tear in the tube is repaired.

Most spiders simply set their "traps" and wait for prey, but others actually manipulate silken structures to catch insects. The ogre-faced spiders (family Deinopidae) produce a rectangular web of cribellate threads, which is a highly modified orb web, and hold it between their front walking legs. Deinopids forage at night and have extraordinary visual capabilities, especially *Deinopis*, with a pair of enormous posterior median eyes that are ultrasensitive to light (Figure 24.21A). When an insect is visually detected, the spider sweeps the net around it. The bolas spiders, such as *Mastophora* (family Araneidae), are among the most bizarre and specialized hunters. While hanging from a suspension thread, the bolas spider "throws" a catching thread tipped with sticky liquid to capture its prey (Figure 24.15H). Bolas spiders of the genus *Mastophora* hunt at night using chemical mimicry: they specialize

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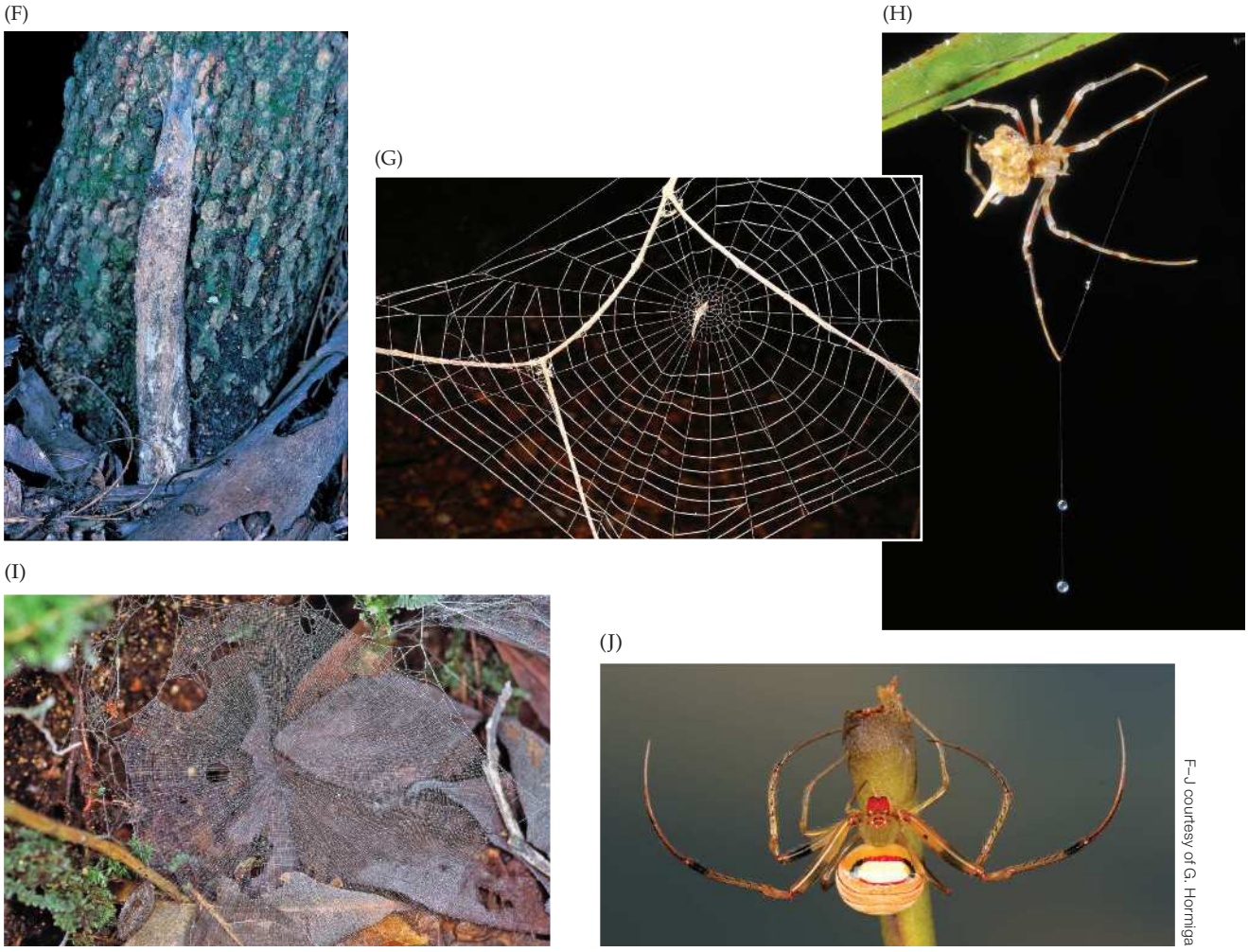

in feeding on male moths of the genus *Spodoptera*. *Mastophora* releases an airborne chemical that mimics the sex pheromone of the female *Spodoptera*, thus attracting males within reach of the catching thread and greatly increasing the likelihood of capture success.

Whereas most sedentary spiders detect their prey by sensing web vibrations, the "wandering" spiders use a variety of methods. Some wolf spiders and most jumping spiders locate prey visually, while many others sense vibrations (e.g., wingbeats or walking movements) or rely simply on accidental contact. Some actually chase prey; others, such as certain trapdoor spiders, lie in ambush and wait for victims to come close enough to grab.

Among jumping spiders, members of the genus *Portia* require special mention. Unlike most spiders, whose behaviors appear to be genetically programmed, *Portia* species exhibit trial and error strategies and learning in their predation on other spiders. *Portia* really doesn't look much like a spider; rather, it resembles crumpled leaves or twigs. Some species utilize this camouflage in what has been described as aggressive mimicry. To do so, *Portia* climbs onto the web of another spider and begins to generate vibrations that mimic those of a trapped insect. When the resident spider responds, *Portia* attacks and kills it. More remarkable is that *Portia* often tries various vibration patterns on a web, and when a successful one is found, it continues to use only that one on the webs of the same prey species in the future. Aggressive mimicry is also used by pirate spiders (Mimetidae) (Figure 24.15J), which feed mainly on other spiders.

Regardless of the method of prey location and capture, once contact is made, spiders pull their prey to their chelicerae and bite it, inserting the fangs and injecting venom from the poison glands within the prosoma (Figure 24.16A). The prey is quickly immobilized or killed by the poison. An interesting exception to this grabbing-and-biting pattern is displayed by the spitting spiders (family Scytodidae), some of which are social. The poison glands of *Scytodes* include a posterior glue-producing portion along with the usual venom-secreting cells in the anterior region. A mixture of venom and glue is shot very fast from pores in the cheliceral fangs by muscular contraction of the glands; thus the prey is captured without direct contact (Figure 24.16B).

Many spiders wrap their prey in silk to some extent prior to feeding, even if silk is not used in the actual capture. Many hold the victim and wrap it prior to

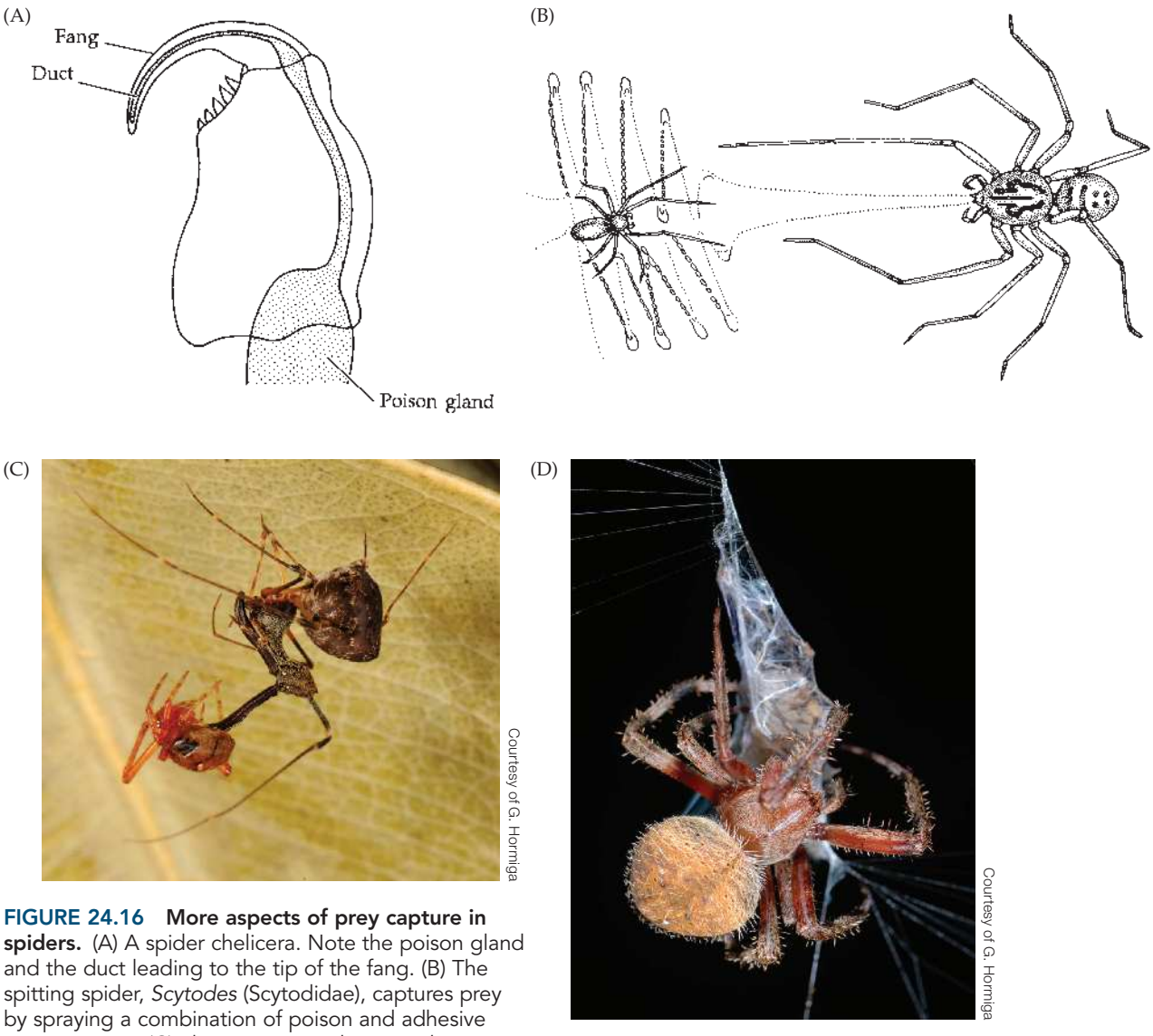

FIGURE 24.16 More aspects of prey capture in spiders. (A) A spider chelicera. Note the poison gland and the duct leading to the tip of the fang. (B) The spitting spider, *Scytodes* (Scytodidae), captures prey by spraying a combination of poison and adhesive over its victim. (C) The assassin spider *Eriauchenus* (Archaeidae), from Madagascar, stalks a theridiid spider. Notice the extremely long chelicerae (only the left chelicera is extended) and the bizarre shape of the cephalothorax with a long and narrow "neck." (D) *Neoscona arabesca*, an araneid orb-weaver, wrapping its insect prey (USA). (B after R. Foelix. 1996. *Biology of Spiders*. Oxford University Press, Oxford.)

biting it (e.g., theridiids and araneids). Very active insects caught in orb webs are generally wrapped immediately, which prevents possible damage to the web or its owner (Figure 24.16D). Potentially dangerous prey, such as large stinging insects, are generally handled in this manner.

Nearly all spiders possess poison glands that produce proteinaceous neurotoxins, although venom composition is highly heterogeneous and varies widely across species. Venom glands have been lost in all members of the family Uloboridae and in the Anapidae genus *Holarchaea*. The toxicity of spider venom is quite variable, and only about two dozen species are considered dangerous to humans. Among these are the black widows (*Latrodectus* species), a Brazilian wolf spider (*Lycosa erythrognatha*), the brown recluse spiders (such as *Loxosceles reclusa*), the Australian funnel-web spiders (such as *Atrax robustus*), and some species belonging to the tropical wandering spider family Ctenidae (e.g., *Phoneutria fera*).

Uloborid spiders lack the poison glands typical of almost all other spiders and wrap their prey with up to hundreds of meters of silk that severely compresses and physically damages the prey's cuticle. This compaction probably functions to facilitate these spiders' unusual method of feeding, which involves covering the entire surface of the prey with digestive fluid, cyclically regurgitating and sucking up the fluid from the outer surface of the prey package. Spiders, like most other chelicerates, ingest their food in a liquid or semiliquid form. The chelicerae of most spiders have dentate gnathobases with which the prey is mechanically pulverized, while at the same time the food is flooded with digestive juices. Except for the hard parts, the prey is thus reduced to a partially digested broth. Bristles bordering the mouth and thousands of overlapping cuticular plates in the

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pharynx serve as filters so that only very small particles (<1 μm) enter the gut. Members of some families (e.g., some species in Theridiidae and Thomisidae) lack cheliceral teeth. These spiders simply puncture their prey's cuticle and then flush digestive juices in and out of the wound. The liquefied innards of the victim are then sucked out of its body and ingested.

The fascinating biology of two species of jumping spiders (Salticidae) that feed preferentially on mosquitoes was recently described; both are highly specialized mosquito assassins. One species, *Evarcha culicivora*, like an eight-legged vampire, is particularly drawn to female mosquitoes whose guts are filled with blood (especially species of *Anopheles*). Eating blood-filled mosquitoes also allows this spider to acquire a scent that is attractive to members of the opposite sex. Another species, *Paracyrba wanlessi*, preferentially feeds on mosquito larvae lurking in pools of water inside bamboo.

Digestion The digestive system of chelicerates follows the basic arthropod plan of foregut, midgut, and hindgut, the first and last parts being lined with cuticle (Figure 24.17). The foregut is often regionally specialized. In the xiphosurans (e.g., *Limulus*), the foregut loops anteriorly to form an esophagus, crop, and gizzard, the last of these bearing sclerotized ridges that grind ingested particles (Figure 24.17A). In many arachnids, portions of the foregut are modified as pumping organs for sucking in liquefied food. In scorpions this function is served by a muscular pharynx, and in spiders by an elaborate sucking stomach (Figure 24.17B). The pharynx of spiders may contain chemosensory cells that function as taste receptors.

The eucheliceratе midgut bears paired digestive ceca and is the site of final chemical digestion and absorption (Figure 24.17C). Xiphosurans have two pairs of ceca arising from the anterior part of the midgut, followed by an intestine, a short rectum (the hindgut), and the anus on the posterior margin of the opisthosoma. In *Limulus*, enzymes are produced by the midgut wall and secreted into the lumen. Apparently only preliminary protein digestion occurs extracellularly, and final breakdown takes place in the cells of the digestive ceca after absorption.

Most spiders possess four pairs of digestive ceca in the prosoma and frequently additional branched ceca in the opisthosoma (Figure 24.17B,C). Near its junction with a short rectum, the midgut expands as a spacious "mixing chamber," called the stercoral pocket. Malpighian tubules arise from the midgut wall near the origin of the stercoral pocket. The anus is located on the opisthosoma near the spinnerets, opening on an anal tubercle that could be homologous with the pygidium of other arachnids.

The midgut of scorpions bears six pairs of digestive ceca (Figure 24.17D). The first pair, the salivary glands, lies within the prosoma and produces much of the digestive juice used in preliminary external digestion. The remaining five pairs are highly convoluted and lie in the opisthosoma. These ceca produce the enzymes for final digestion and are the site of absorption of the digestive products. Two pairs of Malpighian tubules arise from the posterior region of the midgut, just in front of the short rectum. The anus is on the last opisthosomal segment.

Circulation and Gas Exchange

The eucheliceratе circulatory system, like that of other arthropods, consists of a dorsal ostiate heart situated within a pericardial sinus and giving rise to various open-ended vessels (Figures 24.17 and 24.18). Blood leaves these vessels and enters the hemocoel, where it bathes the organs and supplies the structures of gas exchange before returning to the heart. The complexity of the system is primarily a function of body size; some very tiny eucheliceratеs (e.g., palpigrades and some mites) have lost much or all of their circulatory structures—for them, gas exchange is cutaneous. On the other hand, xiphosurans are large animals, and their body plan demands a substantial circulatory mechanism to move the blood around inside the rigid body covering. The large tubular xiphosuran heart bears eight pairs of ostia, and it is attached to the body wall by nine pairs of ligaments that extend through the pericardium (Figure 24.17A). The organs of these big creatures are supplied with blood through an extensive arterial system arising from the heart and opening into the hemocoel close to the organs themselves. In the opisthosoma, a major ventral vessel gives rise to a series of afferent branchial vessels to the book gills. Efferent vessels carry oxygenated blood to a large branchiopericardial vessel leading back toward the heart.

The gas exchange organs of xiphosurans are unique among the chelicerates. The presence of gills is, of course, associated with their aquatic lifestyle. The structure of these opisthosomal book gills provides an extremely large surface area, a necessity for adequate gas exchange by these large animals (Figures 24.2B and 24.18A). Each gill bears hundreds of thin lamellae, like pages in a book. The blood within the lamellae is separated from the surrounding seawater by only a thin wall. Water is moved over the lamellae by metachronal beating of the gills; these movements also cause blood flow into (on the forward strokes) and out of (on the backward strokes) the gill sinuses.

The heart of a spider lies within the opisthosoma and bears two to five pairs of ostia (Figure 24.18B). It is suspended within the pericardial sinus by several ligaments attached to the inside of the exoskeleton. These suspensory ligaments are stretched during systole as blood is pumped from the heart into arteries. The elasticity of the ligaments then effects diastole, expanding the heart and drawing blood into it from the pericardial sinus. The routes of the major arteries ensure that an ample supply of oxygenated blood reaches the major organs,

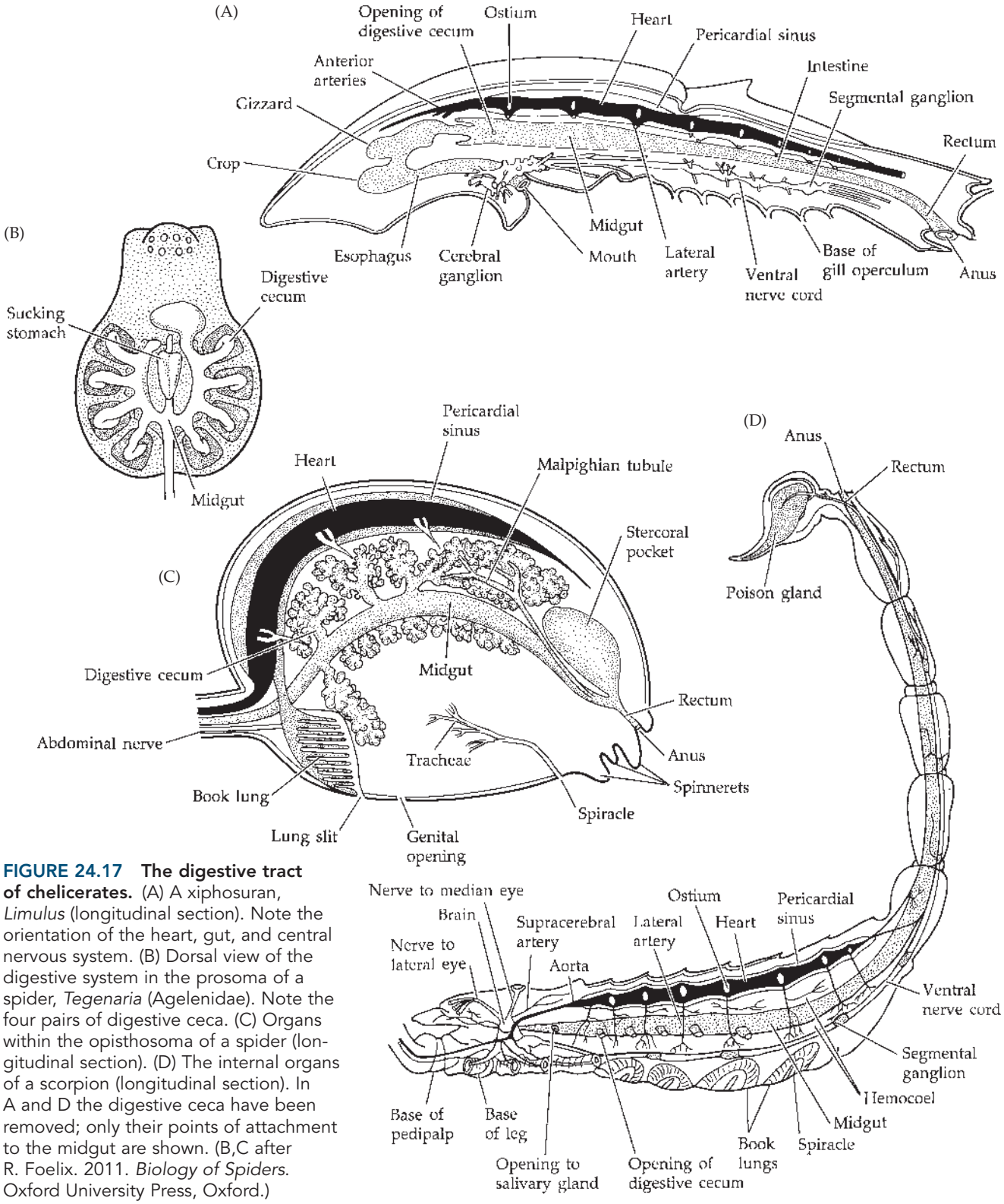

FIGURE 24.17 The digestive tract of chelicerates. (A) A xiphosuran, *Limulus* (longitudinal section). Note the orientation of the heart, gut, and central nervous system. (B) Dorsal view of the digestive system in the prosoma of a spider, *Tegenaria* (Agelenidae). Note the four pairs of digestive ceca. (C) Organs within the opisthosoma of a spider (longitudinal section). (D) The internal organs of a scorpion (longitudinal section). In A and D the digestive ceca have been removed; only their points of attachment to the midgut are shown. (B,C after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

particularly the central nervous system, muscles, and hemocoelic spaces in the limbs in which blood pressure aids in leg extension. From the hemocoel, blood is channeled back to the pericardial sinus and the heart.

Aerial gas exchange structures in spiders include book lungs and tracheae. Generally, liphistiomorphs, mygalomorphs, and some basal araneomorphs have two pairs of book lungs but no tracheae, whereas members of Araneomorphae usually have one pair of anterior book lungs and a posterior system of tracheal tubes. In some groups of very small araneomorphs (such as the minute Synaphridae), the anterior book lungs are modified into tubular tracheae; in other groups there are anterior and posterior tracheal systems, while in a

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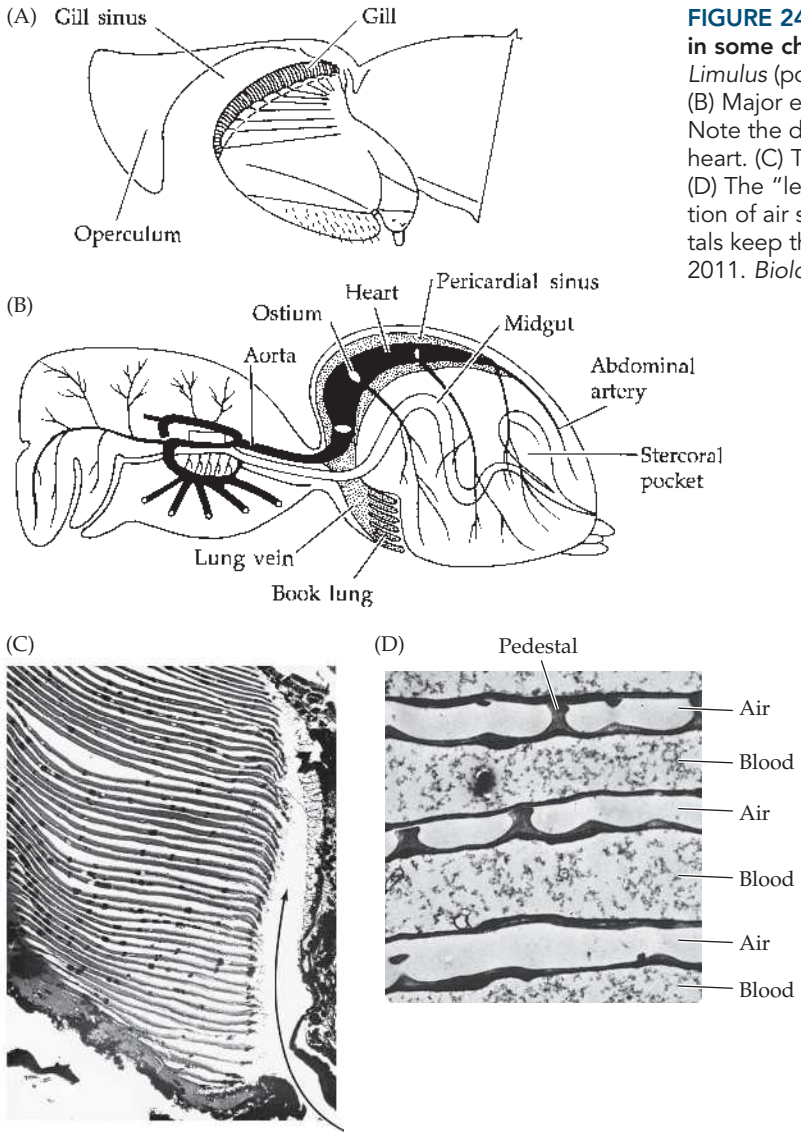

C,D courtesy of R. F. Foelix

FIGURE 24.18 Circulatory and gas exchange structures in some chelicerates. (A) An opisthosomal appendage of *Limulus* (posterior view). Note the gill and opercular parts. (B) Major elements of the circulatory system in a spider. Note the direct route of blood from the book lung to the heart. (C) The book lung of the spider *Lycosa* sp. (section). (D) The "leaves" of a book lung (section). Note the separation of air spaces and blood-filled leaves. Cuticular pedestals keep the air spaces from collapsing. (B after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

few their respiratory system consists of only anterior tracheae. Since the tracheae occur only in more distal groups among spiders, it is likely that they evolved separately from those of other arachnids and, of course, independently from those of insects and myriapods. Phylogenetic analyses, both morphological and molecular, support this contention and place spiders with the other pulmonate arachnid orders, including scorpions.

Spider book lungs are located in the second, or the second and third, segments of the opisthosoma. They open to the outside via spiracles, or lung slits, near the epigastric furrow (Figure 24.5C). Since they are localized and do not extend far into the body, book lungs must receive sufficient circulating blood to ensure adequate distribution of oxygen throughout the body and removal of carbon dioxide from the internal organs. Just inside each lung slit is an expanded chamber, the atrium, from which numerous flattened air spaces extend into the hemocoel (Figure 24.18D). These leaflike pockets of air are separated from one another by thin blood-filled extensions of the hemocoel. Although the book lungs are themselves relatively small, this structural arrangement provides a very large surface area between the "pages" of the book lungs and the circulatory fluid. Blood that has passed by these surfaces returns directly to the pericardial sinus via the lung vein (Figure 24.18B).

Spider tracheae open to the outside through one or two spiracles located posteriorly on the third opisthosomal segment (Figures 24.5B,C and 24.17C). These tracheae probably evolved from the book lungs and muscle apodemes on this segment in more primitive spiders. Tracheal spiracles open inward to simple or branched tubes. In spiders, the open inner ends of the tracheae do not bring the oxygen supply into direct contact with tissues, as they do in many insects; rather, a small amount of blood is necessary as a diffusion medium. When the tracheal system is extensive, there is usually a reduction in the structural components of the circulatory system. There is a great diversity of tracheal structures and arrangements in some groups of spiders. In araneomorph spiders the posterior book lungs evolved convergently into similar tracheal systems multiple times independently after the origin of aerial webs and the evolution of novel silk glands. It has been hypothesized that the evolution of similar tracheal systems via convergence in the early-diverging web-building spiders was prompted by the novel energetic demands for web spinning.

The circulatory system of scorpions is very similar to that of spiders, except that it is constructed to accommodate an elongate and generally larger body. The tubular heart bears seven pairs of ostia and extends through most of the mesosoma (Figure 24.17D). An extensive set of arteries delivers blood to the hemocoel throughout the body and to four pairs of mesosomal book lungs, and a network of capillaries supplies the large prosomal ganglion.

Except where reduced or absent, the circulatory system of other euchelicerates is built along the same general plan as described previously. Gas exchange is cutaneous in palpigrades and some mites, but in other euchelicerate groups it occurs through book lungs (Uropygi, Schizomida, and Amblypygi) or tracheae (Ricinulei, Pseudoscorpiones, Solifugae, Opiliones, and many mites).

The blood of chelicerates has been most extensively studied in spiders and in xiphosurans. Because *Limulus* is large, its blood chemistry has been especially well studied, and many horseshoe crabs have made the supreme sacrifice for science at the hands of laboratory physiologists—so many, in fact, that many populations of the American species (*L. polyphemus*) have become threatened. Hemocyanin, the common respiratory pigment in chelicerates, is dissolved in the blood plasma. At least in spiders, hemocyanin serves primarily for oxygen storage rather than for immediate transport and delivery of oxygen to the tissues. Hemocyanin has a very high affinity for oxygen, releasing it only when surrounding oxygen levels are quite low. Some spiders are able to survive for days after their air supply has been cut off experimentally by covering the spiracles. Apparently they obtain sufficient oxygen from their hemocyanin-bound stores and some cutaneous exchange.

Chelicerate blood also contains various cellular inclusions, but the functions of most of them are not well understood. The blood of *Limulus* includes amebocytes that may provide clotting agents. Several kinds of blood cells occur in spiders. Interestingly, it seems that all of them originate as undifferentiated cells from the muscular portion of the heart wall itself. These cells are released into the blood, where they mature and differentiate. Functions that are attributed to chelicerate blood cells include clotting, storage, combating infections, and aiding in sclerotization of the cuticle.

Excretion and Osmoregulation

Xiphosurans have two sets of four coxal glands each, arranged along each side of the prosoma near the coxae of the walking legs. On each side of the body, the glands converge to a coelomic sac, from which a long, convoluted duct arises. The duct leads to a bladderlike enlargement that connects to an excretory pore at the base of the last walking leg. Surprisingly little is known about excretory physiology in xiphosurans. Apparently the coxal glands extract nitrogenous wastes from the surrounding hemocoelic sinuses and carry them to the outside. The coxal glands and their associated tubule system also function in osmoregulation, as evidenced by the production of a dilute urine when the animal is in a hypotonic medium. The digestive ceca probably aid in excretion of excess calcium by removing it from the blood and releasing it into the gut lumen.

The problems of excretion and water balance are obviously much more critical to terrestrial euchelicerates than to horseshoe crabs, and land-dwelling arachnids display a variety of structural, physiological, and behavioral adaptations to cope with them. The main excretory structures of arachnids are coxal glands and Malpighian tubules, although many groups possess additional supplementary nitrogenous waste removal mechanisms. Coxal glands persist in many arachnids (spiders, scorpions, palpigrades); in these animals, the glands lie within the prosoma and open on the coxae of some walking legs. The degree to which coxal glands function in excretion and osmoregulation varies among arachnids, but they are considered far less important than the Malpighian tubules.

The Malpighian tubules of arachnids arise from the posterior midgut. They are not homologous with the Malpighian tubules of insects or myriapods, which arise from the hindgut and are thus of ectodermal origin. The tubules branch within the hemocoel of the opisthosoma, where they actively accumulate nitrogenous waste products and release them into the gut for elimination along with the feces (Figure 24.17C). In spiders, the wastes from the tubules and the gut are mixed in the stercoral pocket prior to release from the anus. The excretory action of the Malpighian tubules is often supplemented by other mechanisms, such as the coxal glands. Nitrogenous wastes also are accumulated in the cells of the midgut wall and released into the lumen. In addition, waste products are picked up and stored by special cells called nephrocytes, which form distinct clumps in various parts of the prosoma.

Terrestrial arachnids produce complex, insoluble, nitrogen-containing excretory compounds. The major excretory product is guanine, although uric acid and other compounds also occur. Because these compounds are of low toxicity, they can be stored and excreted from the body in semisolid form, thus conserving water.

Terrestrial arachnids also display various behavioral adaptations to avoid desiccation. Most arachnids are nocturnal, remaining in cooler or more-humid protected places during the daytime. Some spiders actively drink water during dry periods or when they lose blood through injury. Desert scorpions must tolerate not only low humidity but also very high daytime temperatures. To avoid this, they typically bury themselves in sand or soil or hide under rocks or tree bark during the day. In addition, some species exhibit an adaptive behavior called stilting, wherein the body is raised off the substratum to allow air to circulate underneath. While thought to be mainly a cooling strategy, this behavior, by lowering the body temperature, probably also slows the rate of evaporative desiccation. Some scorpions are also able to withstand large losses of body water—as much as 40% of their body weight—with no ill effects.

Nervous System and Sense Organs

As in all arthropods, the external body form of euchelicerates is generally reflected in the structure of the

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central nervous system. These animals show various degrees of compaction and fusion of the body somites and the associated nervous system components while still conforming to the basic arthropod plan. The cerebral ganglia, or brain, includes the protocerebrum (which innervates the eyes), the deutocerebrum (which innervates the chelicerae), and the tritocerebrum (which innervates the pedipalps). The deutocerebrum was traditionally thought to be absent in euchelicerates, and therefore the chelicerae were thought to be innervated by the tritocerebrum, until Hox gene expression data showed homology of the chelicerae of euchelicerates with the deutocerebral appendages of mandibulates in the late 1990s. The tritocerebrum generally contributes to the circumenteric connectives, which unite ventrally with a large ganglionic mass formed in part by the fusion of paired anterior ganglia of the ventral nerve cord, and thus it looks like the pedipalps innervation is from the ventral ganglionic mass. In xiphosurans and scorpions this subenteric neuronal mass includes all of the prosomal ganglia, whereas in spiders even the opisthosomal ganglia fuse anteriorly. Thus in most spiders the adult nervous system is no longer obviously segmented (except in some members of the suborder Mesothelae), although a chain of ventral ganglia is evident during early embryonic development. The ventral nerve cord persists in the opisthosoma of xiphosurans and has five segmental ganglia; in scorpions it has seven ganglia (Figures 24.17A,D and 24.19).

The protocerebrum and deutocerebrum give rise to nerves to the eyes and chelicerae, respectively, and are dorsal. The ventral (subenteric) ganglionic mass, which includes the fused segmental prosomal ganglia and the tritocerebrum, gives rise to nerve tracts to the pedipalps and walking legs and, in spiders, bears a pair of abdominal ganglia from which arise branching nerves to the opisthosoma. Segmental ganglia on the ventral nerve cord in xiphosurans and scorpions serve the opisthosomal appendages, muscles, and sense organs.

Chapter 20 discussed some of the qualities of arthropod sense organs in terms of the imposition of the exoskeleton. Xiphosuran sense organs include tactile mechanoreceptors in the form of various spines and bristles, proprioceptors in the joints, chemoreceptors, and photoreceptors. The prosoma bears two simple eyes near the dorsal midline and two lateral compound eyes (Figure 24.2A), in addition to a series of hidden eyes. The median eyes are of the pigment-cup type, but each contains a distinct cuticular lens. The lateral eyes are compound rhabdomeric units—structures not found in any other chelicerate. The thousand or so ommatidia per eye are very large and rather loosely packed together. While the resolving power of xiphosuran eyes has long been debated, certainly *Limulus* can detect movement and changes in light intensity and direction. It has been demonstrated that the light sensitivity of these receptors is regulated on a 24-hour cycle by instructions from the brain. At night, these signals increase the eyes' sensitivity to light by up to a million times over daytime levels. Thus, *Limulus* may see as well at night as it does during daylight hours. It may also be capable of perceiving clear images, as male horseshoe crabs have been experimentally shown to be attracted to "models" of females.

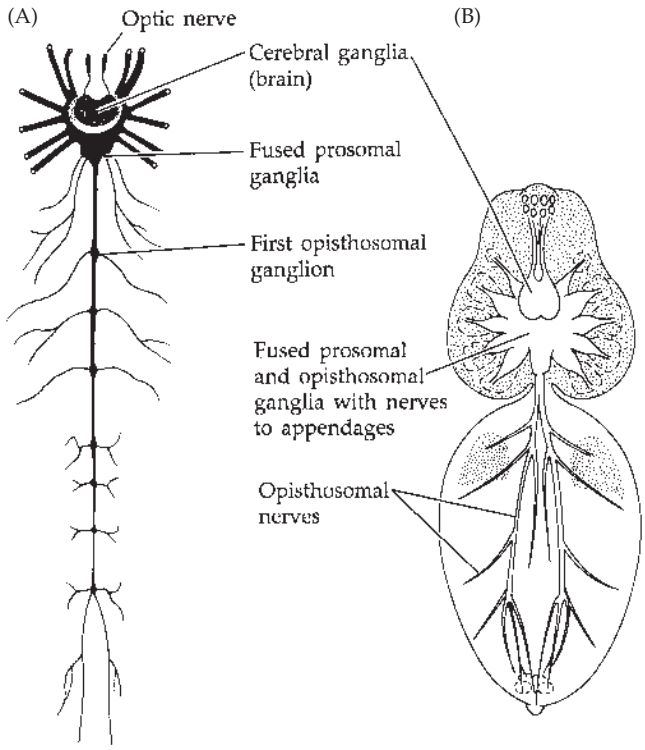

FIGURE 24.19 The central nervous system. (A) Scorpion. (B) Spider. (B after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

Arachnids possess well-developed sense organs upon which much of their complex behavior depends. The typical "hair" on a spider or scorpion body is a mechanoreceptor called a **hair sensillum**, which occurs in several types. Simple tactile hairs (or setae) cover much of the body surface and respond to direct physical contact. Setae of the second type, called trichobothria, are found on the appendages of many arachnids. They are less abundant and much thinner than simple tactile setae and are extremely sensitive (Figure 24.20B). *Cupiennius*, a tropical wandering spider (Trechaleidae) that has been extensively studied as a model organism, has close to one thousand trichobothria in its legs and pedipalps. Trichobothria are stimulated by airborne vibrations, such as those caused by beating insect wings, natural air currents, and probably some sound frequencies.

Additional mechanoreceptors of arachnids include slit sense organs (Figure 24.20A,C). These structures may occur singly, as a **slit sensillum**, or in groups of parallel slits called **lyriform organs**. A slit sensillum is a deep groove in the cuticle associated with sensory neurons. It detects a variety of mechanical stimuli that impose physical deformation on the cuticle around the slit. Depending on its location and orientation, a spider

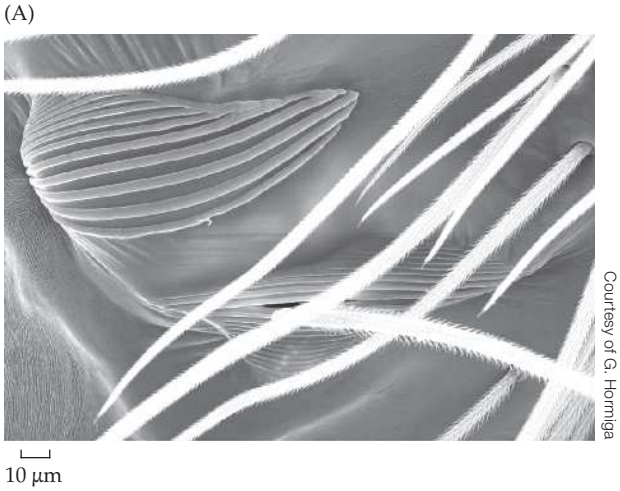

FIGURE 24.20 Mechanoreceptors and chemoreceptors in spiders. (A) Lyriform organs (groups of slit sensilla) on the leg patella of *Amaurobius similis* (SEM, 1.76K×). (B) The organization of a trichobothrium in its socket; from *Tegenaria*. (C) A slit sense organ from the leg of *Cupiennius* (cutaway view). (D) A chemosensitive hair. The mechanoreceptor neurons terminate at the base of the hair (arrow in illustration), whereas the chemoreceptor neurons extend through the hollow shaft to the tip (photo). (E) A humidity receptor, or tarsal organ, of the orb-weaver *Araneus*. (B,C after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford.)

slit sensillum serves as a proprioceptor (by sensing leg movements and position), as a georeceptor (by measuring bending of the pedicel under the weight of the opisthosoma), as a direct mechanoreceptor (by sensing direct external pressure on the cuticle), as a vibration sensor, and even as a phonoreceptor.

Not all of the setae of spiders are sensory in function. We have already described the calamistrum, a row of modified macrosetae in the fourth metatarsus of cribellate spiders that is used to comb the silk produced by the cribellum. Another interesting type of specialized setae is found in the New World tarantulas (Theraphosidae). These mygalomorphs have modified abdominal barbed setae that can be released by their hind legs. These setae become airborne and are highly urticating, providing a defensive mechanism against some predators. Efficient proprioceptors occur in the walking legs and pedipalps

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of all chelicerates and are particularly well developed in arachnids. By virtue of their position and number in different joints, they convey information about the direction and velocity of appendage motion as well as the position of the limbs relative to the body and to one another. These "true" proprioceptors appear to work in concert with the lyriform organs.

Chemoreception in arachnids involves sensing both liquid and airborne chemicals that contact the body. This dual ability can be likened to capacities for both taste (contact chemosensitivity) and smell, or olfaction (distance chemosensitivity). The olfactory sense plays major roles in prey location and, for those species in which females release sex pheromones, in mating. The most important chemoreceptors are probably the hundreds of erect, hollow setae (called **sensilla chaetica**) with open tips that are present on the pedipalps and other areas around the mouth and are most abundant on the tips of limbs that contact the substratum. Dendrites of sensory neurons extend through the hollow hair shaft to the open tip, where they are directly stimulated by chemicals (Figure 24.20D). Spiders also bear humidity detectors called tarsal organs (Figure 24.20E).

Scorpions have a pair of large, unique, comblike structures, the pectines, on the ventral surface of the mesosoma (Figure 24.6C). After detailed studies of their innervation, Foelix and Schabronath (1983) suggested that the pectines act as both mechanoreceptors and chemoreceptors. Other work has shown them to be capable of detecting subtle differences in sand grain size. These versatile structures are usually held laterally erect, free to swing back and forth while the scorpion is actively moving about. Solifuges have other mysterious sensory structures called malleoli (or racquet organs) on the coxae and trochanters of the fourth pair of legs.

The importance of vision varies greatly among the arachnids. Most species possess some sort of photoreceptors, although Ricinulei and Palpigradi are entirely blind. At least some species in the other groups are also blind (e.g., some members of the orders Schizomida, Pseudoscorpiones, and different mite orders), and within the Opiliones suborder Cyphophthalmi, four of the six families are entirely blind. Certain spiders depend on photoreception for prey and mate location, particularly the errant hunters (e.g., some lycosids and most salticids) (Figure 24.21B,C). Vision is relatively unimportant to many sedentary species, such as many web builders that depend more on tactile cues, vibrations, and chemosensitivity. Web builders are not blind, however, and many respond behaviorally to variations in light intensity, while some exhibit distinct escape responses when they visually detect potential predators. Nevertheless, these spiders are generally able to build their webs, capture prey, and mate with little or no visual input. Some spiders are capable of perceiving polarized light, presumably as a means of spatial orientation.

Spiders possess single-lensed rhabdomeric eyes, but the sensory units of each are simple ocelli in a cluster. Thus they are quite different from the compound eyes of xiphosurans and most other arthropods. Each eye includes a thickened cuticular lens over a vitreous body, which is a layer of cells derived from the epidermis and covering the retina (Figure 24.21D). The retina is composed of the sensory (receptor) cells and the pigment cells. The membranes of the sensory cells bear interdigitating microvilli, confirming the rhabdomeric nature of the eyes.

Two forms of this basic eye structure occur among spiders. The anterior median eyes—the main eyes—have the light-sensitive portions of the sensory cells directed toward the lens, whereas other eyes—secondary eyes—are inverted, with the light receptor elements directed away from the lens (Figure 24.21D,E). Most of these secondary eyes contain a crystalline reflective layer called the tapetum, which may serve to collect and concentrate light in poorly lit conditions (e.g., during night hunting). The reflective nature of the tapetum produces the effect in some spiders of eyes that "shine in the dark" (Figure 24.21F).

Scorpion eyes are of the direct type and differ from spider eyes in having the retinal layer external to the epidermis. Most work suggests that scorpions depend much more on mechanoreception and chemoreception than on visual input.

There is no question that spiders, and perhaps other arachnids, are capable of modifying their behavior based on experience—that is, they can learn. Some examples of such activity were noted earlier. Memory and association centers in the protocerebrum are responsible for much of this integrative activity. No doubt, at least in spiders, the ability to remember, learn, and make appropriate adaptations in behavior has played an important role in their evolutionary success. A recent collection of papers on spider behavior can be found in Herberstein (2011).

Reproduction and Development

Eucheliceratesare gonochoristic and generally engage in complex mating behaviors that ensure fertilization. A few are known to be parthenogenetic (e.g., some scorpions, harvestmen, and schizomids). A penis (sometimes a spermatopositor organ) occurs only in the males of harvestmen and some mites. Free spawning never occurs, and fertilization takes place either internally or as the eggs leave the body of the female. The eggs are generally very yolky except in xiphosurans; the developmental strategy is direct in spite of the various juvenile stages through which most eucheliceratespass. We first present a summary of reproduction and development in *Limulus*, then turn to the arachnids, concentrating again on spiders (the best known arachnid developmental model) and scorpions. More recently,

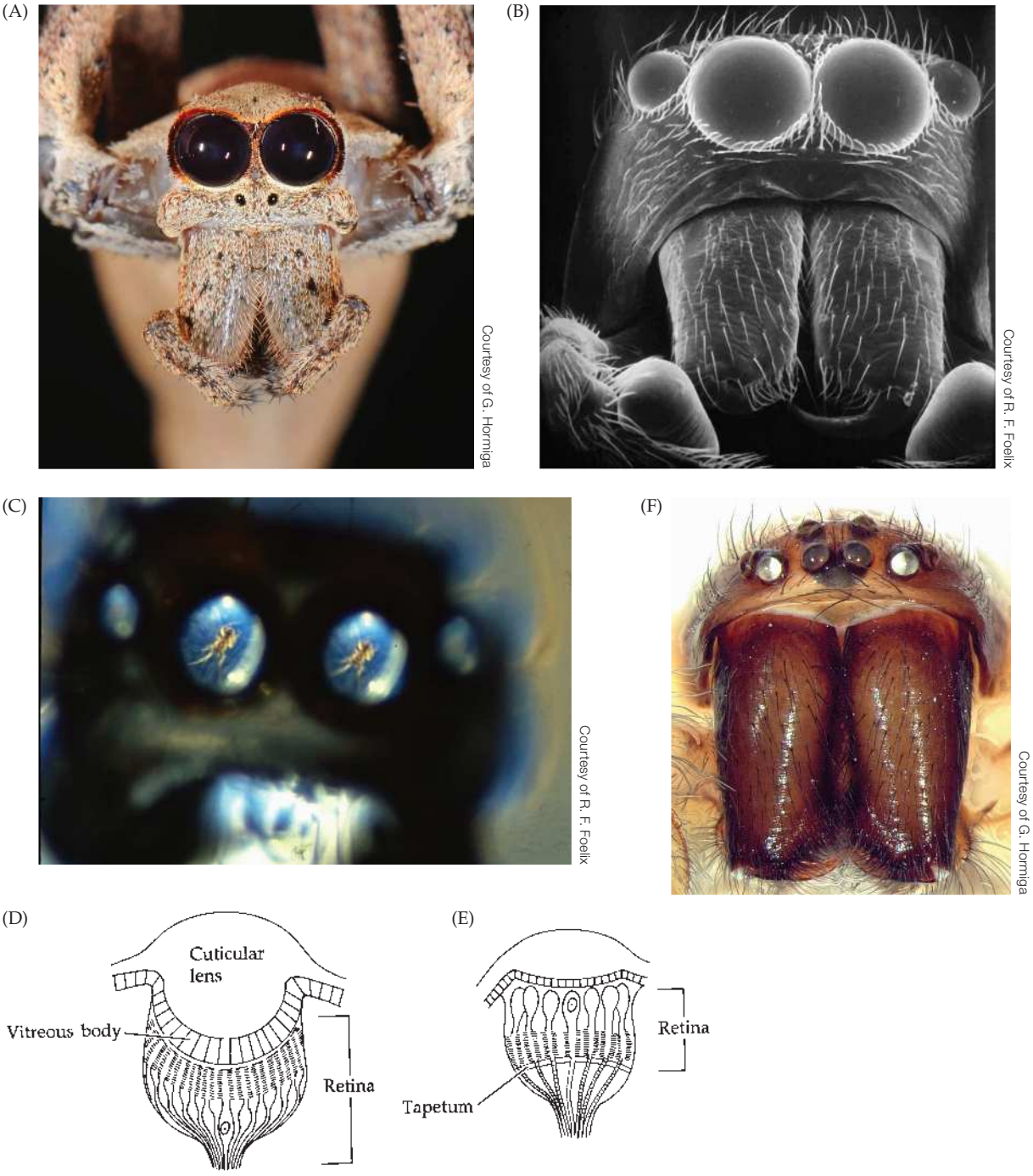

FIGURE 24.21 Spider eyes. (A) Eye pattern of an ogre-faced spider, *Deinopis* from Australia, a nocturnal predator with enormous posterior median eyes extremely sensitive to light. (B) "Looking into the eyes" of *Heliophanus* (Salticidae), with enormous anterior median eyes. (C) Image of another spider as "seen through the eyes" of *Portia*, a jumping spider. (D) Section through a main eye. (E) Section through a secondary eye, showing inverted arrangement of the retinular cells and tapetum. (F) Head-on view of *Amaurobius similis* (Amaurobiidae). Note the highly reflective tapetum in the anterior lateral eyes (secondary eyes). The median eyes are the main eyes and lack a tapetum. (D,E after R. Foelix. 2011. *Biology of Spiders.* Oxford University Press, Oxford.)

development in Opiliones has received more attention, from both behavioral and genetic points of view.

The reproductive system of male and female xiphosurans is similar. In both sexes the gonad is a single, irregularly branched mass of tissue (Figure 24.22A). Paired gonoducts lead from the gonad to a pair of pores on the ventral midline. The first pair of opisthosomal appendages lies over the gonopores, forming a genital operculum.

At the onset of the breeding season, horseshoe crabs migrate into the shallow waters of protected bays and estuaries. On the east coast of North America, this

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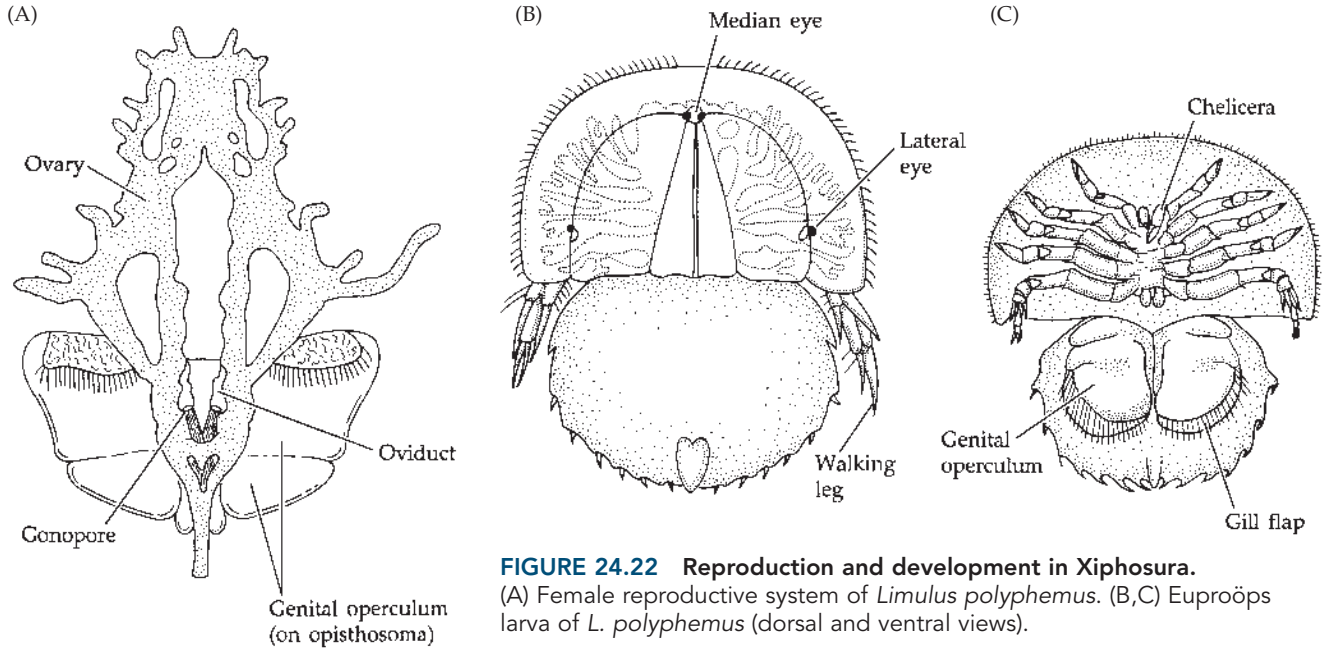

FIGURE 24.22 Reproduction and development in Xiphosura. (A) Female reproductive system of *Limulus polyphemus*. (B,C) Euproöps larva of *L. polyphemus* (dorsal and ventral views).

migration takes place in the spring and summer, and huge numbers of *Limulus* can be seen gathering near the shore in preparation for mating (Figure 24.2C). Mating is initiated when the male climbs onto the back of the female and grasps her with his modified first pair of walking legs, which are the pedipalps. The clasped pair moves to the shallow water, usually at a high spring tide, and the female excavates one or more shallow depressions in the sand and deposits her eggs (2,000 to 30,000 eggs per mating). The male releases sperm directly onto the eggs as they are deposited. Then the mates separate, and the female covers the fertilized eggs with sand. As the waters recede, it is common to find these mating pairs outside of the water or covered with wet sand.

Early development takes place in the sand or mud "nest." Cleavage is holoblastic, producing a stereoblastula with most of the yolk contained in the inner cells. As development continues, the surface cells at the anterior and posterior ends of the embryo divide rapidly, forming two germinal centers. Some of these rapidly proliferating cells migrate inward as the presumptive endoderm and mesoderm. The anterior germinal center gives rise to the first four segments of the prosoma, and the posterior center to the rest of the body. All of the prosomal segments fuse and are eventually covered by the developing carapace-like dorsal shield.

As the yolk reserves become depleted, the embryo emerges from the sediment as a **euproöps larva** (or "trilobite larva"), so named because of its resemblance to the fossil Carboniferous xiphosuran *Euproöps* (which superficially resembled trilobites; Figure 24.22B,C). The larvae swim about and periodically burrow in the sand. Segments are formed and appendages added through a series of molts until the adult form is reached, a typical mode of development observed in other arthropod groups. The early developmental stages are supplied with an investment of yolk by the female and are protected by the nest she constructs, but the young emerge as independent feeding larvae prior to maturation.

The reproductive biology of arachnids is directly related to their success on land. They have evolved a variety of sophisticated mating behaviors, clever methods of sperm transfer, and various devices for protecting developing embryos, thereby ensuring successful procreation in terrestrial habitats. A comparison of the functional anatomy of the reproductive systems of spiders and scorpions provides a background for discussing arachnid courtship behavior and developmental patterns. But many other interesting behaviors are known from groups like amblypygids, uropygids, ricinuleids, and harvestmen, among others.

The male reproductive system of spiders consists of a pair of straight or convoluted tubular testes in the opisthosoma, which lead to a common sperm duct that opens into the epigastric furrow through a gonopore (Figure 24.23A). Each developing sperm usually bears a distinct flagellum with an unusual 9+3 axonemal pattern of microtubules (Figure 24.23B) (members of the sister families Pimoidae and Linyphiidae share a unique 9+0 pattern). The spermatozoa of spiders exhibit remarkably high structural diversity. Prior to copulation, the flagellum wraps around the head of the sperm, and a protein capsule forms around the gamete (Figure 24.23C). The sperm remains in this nonmotile state until after mating.

Although male spiders lack a penis (like almost all other arachnids), the pedipalps of the adults are modified for sperm storage and transfer and serve as copulatory organs. Sperm released from the male gonopore are placed on a specially constructed silken sperm web

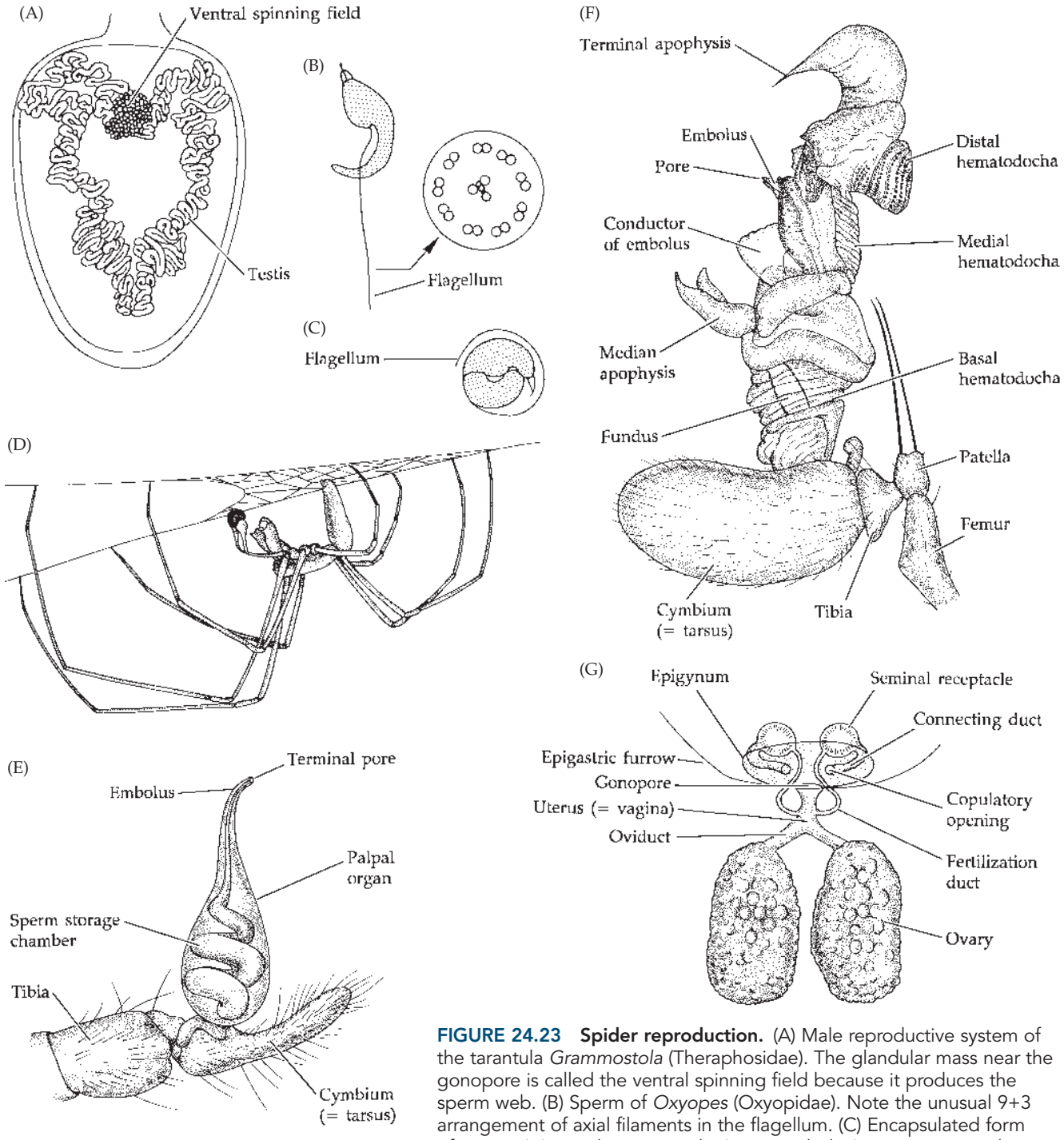

FIGURE 24.23 Spider reproduction. (A) Male reproductive system of the tarantula *Grammostola* (Theraphosidae). The glandular mass near the gonopore is called the ventral spinning field because it produces the sperm web. (B) Sperm of *Oxyopes* (Oxyopidae). Note the unusual 9+3 arrangement of axial filaments in the flagellum. (C) Encapsulated form of sperm. (D) A male *Tetragnatha* (Tetragnathidae) on its sperm web, drawing sperm into its palpal organs. (E) Simple male pedipalp copulatory structure (palpal organ) (*Segestria*, Segestriidae). (F) Complex palpal organ (*Araneus*, Araneidae). (G) Female spider reproductive system. (A after M. Melchers. 1964. *Z Morph Ökol Tiere* 53: 517–536. https://link.springer.com/article/10.1007/BF00408073; C–E after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford; F after J. H. Comstock. 1910. *Ann Entomol Soc Am* 3: 161–185.)

(Figure 24.23D). From here the sperm are picked up by the pedipalps, where they are held in special pouches or chambers, and eventually transferred to the female. The pedipalps of adult male spiders vary greatly in form and complexity, generally being simple in certain mygalomorphs and more complex in most araneomorphs. In the simplest form, each pedipalp bears on its modified tarsus (called the **cymbium**) a teardrop-shaped process known as the palpal organ (Figure 24.23E). A pointed tip, or **embolus**, bears a pore that leads inward to a blind coiled sperm duct (the spermophor). Sperm are drawn into this tube from the sperm web and held until transferred to the female. Until very recently no nerves or sensory organs had been found in the palpal bulb, suggesting that spider male copulatory organs are numb and blind to sensorial stimuli. The presence of neurons and a nerve inside the male palpal organ was documented for the first time in the Tasmanian cave spider *Hickmania troglodytes* (Gradungulidae) in 2015. Subsequent studies across many spider lineages have

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demonstrated that the innervation of the male copulatory organ is part of the ground pattern of spiders.

The more complex male copulatory organs are formed of structures with varying degrees of sclerotization (sclerites) and a diversity of soft parts, such as sacs that can expand through increased hemolymph pressure (hematodochae) and various types of membranes. Often some of these cymbial sclerites, as well as the cymbium itself, and other pedipalpal articles bear processes called apophyses of wildly diverse morphology (Figure 24.23F), such as the "retrolateral tibial apophysis," which characterizes a large lineage of araneomorph families (the "RTA Clade") that includes, among others, the salticids and the wolf spiders. Although often difficult, assessing the homology of the highly variable structures across species is an important part of morphological phylogenetic inference, particularly in araneomorphs. Because genitalia vary across species, and because in closely related species somatic morphological features often vary little, genitalia, both male and female, are extensively used in spider taxonomy. Although male genitalia need to fit with the mating organs of conspecific females, the key-and-lock hypothesis to explain the evolution and huge interspecific diversity of genitalic structures of spiders has been empirically rejected. This variation is probably part of a series of mechanisms to prevent interspecific mating, although nonproductive interspecific encounters are prevented primarily by species-specific courtship behaviors (discussed below). Following the uptake of sperm through the embolus and insertion of the palpal organ into the female's receiving structure (the epigynum), the soft hematodochae are inflated with hemocoelic fluid, thereby causing an erection of the sclerites within the female parts. Once the partners are thus coupled, sperm are injected into the female's copulatory openings and ducts. In some species, sperm transfer is preceded by copulation before the palps are charged with sperm ("pseudocopulations"). A somehow analogous mechanism of sperm transfer with a diversity of sclerites and hemocoelic fluid pressure occurs in Ricinulei, where adult males have the third pair of legs modified for sperm transfer.

Female spiders have a pair of ovaries in the opisthosoma. The lumen of each ovary leads to an oviduct, and the two oviducts unite to form a uterus (also called the vagina), which opens to the outside in the epigastric furrow (Figure 24.23G). Eggs are produced mainly on the exterior of the ovaries, giving the ovaries a bubbled texture; how the eggs move to the internal ovarian lumen is not well understood.

Just inside, or lateral to, the female gonopore, there is usually a pair of copulatory openings that lead through coiled connecting ducts to paired seminal receptacles (or spermathecae). In entelegyne spiders a second pair of tubes, called the fertilization ducts, connects the seminal receptacles to the uterus (Figure 24.23G). Many spiders have a complexly structured sclerotized plate just in front of the epigastric furrow. This plate, called the epigynum, extends over the genital pore and bears the copulatory openings to the seminal receptacles through copulatory ducts or folds. The morphology of the epigynum, the position and length of the copulatory openings and connecting ducts, and other external features provide a particular topography that matches the palpal organs of conspecific males. As with male pedipalps, the morphology of the female genitalia is used by taxonomists to discriminate species. These differences in external anatomy, as well as in body size and overall courtship behavior, result in a variety of species-specific copulatory positions among spiders. Once sperm are inside the seminal receptacles, they are stored there until the female deposits her eggs, which may be months after copulation. At that time, the sperm pass through the fertilization ducts to fertilize the ova during egg laying.

The reproductive system of scorpions lies within the mesosoma, and both testes in males and ovaries in females are in the form of interconnected tubules (Figure 24.24). The gonads are drained by lateral sperm ducts or oviducts. The sperm ducts bear various storage chambers (seminal vesicles) and accessory glands and unite

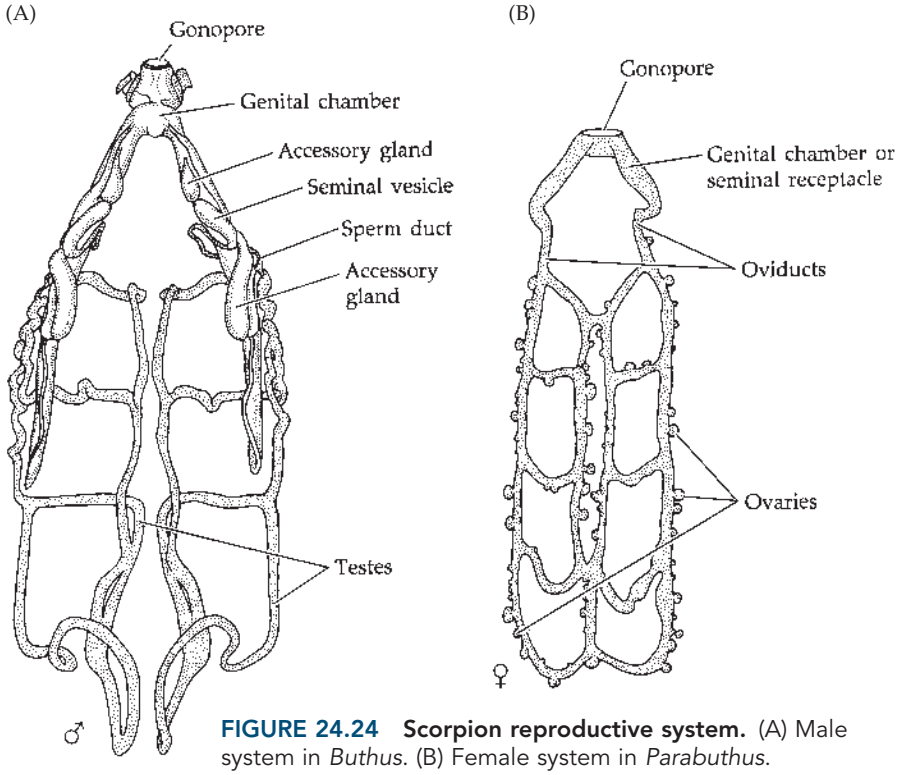

FIGURE 24.24 Scorpion reproductive system. (A) Male system in *Buthus*. (B) Female system in *Parabuthus*.

as a genital chamber just inside the gonopore on the first segment of the mesosoma. Some accessory glands are responsible for the production of spermatophores. Each oviduct is enlarged as a genital chamber, or seminal receptacle, near its union with the gonopore.

With few exceptions, sperm transfer in arachnids is indirect, as described above for the spiders. That is, the sperm leave the body of the male and are then somehow manipulated into the body of the female or deposited on the eggs outside the female's body. The only exceptions to this rule occur in most harvestmen (all members of the Phalangida) and some mites, in which the male possesses a penis through which sperm pass directly to the reproductive tract of the female. In all other arachnids, including mite harvestmen in the suborder Cyphophthalmi and many mites, either the sperm are inserted into the female's body by modified appendages of the male, or they are placed on the ground in spermatophores and then retrieved by the female. Modified appendages are used to transfer sperm in the orders Araneae (pedipalps), Uropygi (pedipalps), Ricinulei (third walking legs), some members of Solifugae (chelicerae), and some mites (chelicerae or third legs). In other arachnids (orders Scorpiones, Schizomida, Amblypygi, Pseudoscorpiones, and many Solifugae and mites), the males deposit spermatophores on the ground and the females simply pick them up, but in Cyphophthalmi (Opiliones) it seems that the male may deposit a spermatophore with a spermatopositor organ near the female gonostome. We hasten to point out, however, that the reproductive biology of many species in these taxa, and of some entire groups (e.g., Palpigradi), has been little studied.

The events leading up to insemination often include species-specific courtship behaviors that serve as cues for species recognition. These behaviors must, of course, be compatible with the particular method of sperm transfer (Figures 24.25 and 24.26). Again, we can look to spiders and scorpions for examples. Among spiders, courtship behaviors not only ensure conspecific copulation, but also prevent the usually smaller males from being mistaken for prey by the females, as well as having an arousal function. Platnick (1971) classified spider courtship behaviors into three general levels. First-level courtship involves necessary contact between male and female. Among many thomisids and clubionids, mating involves the male simply climbing over the female, positioning her abdomen, and inserting a palpal organ. The males of some thomisids (e.g., *Xysticus*) and at least some species of the golden orb-weaver *Nephila* (Araneidae) place silk threads over the bodies or legs of the female preparatory to copulation. These threads are apparently only part of the recognition ritual, because they are not strong enough to actually restrain the female (Figure 24.25C). A few other spiders, including certain tarantulas (Theraphosidae), also use body contact and leg touching as courtship behavior.

Second-level courtship behaviors involve the release of sex pheromones by the female spider. Some of the most complex behavior patterns occur in male spiders that detect females by olfaction, although other recognition devices may also be involved. Some male araneids are apparently led to the female's orb web by her pheromones, and the web is then recognized by contact chemoreception. Once in touch with the edge of the web, the male announces his presence to the female by plucking the threads of the orb itself or by attaching a special mating thread to her orb, which he then plucks (Figure 24.25E). If properly orchestrated, the male's "tune" eventually attracts the female, and contact is made.

Males of some species of wolf spiders (Lycosidae) respond to pheromones emitted along with the female's dragline. When he detects a female visually, the male begins a specific set of actions in an effort to win her favor. These male behaviors involve abdomen bobbing and pedipalp waving, coupled with drumming of the pedipalps on the substratum and stridulation (Figure 24.25F). If attracted by these cues, the female responds by slowly approaching the male and sending out signals of her own in the form of particular leg movements. Stridulation, using modified pedipalps, also occurs in some uloborids and many other families (Figure 24.25G).

Among the most interesting second-level courtship behaviors are those of certain nursery-web spiders (*Pisaura*; Pisauridae). After locating a female emitting pheromones, the male captures an insect (usually a fly), spins a silk wrapping around it, and offers it to the female. Acceptance of the nuptial gift and of the male are one and the same, for the successful male copulates with the female while she devours the insect. Alas, unsuccessful males are eaten along with the offering. Postcopulatory cannibalism by females is not uncommon in certain groups of spiders. Contrary to popular belief, the males of the North American black widow (*Latrodectus mactans*) are often unharmed after copulation. In other widow species, such as *L. geometricus* and *L. hasselti*, males are cannibalized by the females.

Another interesting second-level courtship behavior occurs in the Sierra dome spider (*Neriene litigiosa*) of western North America. Upon encountering a mature virgin female, a male attacks her pheromone-laden web and packs it into a small, tight mass. This behavior hinders the evaporation and dispersal of the male-attracting pheromone, thereby reducing the likelihood of additional males locating the female and competing for her favors.

Third-level courtship behaviors depend primarily on visual recognition of prospective mates and are best known in jumping spiders (Salticidae), which often exhibit conspicuous sexual dimorphism and striking coloration. A male locates a female and then begins a series of behaviors that identify him as a conspecific individual. Usually the male approaches the

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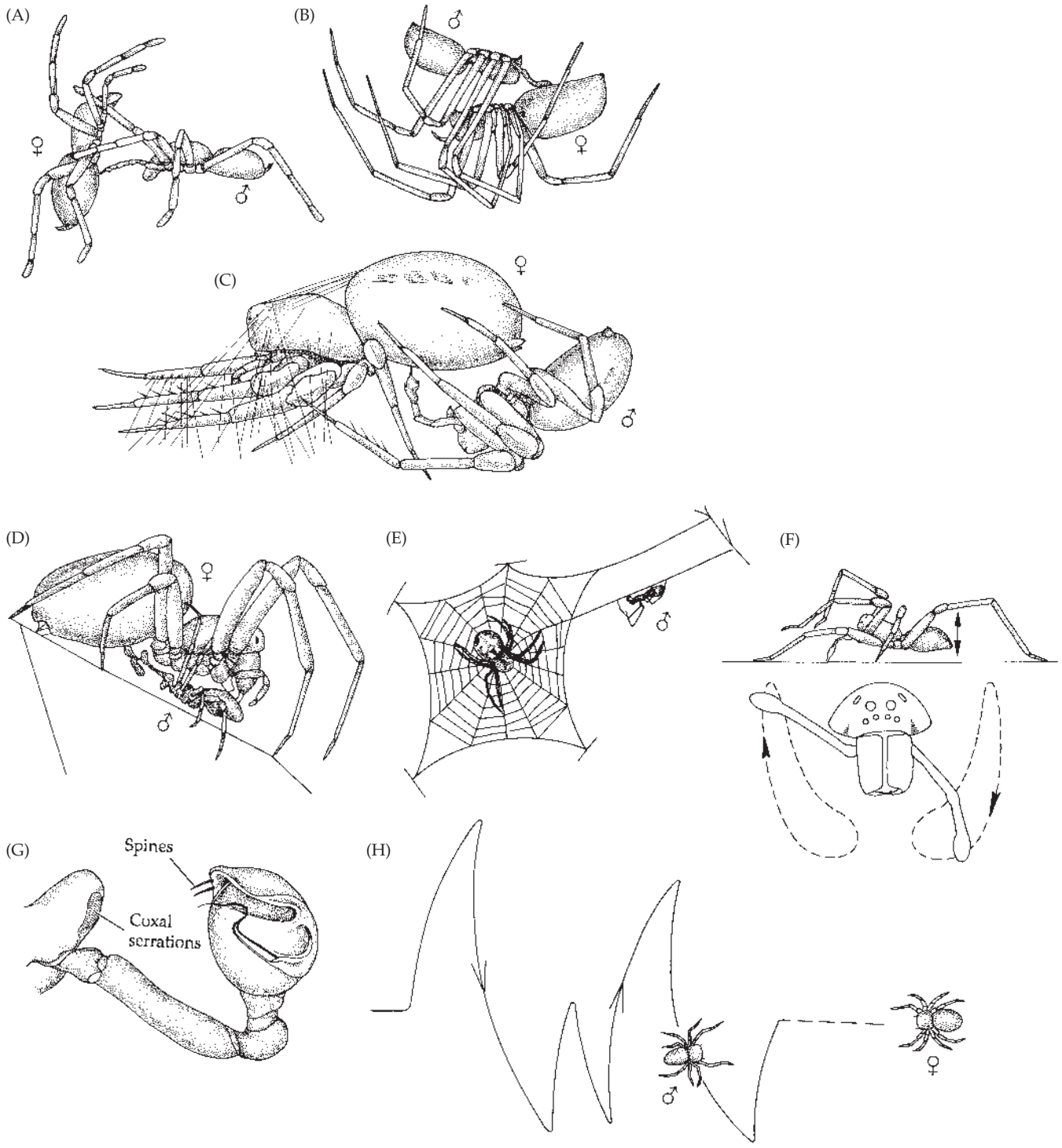

FIGURE 24.25 Courtship and mating in spiders. (A) Mating position in tarantulas. (B) Mating position in linyphiids. (C) Mating position in *Xysticus* (Thomisidae). Mating occurs after the male has placed a series of threads over the female's body. (D) Mating position in *Araneus diadematus* (Araneidae). (E) Use of a mating thread by some orb-weavers. In this general example, the male has spun a mating thread from an object to the female's web. When properly plucked, the thread transmits vibrations to the web, and the female responds by approaching the male and assuming a mating posture. (F) The courtship behavior of a male lycosid (*Lycosa rabida*) includes movements of the anterior legs, abdomen bobbing, and pedipalp movements. (G) The pedipalp of *Tangaroa tahitiensis* (Uloboridae) bears organs of stridulation. The spines are scraped against the filelike serrations on the coxa. (H) The zigzag approach and courtship display of a male jumping spider (Salticidae). (A–D,F after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford; E after B. Robinson and M. H. Robinson. 1978. In P. Merrett [Ed.], *Arachnology. Symposia of the Zoological Society of London, Number 42*, pp. 17–29. Academic Press, London.)

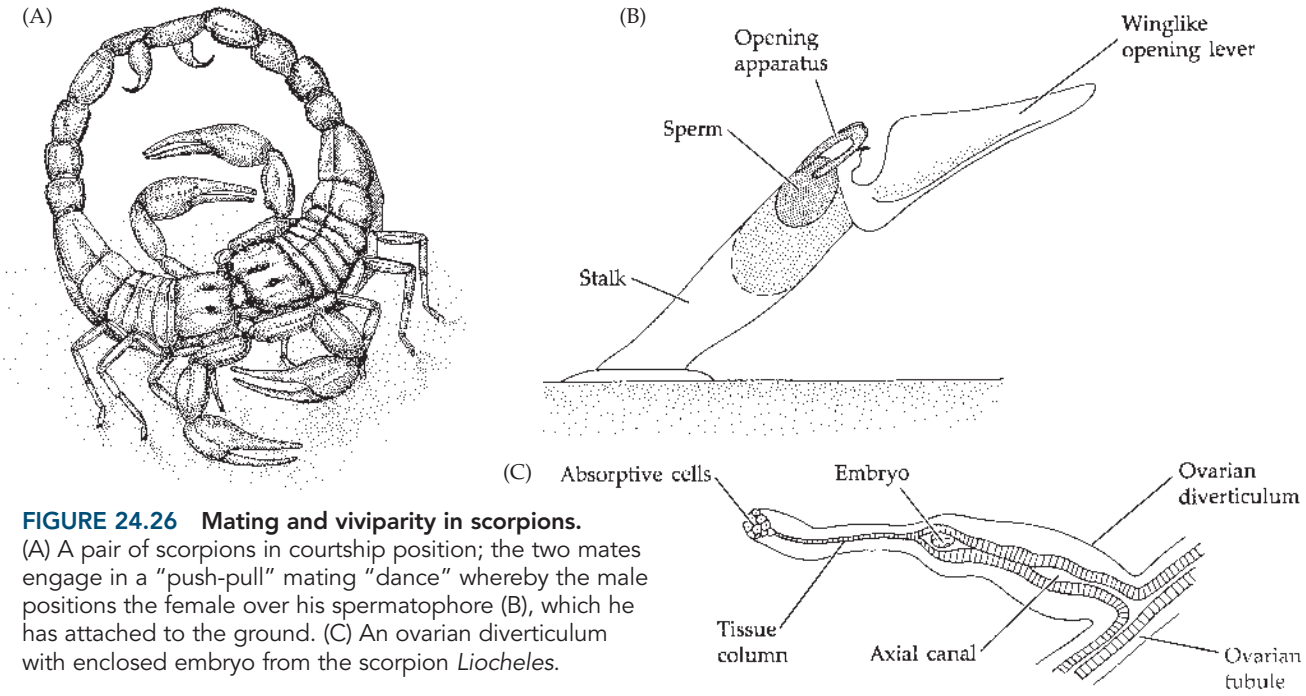

FIGURE 24.26 Mating and viviparity in scorpions. (A) A pair of scorpions in courtship position; the two mates engage in a "push-pull" mating "dance" whereby the male positions the female over his spermatophore (B), which he has attached to the ground. (C) An ovarian diverticulum with enclosed embryo from the scorpion *Liocheles*.

female along a zigzag path and then performs specific movements of the opisthosoma, pedipalps, and front walking legs (Figure 24.25H). The female signals her approval and receptiveness by sitting still in a visually recognizable position. The male eventually contacts her, caresses her briefly, mounts her, and copulates.

Sex-related behaviors among spiders are not restricted to male-female encounters. Conspecific males frequently exhibit agonistic behavior in competition for a mate. When males encounter one another in the presence of a female, or even in a mating "territory" (such as on the web of a female), they may assume various threatening postures and in some cases actually engage in combat. Usually, however, one of the males retreats before any real damage is done, leaving the dominant male free to pursue his sexual interests.

The courtship behavior of scorpions does not involve copulation in any form, but instead involves deposition of spermatophores onto the ground. Courtship behaviors appear to be relatively similar among those species that have been studied, although subtle species-specific differences allowing species recognition undoubtedly occur. In a typical case, the male initiates the ritual by grasping the female's pedipalps in his and, in this face-to-face position, dances her around in a series of back-and-forth steps (Figure 24.26A). Eventually the male releases a spermatophore and cements it to the ground. He then continues to move the female around until she is precisely positioned with her genital operculum over the packet of sperm. The spermatophore is a complex, species-specific structure, and it bears a special process called an opening lever (Figure 24.26B). The pressure of the female's body on this lever causes the spermatophore to burst, releasing the sperm, which can then enter her gonopore.

Arachnids undergo a variety of developmental patterns, all of which may be considered direct in terms of their life history strategies. Most species produce very yolky eggs, providing the embryos with nourishment through much of their development. By the time of hatching, many resemble miniature adults or still contain enough yolk to carry them through subsequent development to the juvenile stage. In some acarines and all ricinuleids, the young hatch as six-legged "hexapod larvae" (Figure 24.27L). These immature individuals add the last pair of legs later through molting. In most arachnids the developing embryos are protected by some sort of egg case or cocoon, or they are brooded in or on the body of the female.

Nearly all spiders cement their eggs together in clusters and wrap them in silken egg sacs, the sizes and shapes of which vary among species (Figure 24.27). The egg sac provides physical protection for the embryos and also insulates them from fluctuations in environmental conditions, particularly changes in humidity. Additional

FIGURE 24.27 Egg cases, hatching, and parental care. ▶ (A) The ogre-faced spider *Deinopis* (Deinopidae) building an egg sac in Costa Rica. (B) The egg sac (section) of *Agroeca brunnea* (Liocranidae); the female constructs the egg sac and coats it with bits of soil. Note the eggs above the molting chamber. (C) The subterranean, silk-lined nest of the jumping spider *Heliophanus cupreus* (Salticidae). (D) Female *Theridion* tending a spiderling and feeding it with regurgitated food. (E) A female wolf spider, *Lycosa* (Lycosidae), carrying young on her back. (F) Female of *Chibchea mapuche* (Pholcidae) from Chile carrying her egg case. (G) Surface of the egg sac of the pirate spider *Ero furcata* (Mimetidae). (H) A spider hatchling emerging from its egg case. (I–K) Prelarval, larval, and nymphal forms of a spider.

(*Continued*)

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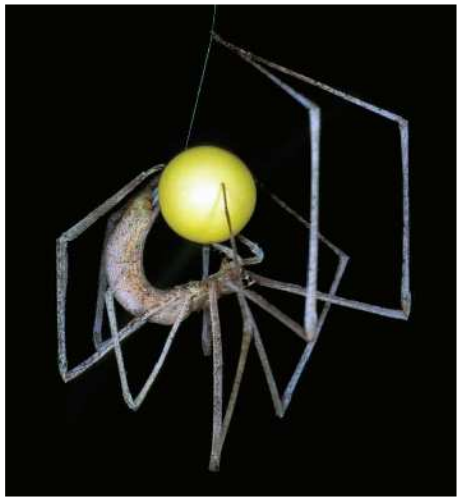

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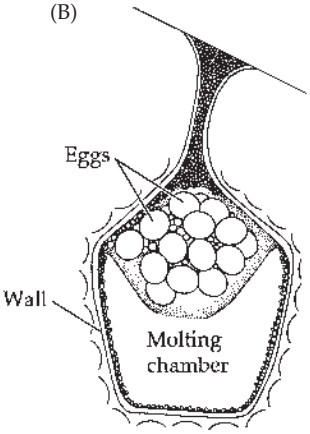

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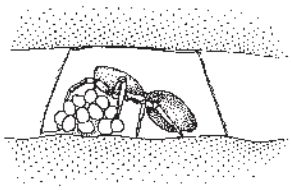

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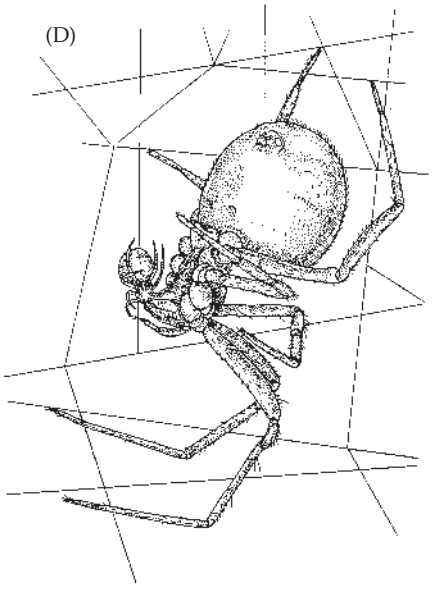

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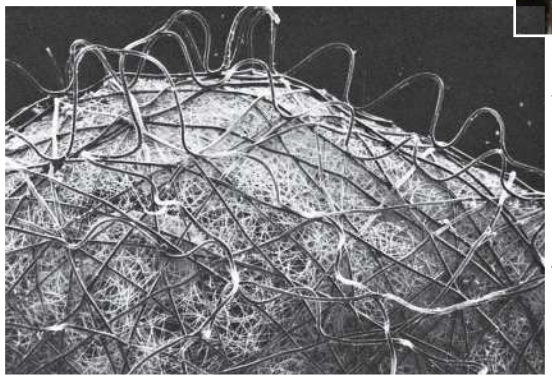

G,H from R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford

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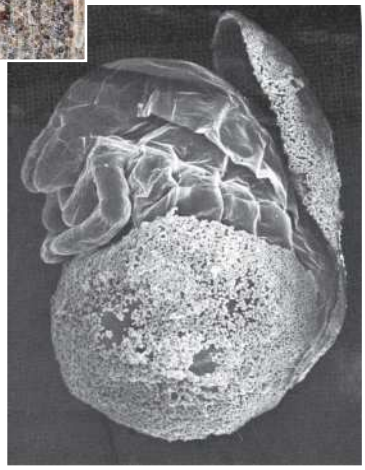

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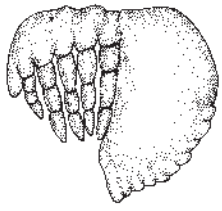

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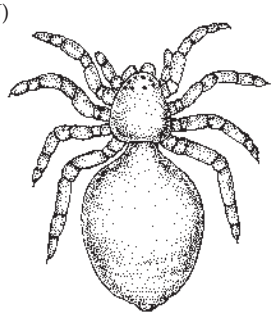

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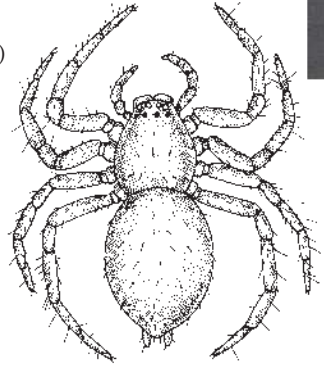

(L)

(M)

L,M courtesy of G. Giribet

FIGURE 24.27 (*continued*) Egg cases, hatching, and parental care. (L) Hexapod larva of an undescribed species of *Cryptocellus* from Panama. (M) A female armored harvestman, *Phareicranaus manauara*, tending her eggs. (B,C,I,J,K after R. Foelix. 2011. *Biology of Spiders*. Oxford University Press, Oxford; D from P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

protection results from placing the egg sac underground, in a nest, or in other secluded spots. Some species camouflage their cocoons with bits of detritus; others guard their cocoons or actually carry them on their bodies.

The early development of spiders includes intralecithal nuclear divisions followed by migration of the nuclei to the periphery of the embryo. The nuclei are then isolated by cytoplasmic partitioning, a process that produces a periblastula around an inner yolky mass. Gastrulation follows by formation of a germinal center of presumptive endodermal and mesodermal cells that migrate inward. Additional germinal centers produce the precursors of segments and limbs. The immature individuals of different spider species hatch from their egg membranes at different stages, but they always remain inside the cocoon and utilize their yolk reserves until they are able to feed. Most workers recognize three postembryonic, preadult stages in spider development (Figure 24.27I–K). The majority of spiders hatch from their egg membranes as immobile "prelarvae," characterized by incomplete segmentation and poorly developed appendages. The "prelarva" matures into a "larva" and then into a "nymph," or juvenile, which physically resembles the adult. In some spiders these early developmental changes take place in a special molting chamber inside the cocoon (Figure 24.27B). The emergence from the cocoon usually occurs at an early "nymphal" stage, when the young are fully formed spiderlings. Many female spiders even engage in postnatal care by carrying their young on their bodies or by feeding them (Figure 24.27E). (It is important to note that the terms "prelarva," "larva," and "nymph," as used here, do not carry the same meanings as they do when used to describe indirect or mixed development, in which the larva is an independent, free-living individual, as in insects or crustaceans.)

Scorpion development is direct and may be either ovoviviparous or viviparous. Viviparity is perhaps best studied in the Asian scorpion *Liocheles australasiae*. In this species the zygotes lie in tiny diverticula on the walls of the ovarian tubules (Figure 24.26C). Certain cells of the tubule wall absorb nutrients from the adjacent digestive ceca and supply them to the developing embryos. The eggs of *Liocheles* contain very little yolk and undergo holoblastic, equal cleavage. Ovoviviparous scorpions, on the other hand, produce yolky eggs that cleave meroblastically. The embryos of these species are brooded in the ovarian tubules but depend on their yolk supplies for nutrients. The young eventually emerge from the female's gonopore and crawl onto her back. Here they stay until they are old enough to make periodic excursions away from their parent and eventually assume an independent life. Juvenile scorpions molt through several instars until they mature, about a year after birth.

Many other arachnids also brood their embryos, usually externally on the mother's body, as in Amblypygi, Uropygi, Ricinulei, and Schizomida. Members of these groups carry their young in some sort of sac near the female gonopore. Pseudoscorpions spin cocoons from their cheliceral silk glands. Solifuges and harvestmen are oviparous, and some deposit their eggs in the soil or in leaves or logs. In all cases the young hatch and pass through a few or many instars before they mature, and the maturation process may take several years in groups like Ricinulei. Again, except for the "hexapod larvae" of mites and ricinuleids (Figure 24.27L), arachnids hatch as small immature adults, and although various names are given to these immature stages, development is strategically direct. Some harvestmen are known for their parental care, which can be in the form of maternal (Figure 24.27M), paternal, or biparental care. Paternal care is extremely rare in other groups of animals, but it is the norm in sea spiders, discussed in the following section.

The Class Pycnogonida

Pycnogonids (Greek *pyc*, "thick," "knobby"; *gonida*, "knees"), or pantopods, are usually called "sea spiders" because of their superficial similarity to true, terrestrial spiders (Figures 24.28 and 24.29). Pycnogonids

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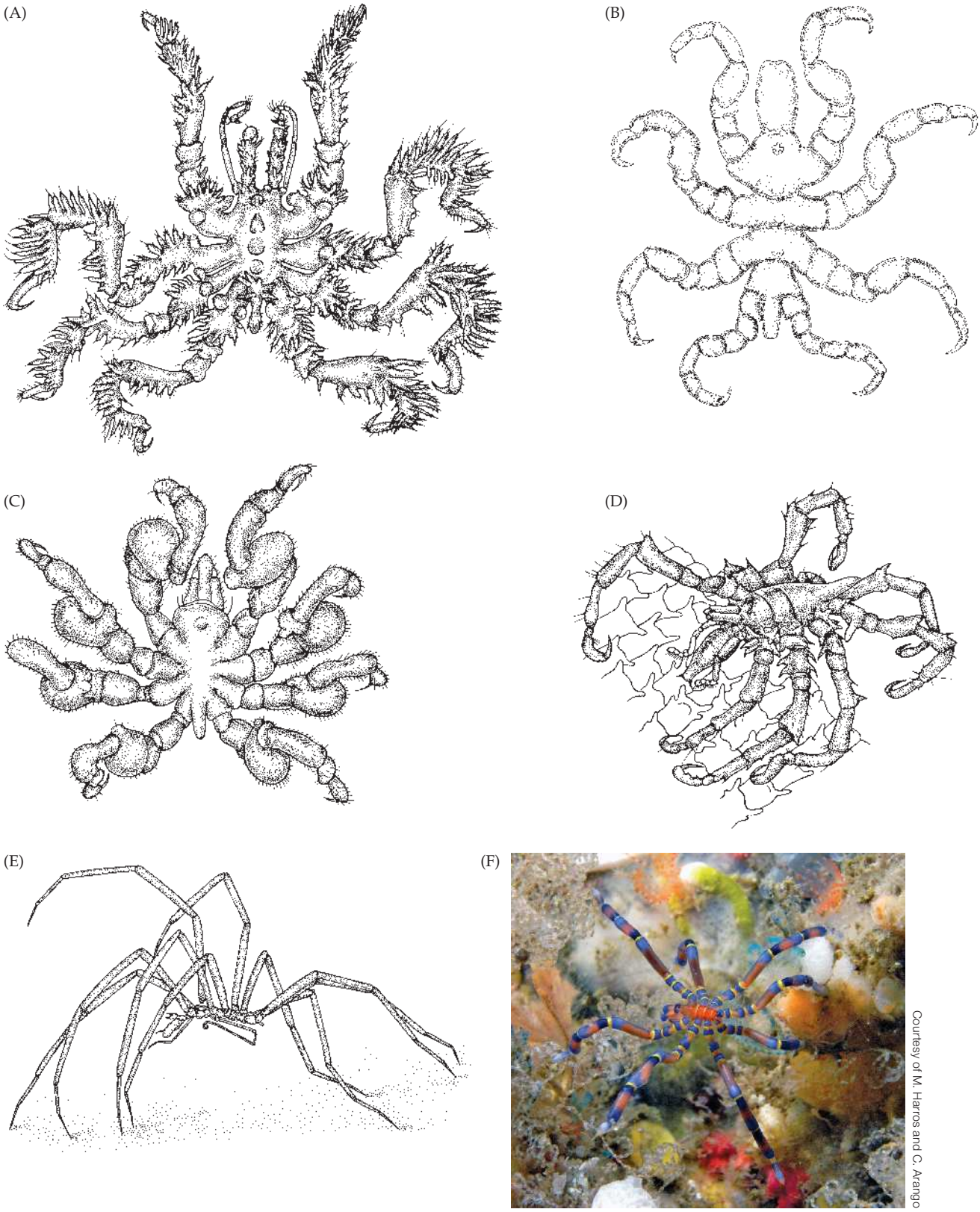

FIGURE 24.28 Representative pycnogonids. (A) *Nymphopsis spinosissimum* (Ammotheidae). (B) *Pycnogonum stearnsi* (Pycnogonidae). (C) *Tanystylum grossifemorum* (Ammotheidae). (D) *Achelia echinata* (Ammotheidae) feeding on a bryozoan colony, one zooid at a time. (E) The ten-legged *Decolopoda australis* (Colossendeidae) (side view of animal walking). (F) *Anoplodactylus evansi* (Phoxichilidiidae) from Australia. (D after D. W. Wyer and P. E. King. 1973. In G. P. Larwood [Ed.], *Living and Fossil Bryozoa*, pp. 199–207. Academic Press, London; E after F. R. Schram and J. W. Hedgpeth. 1978. *Zool J Linn Soc* 63: 145–169.)

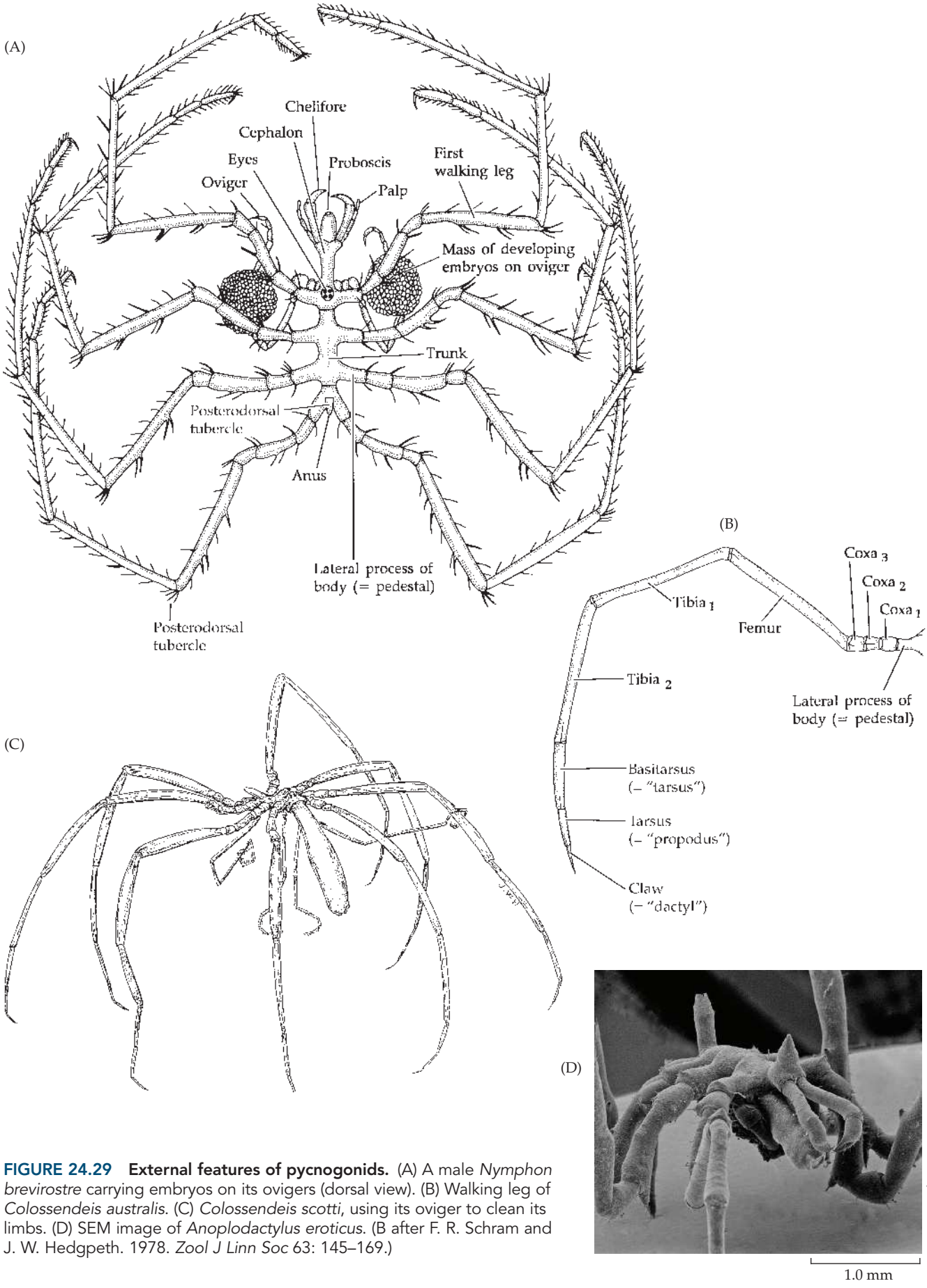

FIGURE 24.29 External features of pycnogonids. (A) A male *Nymphon brevirostre* carrying embryos on its ovigers (dorsal view). (B) Walking leg of *Colossendeis australis*. (C) *Colossendeis scotti*, using its oviger to clean its limbs. (D) SEM image of *Anoplodactylus eroticus*. (B after F. R. Schram and J. W. Hedgpeth. 1978. *Zool J Linn Soc* 63: 145–169.)

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had been problematic in terms of their placement among the other arthropod taxa for decades. Since the turn of the twentieth century they have been associated at one time or another with virtually every major group of arthropods, as well as with the onychophorans and polychaetes. The principal problem has been uncertainty concerning homologies of the various body regions and appendages. The unique pycnogonid "proboscis," for example, has been homologized with everything from the prostomium of polychaete worms to the lips of onychophorans to various anterior regions of other arthropods. However, recent anatomical and molecular studies place the pycnogonids solidly within arthropods, as the sister group to all other chelicerates (what we call euchelicerates).

Several characters are apparent shared apomorphies between the euchelicerates and pycnogonids, including the first appendages (chelicerae/chelifores) and second appendages (pedipalps/palps)—based on the assumption that these appendage pairs, and their somites, are indeed homologous, and nervous innervation tends to support this contention. Two other apparent synapomorphies are the stenopodous uniramous legs (with certain functional similarities) and a feeding method that is largely liquid/suctorial. Pycnogonids also possess several striking unique features, synapomorphies not found in any euchelicerate or in any other arthropod group, such as the odd anterior "proboscis," the **ovigers** (specialized appendages between the pedipalps and first walking legs, used for a variety of purposes but most notably for brooding in males), multiple gonopores (on the second coxal segment of some or all of the walking legs), and the unique body form, discussed in the Pycnogonid Body Plan section, with a reduced abdomen. When compared with euchelicerates, pycnogonids are much more labile in the presence or absence of several appendages (including chelifores, palps and ovigers), and even the number of segments sometimes varies within species or closely related groups.

There are about 1,368 described extant species of pycnogonids, in nearly a hundred genera, with many more yet to be discovered. Pycnogonids are strictly marine; they occur intertidally and to depths of nearly 7,000 m and are distributed worldwide. Most are small, with leg spans less than a centimeter (*Austrodecus palauense* has a leg span of only 2 mm); however, some deep-sea and polar species have leg spans to almost 60 cm. The largest species are members of the genus *Colossendeis*, which live in deep waters worldwide and are common, together with other giants, near shore in Antarctica. Many are errant benthic animals, but others live on seaweeds or on other invertebrates, particularly sea anemones, hydroids, bryozoans, and tunicates. One or two species live on the bells of pelagic medusae, and six species have been collected in hydrothermal vents often associated with, or on the huge vestimentiferan tube worms. A review of the biology of sea spiders can be found in Arnaud and Bamber (1987).

Pycnogonid systematics has remained unsettled for a while, but recently a large community effort has produced a comprehensive tree of life for pycnogonids using a multidisciplinary approach (Ballesteros et al., 2021). Historically, the few known fossil species (which date back to the Upper Carboniferous, as the Cambrian fossil *Cambropycnogon klausmuelleri* is not considered a pycnogonid by most authors) were "dumped" into the single order Palaeopantopoda, and the living forms into the order Pantopoda. The most commonly used classification, with subsequent modifications, was that of Hedgpeth (1982), who recognized just 8 families, based largely on appendage structure (particularly the reduction or loss of various appendages), but many of these families are not monophyletic. Several updates of this system have been proposed in the past two decades and currently pycnogonids include 11 families, 2 of which (Ascorhynchidae and Callipallenidae) are not monophyletic.

The Pycnogonid Body Plan

External Anatomy

The bodies of pycnogonids are not as clearly divided into recognizable tagmata as are those of other arthropods (Figures 24.28 and 24.29), especially since they have a miniaturized abdomen. The first body "region" bears an anteriorly directed proboscis with a terminal mouth, which varies in size and shape among species. The proboscis contains a chamber and bears an opening at its distal end (Figure 24.29A); most researchers now consider the mouth to be at the end (tip) of the proboscis. This anterior-most body "region" also bears paired appendages in the forms of **chelifores**, palps, first walking legs, and, when present, ovigers (Figures 24.29A and 24.31). The chelifores may be chelate or achelate, or absent altogether; they receive a different name from that of the similar appendages in other chelicerates, the **cheliceres**, but it is now clear that these appendages are homologous and innervated by the deutocerebrum. The ovigers are modified legs that serve a variety of functions, including grooming (Figure 24.29C), food handling in some species, courtship, mating, egg transfer (female to male) in many species, and brooding of the embryos by males in most species. Also located on the first segment of most species is a tubercle with four simple median eyes.

The following body segments form the "trunk" and may be variably fused, but each bears a pair of lateral processes, called **pedestals**, on which are borne the walking legs. Because of the orientation of the pedestals, the walking legs are arranged somewhat radially around the body. The posterior-most body segment

carries a dorsally inserted posterodorsal tubercle, which may be a vestigial abdomen and which bears the anus. Perhaps the most distinctive synapomorphy of the pycnogonids, compared with other arthropods, is the presence of multiple gonopores, found on some or all of the walking legs.

One of the most unusual aspects of pycnogonid morphology is the existence of polymerous species, which have more than four pairs of walking legs. This phenomenon is unique to pycnogonids and occurs in the genera *Pentanymphon*, *Pentapycnon*, and *Decolopoda* (with five pairs of legs; decapodous), and *Sexanymphon* and *Dodecolopoda* (with six pairs of legs; dodecapodous). *Callipallene brevirostris* typically bears four pairs of legs, but one specimen has been found with only three pairs. This polymery is poorly understood phylogenetically and developmentally.

Variation among different pycnogonids also occurs in appendage shape and length, spination, proboscis structure, reduction or loss of chelifores and palps, and many other external features. Several examples are shown in Figures 24.28 and 24.29 to illustrate this diversity. In all, however, the body is remarkably reduced and narrow, a feature compensated for by extensions of the gut ceca and gonads into the legs.

Locomotion

The walking legs of pycnogonids are typically nine-segmented. The junction of the first coxal segment and the pedestal is a more or less immovable joint and does not contribute to the action of the leg. The joint between the first and second coxae is hinged to provide antero-posterior movement, and the rest of the joints provide the usual flexion and extension. However, the coxal joints also allow a certain amount of "twisting" and thus accentuate the anterior–posterior swing of the appendage tips during the power and recovery strokes. Some joints lack extensor muscles, and limb extension is effected by hydrostatic pressure, as in many arachnids. Note that pycnogonid specialists have given names to the leg articles that do not parallel those used for any other arthropod group (Figure 24.29B).

Most of the commonly encountered intertidal pycnogonids are quite sedentary and move very slowly. These small forms have short, thick legs that are somewhat prehensile and serve more for clinging to other invertebrates or algae than for rapid locomotion. Deep-water benthic pycnogonids tend to be more active, and these errant pycnogonids have longer and thinner legs than the sedentary forms, and they tend to walk on the tips of the legs (Figures 24.28E and 24.29C). However, some of the very large forms (e.g., *Colossendeis*) may depend more on slow ocean currents to roll them around on the bottom than on their own locomotory powers.

Many pycnogonids are also known to swim periodically by employing leg motions similar to those used in walking. Some species are known to "hang" from the water's surface, utilizing a combination of small body mass and surface tension. Several studies also report a characteristic "sinking behavior" in a number of species. When dropping to the bottom, these pycnogonids elevate all of the appendages over the dorsal surface of the body in a basket configuration. This behavior eliminates much of the frictional resistance to sinking and allows the animal to drop quickly through the water column (presumably to avoid predation), a behavior also commonly found in some ophiuroids.

Feeding and Digestion

In most species of pycnogonids, feeding habits are dictated by the form of the proboscis, and food is limited to material that can be sucked into the gut. Even with this basic structural constraint, pycnogonids feed on a variety of organisms.

A few pycnogonids feed on algae, but most are carnivorous, many being generalized predators on hydroids, polychaetes, nudibranchs, and other small invertebrates. Some, perhaps many, also scavenge. Species that consume other animals usually use three cuticular teeth at the tip of the proboscis to pierce the body of their prey, and then they suck out body fluids and tissue fragments. Some pycnogonids that live on hydroids use the chelifores to pick off pieces of the host and pass them to the proboscis opening. In most species, however, the chelifores cannot reach the tip of the proboscis, and their function in feeding is questionable. Some species (e.g., *Achelia echinata*) feed on bryozoans by inserting the proboscis into the chamber that houses an individual and sucking out the zooid (Figure 24.28D). An interesting phenomenon in Antarctic pycnogonids is the large number of species and individuals that carry, on their cuticle, bryozoans—a major source of food for them! This may be advantageous to the bryozoan colonies, even if used as a food source by the pycnogonids, as they get some protection from ice scour. Others (e.g., *Pycnogonum litorale*, *P. rickettsi*) feed on sea anemones in a similar fashion, but the anemones are rarely killed, due to the large difference in size between predator and prey.

Very little is known about the feeding habits of the deep-sea benthic forms. Undersea photographs and direct observations of aquarium specimens of the giant *Colossendeis colossea* indicate that it may walk slowly along the bottom, sweeping its palps across the substratum to sense prey that it might suck from the mud.

The digestive tract extends from the mouth, at the tip of the proboscis, to the anus, which opens on the posterodorsal tubercle on the peglike abdomen (Figure 24.30A). A chamber within the proboscis bears dense bristles that strain and mechanically mix ingested food, which continues to the pharynx. The pharyngeal and the esophageal regions have a foregut lumen that is

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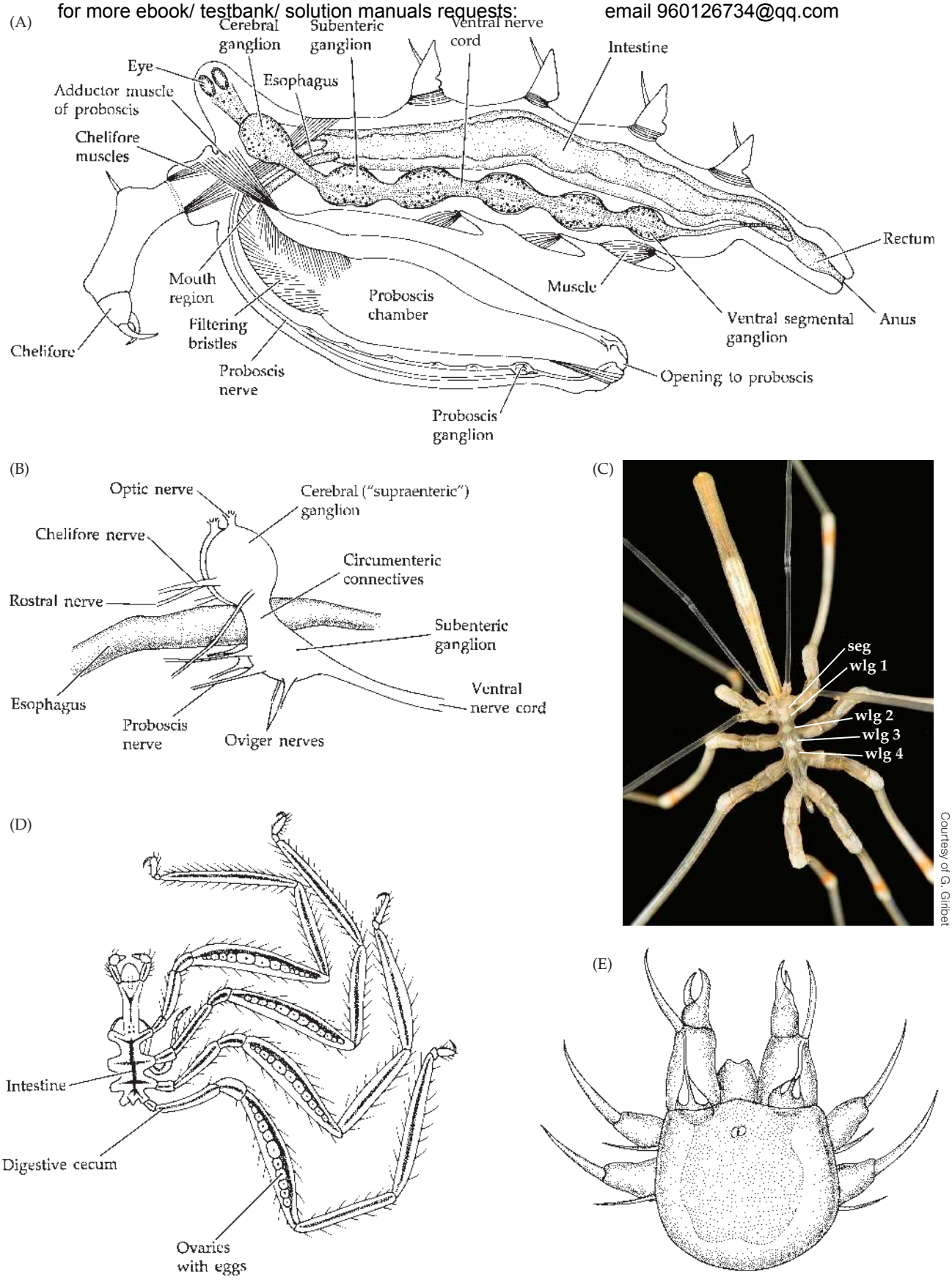

FIGURE 24.30 Internal anatomy of pycnogonids. (A) The body of the pycnogonid *Ascorhynchus* (longitudinal section). (B) Anterior portion of the nervous system of *Nymphon*. (C) Ventral view of *Colossendeis* sp. from the Antarctic Peninsula showing the subesophageal ganglion (seg) and the ventral ganglia anterior to each pair of walking legs (wlg1 to 4) and efferent nerves. (D) A female pycnogonid with developing ova stored in the femoral portions of the gonad diverticula. (E) Protonymphon larva.

Y-shaped in transverse section. The muscles of the foregut supply the suction for ingestion. A short esophagus connects with the elongate midgut or intestine, from which digestive ceca extend into the bases of each leg, providing a high surface area for digestion and absorption. A short proctodeal rectum leads to the anus.

Digestion is predominantly, if not exclusively, intracellular. The cells of the midgut and cecal walls differentiate from the basal layer and contain a bewildering array of secretion droplets, lysosomes and phagosomes, and include phagocytes that engulf ingested food materials. Some of these cells actually break free from the gut lining and phagocytize food particles while drifting in the gut lumen. Apparently these loose cells reattach to the gut wall after they have "fed." It has been suggested that upon reattachment these errant cells first pass their digested food contents to the fixed cells of the gut wall, then assume an excretory function by picking up metabolic wastes, detaching again, and being eliminated via the anus. In the absence of a hepatopancreas, the midgut serves both digestive and absorptive functions.

Circulation, Gas Exchange, and Excretion

Pycnogonids lack special organs for gas exchange. The digestive ceca and the overall body plan together present a very high surface-area-to-volume ratio, and exchange of gases probably occurs largely by diffusion across the body and gut wall, through gut peristalsis. However, cutaneous respiration often poses a limit to size in arthropods, as the cuticle also has a structural function. Recent studies have shown that larger pycnogonids maintain steeper oxygen gradients and higher effective diffusion coefficients of oxygen in the cuticle than vertebrates do, and diffusion modeling has shown that gas exchange occurs mostly through pores in the cuticle.

Traditionally, pycnogonids have been thought to have no excretory organs at all and to use the high surface-area-to-volume ratio or the wandering cells of the midgut for excretion. Recently an excretory structure has been located in at least one ammotheid, *Nymphopsis spinosissimum*, in which a simple, but standard, excretory gland has been found in the scape of the chelifore. It consists of an end sac, a straight proximal tubule, a short distal tubule, and a raised nephropore.

The circulatory system includes an elongate heart with incurrent ostia, but no blood vessels. As in other arthropods, the heart is located dorsally, within a pericardial chamber separated from the ventral hemocoel by a perforated membrane. Blood leaves the heart anteriorly and flows through the hemocoelic spaces of the body and appendages. Contraction of the heart causes a lowered pressure within the dorsal pericardial body chamber, and blood is thus drawn through the perforations in the membrane and toward the heart. Upon relaxation, the blood flows through the ostia into the heart lumen.

Nervous System and Sense Organs

The central nervous system of pycnogonids includes cerebral ganglia above the esophagus, circumenteric connectives, a subenteric ganglion, and a ganglionated ventral nerve cord (Figure 24.30A,B). The nerve cord bears a ganglion for each pair of walking legs, with additional ganglia present in the polymerous species.

The cerebral ganglia, as in most extant arthropods, include protocerebrum, deutocerebrum, and the subesophageal tritocerebrum. The protocerebrum innervates the eyes, and the deutocerebrum innervates the chelifores, an arrangement similar to that in euchelicerates. Recently some authors postulated that the chelifores were innervated by the protocerebrum, as in the "great appendages" of some Cambrian stem-group arthropods, but this was later shown to be an artifact due to the fusion of protocerebrum and deutocerebrum in the second embryonic stage. The cerebral ganglia also give rise to a well-developed ganglionated proboscis nerve.

Little work has been done on pycnogonid sense organs. Tactile reception is provided by touch-sensitive setae and probably by the palps. On the body surface, just dorsal to the cerebral ganglia, is a central tubercle with four simple eyes that provide 360° vision. Some deep-sea species lack eyes entirely.

Reproduction and Development

Pycnogonids are gonochoristic. Mating is typically followed by a period of brooding, during which the embryos are held by the male's ventrally articulated ovigers, then by the release of unique **protonymphon larvae** (Figure 24.30E). The protonymphon has six legs and usually lives in a symbiotic relationship with cnidarians, molluscs, or echinoderms. These relationships are poorly understood, but in some cases they appear to be parasitic or commensalistic, encysting in the cnidarian host. This life cycle strategy has been replaced by direct development in some species wherein the larval stage is passed within an egg case.

Sexual dimorphism is common among pycnogonids. The males bear the unique ovigers associated with the first body segment; these appendages are absent in females of some families (e.g., Phoxichilidiidae, Endeidae, and Pycnogonidae) and reduced in the females of other families (Figure 24.31). Female pycnogonids usually have enlarged limb femora.

Internally, the reproductive system of males and females is similar and relatively simple. In both, the gonad is single and U-shaped, with extensions into the legs where gametes are produced and stored. The expanded femora in females provide space for storing unfertilized eggs (Figure 24.30D). The multiple gonopores are usually located on the ventral surface of the second coxae of two or all pairs of legs and are thus close to the regions of gamete storage. During mating, the male typically hangs beneath the female or

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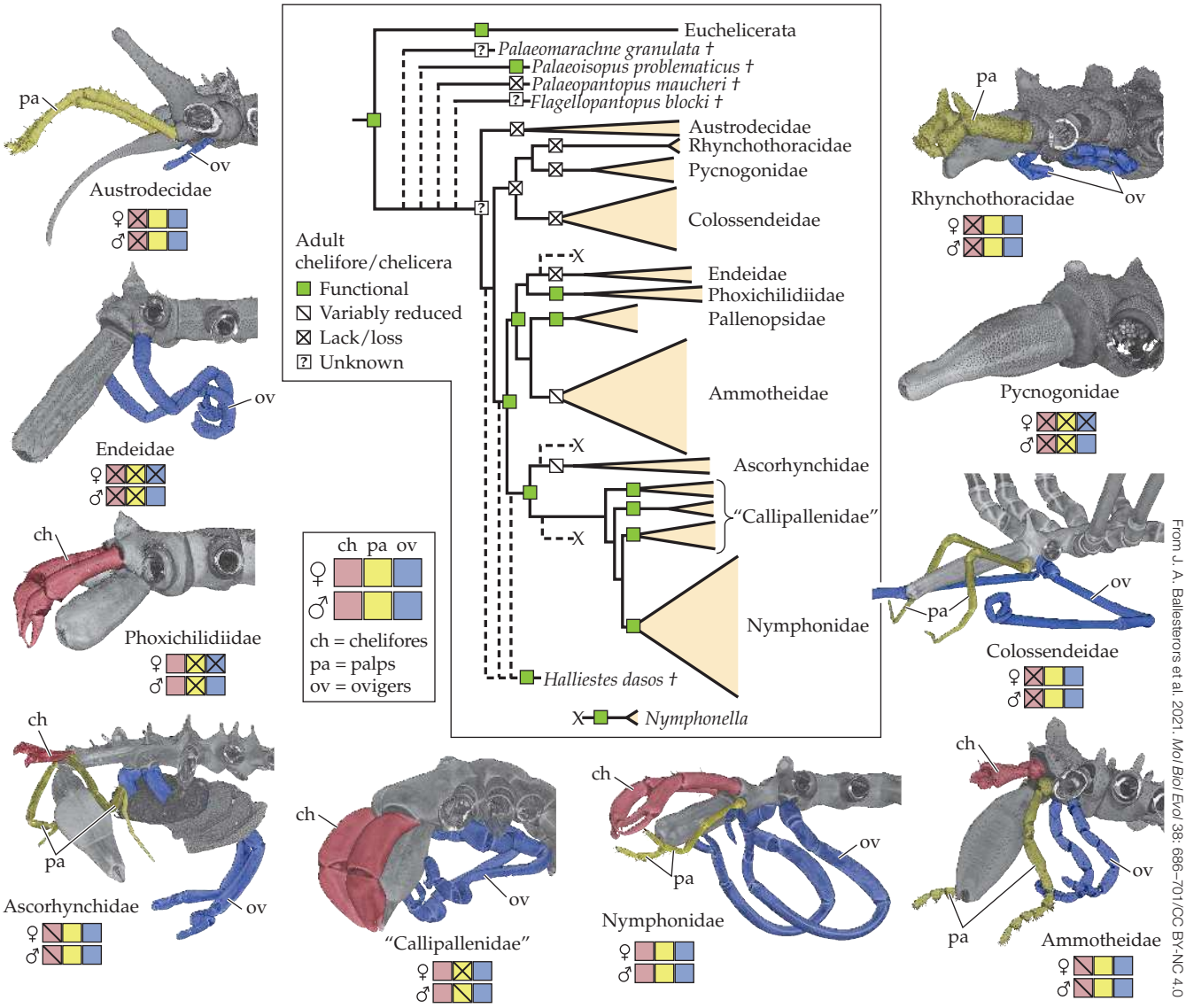
assumes a stance over her back. As the female releases her eggs, the male fertilizes them. Following fertilization, the male gathers the eggs, either one by one or as a single mass, and glues them to his ovigers using a sticky secretion from special femoral glands (Figure 24.29A). Pycnogonids are one of the few groups of animals in which brooding of eggs and developing embryos is conducted exclusively by the males, and in some species males also brood the young.

Knowledge of pycnogonid development has increased considerably in the past few years, with several studies focusing on the identity of the pycnogonid appendages with those of other arthropods, using neurogenesis and Hox gene expression. Earlier in embryogenesis, there is some variation among members of different genera, but cleavage is usually holoblastic and leads to the formation of a stereoblastula. The inward movement of the presumptive endodermal and mesodermal cells is frequently accompanied by a disappearance of some cell membranes, a process leading to the formation of some syncytial tissues in the gastrula. Germinal centers become apparent as appendage buds form. The most common hatching stage is a free-swimming protonymphon larva. Through a



From J. A. Ballesteros et al. 2021. *Mol Biol Evol* 38: 686–701/CC BY-NC 4.0

FIGURE 24.31 Proposed phylogeny of the pycnogonid families and reconstruction of the cephalic appendage evolution, with emphasis on the chelifore. Reconstruction of adult chelifores is mapped on the topology, and appendage complement for males and females is indicated for each family. Ancestral state reconstruction is based on equally weighted parsimony. Note the omission of functional adult chelifores in colossendeids with supernumerary segments (a derived state within the genus *Colossendeis*). Specimens in counterclockwise order from top left: male *Austrodecus glaciale*, male *Endeis spinosa*, female *Phoxichilidium femoratum*, egg-bearing male *Ascorhynchus ramipes*, male *Stylopallene cheilorhynchus*, male *Nymphon gracile*, female *Ammothella longipes*, female *Colossendeis angusta*, female *Pycnogonum litorale*, female *Rhynchothorax australis*.

series of molts, the protonymphon adds segments and appendages to produce a juvenile. In some species, the developing larva becomes encysted in a hydroid or stylasterine coral, emerging later with three pairs of legs. A few species are known to produce all of the appendages at once, with subsequent molts simply increasing the size and segment number of the legs (the "atypical protonymphon larva"). In *Pycnogonum litorale*, at the fifth larval molt, the three pairs of larval legs and the larval proboscis are lost; the adult proboscis appears and, at later molts, the adult limbs develop.

Chelicerate Phylogeny

Although over 150 years have passed since the discovery of pycnogonids, arguments still ensue as to their phylogenetic relationships. However, as we mentioned earlier, recent morphological, paleontological, and molecular studies point to a chelicerate ancestry. The chelifores and palps of pycnogonids are now considered homologous with the chelicerae and pedipalps of the other chelicerates. We thus recognize Pycnogonida as the sister group to the remaining Chelicerata, or Euchelicerata.

Figure 24.32 is a cladogram depicting a working hypothesis of the relationships among the major chelicerate clades. However, we caution readers that the phylogenetic relationships among the Chelicerata are still being debated. Resolving the phylogenetic relationships of chelicerates remains remarkably difficult due to their ancient rapid radiation and the elevated evolutionary rates in several lineages. Until recently, the subclass Arachnida was considered a monophyletic group, although some workers have suggested that it might be diphyletic, having arisen from two separate invasions of land (one leading to the scorpions, the second to all other orders), a view that no longer has much support. Phylogenetic relationships among the orders of Arachnida remain controversial; see Ballesteros and Sharma (2019) for a recent study using transcriptomic data and Shultz (2007) for a recent analysis based on morphological data. Recent phylogenomic studies, even when integrating morphological data, place Xiphosura

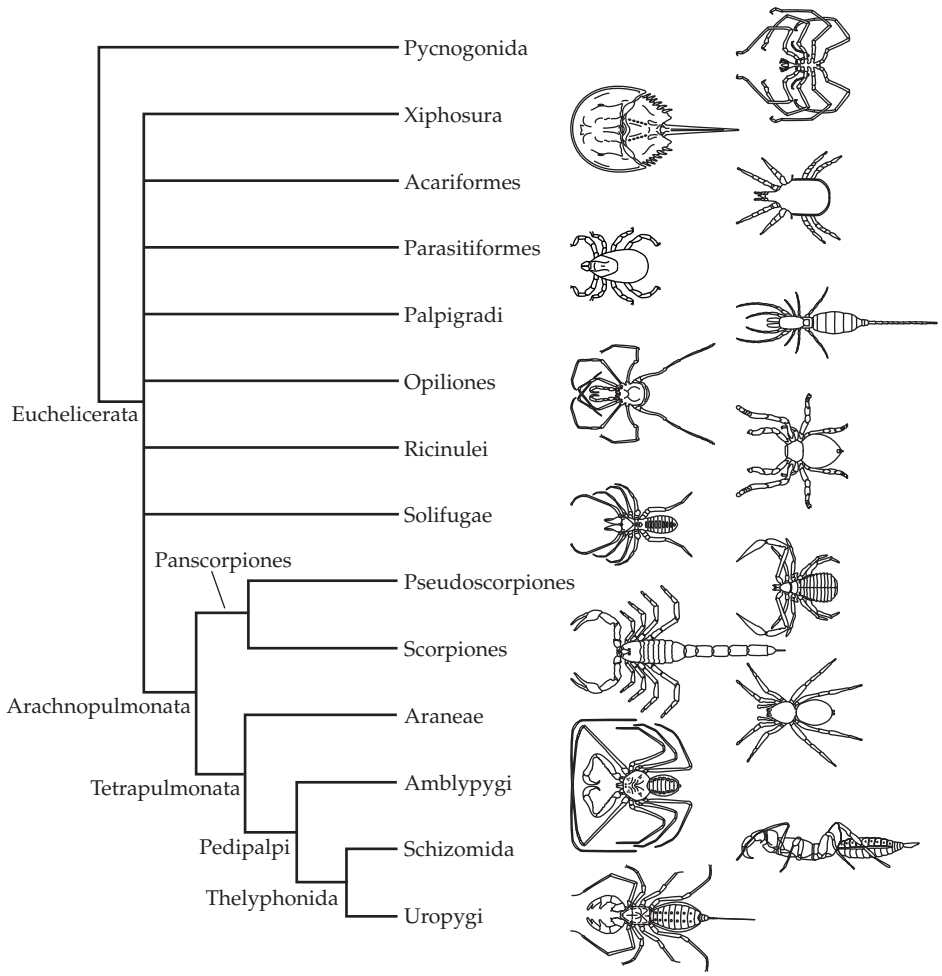


FIGURE 24.32 A cladogram depicting a working hypothesis for the relationships among Chelicerata. Note the unresolved positions for a good number of arachnid orders as well as the unresolved position of Xiphosura with respect to the other orders.

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(horseshoe crabs) as distally placed arachnids, with combined analyses recovering Merostomata (the marine orders Xiphosura, Eurypterida, and Chasmataspidida) as nested within Arachnida. These studies recover older origins of chelicerate groups than previously inferred, suggesting a more complex history of terrestrialization in chelicerates than previously envisioned, with multiple recolonizations of aquatic habitats.

The earliest xiphosuran, eurypterid, and chasmataspidid fossils are from the Ordovician, but putative chasmataspidid impressions are found in the late Cambrian. Like the myriapods (and perhaps the insects), arachnids probably invaded land early in the Silurian, at the same time the land plants were becoming well established, although molecular calibrations suggest an earlier origin of arachnids, probably Ordovician or even earlier. Whether the earliest Paleozoic scorpions (Silurian) were aquatic remains contentious, but fully articulated fossil scorpions have been found in the marine Devonian Hunsrück Slate environment.

A series of phosphatized larval instars from the late Cambrian Orsten of Sweden were considered the oldest putative pycnogonids, but the consensus now is to exclude the Orsten fossils from Pycnogonida, at least from the crown group. The oldest sea spiders come from the Upper Ordovician William Lake Konservat-Lagerstätte deposit in Manitoba, Canada, followed by fossils from the Silurian Herefordshire Konservat-Lagerstätte in England and a suite of taxa from the Early Devonian Hunsrück Slate of Germany.

Chapter Summary

This chapter introduced you to the oldest group of extant arthropods (the first to appear in the fossil record), the Chelicerata, a clade that includes some primitive marine groups (Pycnogonida, Xiphosura) and a plethora of terrestrial counterparts, including large numbers of predators (spiders, scorpions) and parasites (many acarine lineages). Despite their variety of form, chelicerates are characterized by a common body plan with chelicerae as the first pair of appendages (deutocerebral), followed by more or less modified pedipalps (tritocerebral), and then four pairs of walking legs. All of these appendages concentrate in a body region called the prosoma. The prosoma also bears the eyes, with a variety of simple eyes in the different chelicerate lineages, and also with compound eyes in the horseshoe crabs. The opisthosoma, or second body tagma, is externally segmented in most groups (but not in most spiders), although tagmosis in the acarine groups follows a different scheme. The opisthosoma may bear appendage-derived structures, such as the spinnerets of spiders or the pectines of scorpions. Among the chelicerates, the taxon Arachnida has been recognized for a long time, but current molecular phylogenetic analyses have questioned the monophyly of this group, placing horseshoe crabs within the terrestrial arachnids, a result that has raised skepticism among some biologists and that would imply a return to a marine environment for the horseshoe crab ancestors. Arachnids are an important component of terrestrial ecosystems and have developed some of the most fascinating tools used in the animal kingdom for prey capture, venoms and silk.

In addition to the question of the position of horseshoe crabs there is the challenge of classifying arachnids, especially the apulmonate groups (those that typically use tracheae for respiration). Currently, the monophyly of those with book lungs is strongly supported molecularly and morphologically, in a clade known as Arachnopulmonata, which includes Araneae, Amblypygi, Uropygi, Schizomida, Scorpiones, and probably the apulmonate Pseudoscorpiones. Understanding the relationship of the other apulmonates and the plethora of extinct arachnid lineages has been a fruitful but relatively frustrating area of inquiry.

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CHAPTER 25

Introduction to Deuterostomia, and the Phylum Hemichordata

The two great clades of Bilateria—Protostomia and Deuterostomia—have been recognized for well over a century. You were briefly introduced to these clades in Chapters 8 and 10. With this chapter, we begin our formal studies of the deuterostomes. Although there are only three phyla in the clade Deuterostomia, the clade has long loomed large in zoological lore because one of them, the phylum Chordata, contains the vertebrates (which happens to include *Homo sapiens*), and another contains perhaps the most iconic of marine invertebrates, the echinoderms (Figure 25.1). The third deuterostome phylum, Hemichordata, is little known to most zoologists except through courses in invertebrate zoology. Four other phyla were formerly assigned to Deuterostomia (Chaetognatha, Phoronida, Bryozoa and Brachiopoda), but some years ago molecular phylogenetics showed these to belong to the clade Protostomia. In addition, some authors consider Chordata to be three phyla instead of one: Cephalochordata, Urochordata (or Tunicata), and Vertebrata (or Craniata).

Introduction to the Deuterostomia

The groups Protostomia and Deuterostomia were long defined on the basis of embryological principles. In protostomes the blastopore (the region in the embryo that typically gives rise to endodermal tissues) was said to give rise to the mouth (protostome meaning "mouth first"). Typically in deuterostomes, the blastopore gives rise to the adult anus, the mouth thus forming secondarily at a different location (deuterostome means "secondary mouth"). In both lineages, the blastopore sits at the vegetal pole of the embryo when gastrulation begins. Also, it was long thought that

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

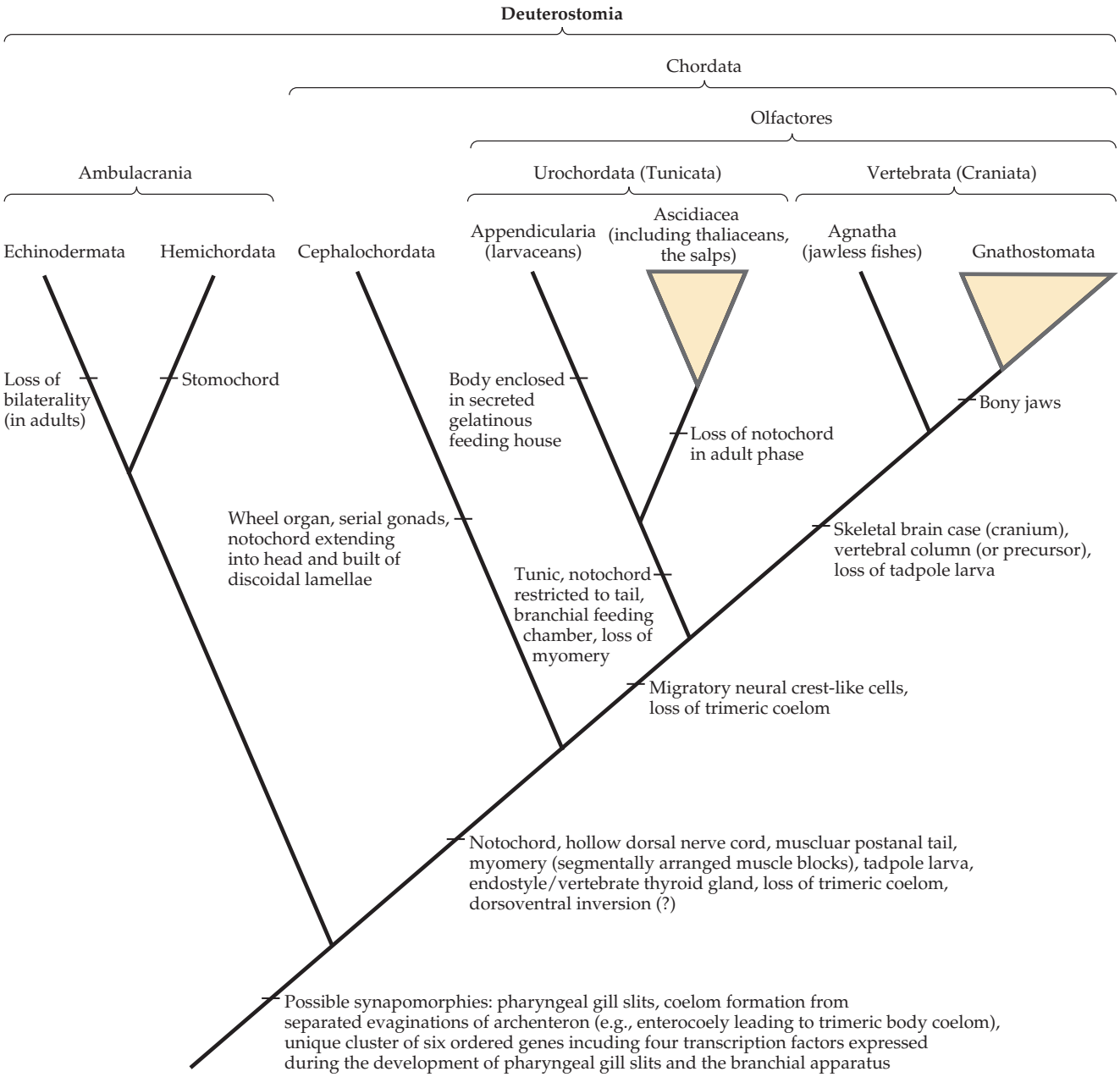

FIGURE 25.1 A phylogeny of Deuterostomia.

radial cleavage defined deuterostomes. However, new embryological patterns have begun to emerge.

It turns out that the blastopore doesn't consistently give rise to the anus in deuterostomes. And among the protostomes, gastrulation is now known to be much more variable, and some protostome phyla display deuterostomous development (e.g., Nematomorpha, Priapula, some Brachiopoda); that is, the mouth opens separately from the blastopore, which may become the anus. And it has been long known that radial cleavage occurs in some nondeuterostomes. So, evidence is accumulating that mouth formation from oral ectoderm (in the animal hemisphere), development of the anus from the blastopore, and radial cleavage, all once thought to define deuterostome embryogeny, may be ancestral in both protostomes and deuterostomes, and thus in Bilateria itself. Hence, most of the embryological features that once defined these two great clades of bilaterians no longer unambiguously do so, and our current definition of Protostomia and Deuterostomia is based primarily on molecular phylogenetic evidence. However, the legacy names Protostomia and Deuterostomia continue to be used for these two animal lineages. Unambiguous morphological or developmental synapomorphies probably exist that define these two clades, but they have not yet been fully identified.

One possible synapomorphy of the Deuterostomia is enterocoelic development and a trimeric condition of its coelomic cavities, at least primitively, but this feature is lacking in the phylum Chordata, and therefore it could be a feature of Ambulacraria. During deuterostome enterocoelic embryogeny, the coelomic cavities form via

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archenteric pouching, in which each of the three coeloms forms from the gut, pinching off and becoming a coelomic cavity (Figure 4.12). These coelomic compartments are called (anterior to posterior) protocoel, mesocoel, and metacoel; the equivalent body regions are the prosome, mesosome, and metasome. By definition, the walls of the pouches are mesoderm. However, schizocoelic coelom formation (Figure 4.11) has also been reported from a few deuterostomes, including scattered mesodermal cells in the tornariae of some enteropneusts. Another probable synapomorphy of Deuterostomia is a widely conserved cluster of six ordered genes, including four transcription factors expressed during the development of pharyngeal gill slits and the branchial apparatus.

Within the deuterostome clade, recent morphological and molecular work (and also Hox gene motifs) suggest that echinoderms and hemichordates are sister groups, constituting a clade called Ambulacraria, and this is the sister group to the phylum Chordata. If this assessment is correct, it means the features shared between chordates and hemichordates (formerly long thought to comprise sister groups), such as gill slits, may have been ancestral within Deuterostomia but lost in the echinoderm line (and also in some hemichordate lineages), as suggested by the putative presence of gill slits in some extinct echinoderms. Gill slits in Deuterostomia have been shown to be homologous based on their gene expression patterns. Several other deuterostome animals with gill slits are known from the fossil record (Saccorhytida, Vetulocystida, Vetulicolia, Yunnanozoa), although it is not yet certain whether these belong to stem urochordates, to stem echinoderms, to stem chordates, or to unique but extinct lineages.

A long-recognized feature shared between the Hemichordata and Chordata is the stomochord/notochord, once viewed as homologues. It is now thought that these structures might have had much earlier origins and may or may not be homologous, or that a group of vacuolated cells in ancestral deuterostomes gave rise to these structures independently in hemichordates and chordates. Within Chordata, Urochordata is the sister group to Vertebrata (a clade known as Olfactores), and Cephalochordata is the sister group to those (Figure 25.1). There is some older evidence that a fourth group, Xenoturbellida (or even the whole clade Xenacoelomorpha) might be near the base of the deuterostome line, but more convincing evidence suggests Xenacoelomorpha as an ancestral bilaterian clade that arose prior to the divergence between protostomes and deuterostomes, and that is the view we follow in this book.

Deuterostomia is an ancient lineage, and dated phylogenetic trees (using fossils to date branching points) suggest the ancestral line existed well into the Precambrian. The oldest definitive fossil of Deuterostomia is a 530-million-year-old creature called *Yunnanozoon*, from the lower Cambrian Chengjiang biota of the Yunnan Province, China, although the affinities of yunnanozoans are still uncertain. An even older fossil from the basal Cambrian of Shaanxi, China, is the meiofaunal *Saccorhytus coronarius*, although the affinities of this fossil are a bit more controversial.

Phylum Hemichordata: Acorn Worms and Pterobranchs

The hemichordates constitute a phylum of exclusively marine, benthic, bilaterally symmetrical deuterostome invertebrates (Box 25A). They inhabit all sea bottoms of the world, from intertidal environments to abyssal depths. The phylum includes about 140 species,

The section on phylum Hemichordata was revised by Christopher Lowe.

BOX 25A Characteristics of the Phylum Hemichordata

1. Bilaterally symmetrical deuterostomes, body vermiform or saccate and fundamentally trimeric, with prosome, mesosome, and metasome, each with coelomic compartments; solitary or colonial; pterobranchs with mesocoelic extensions into the arms and tentacles
2. With mesocoelic ducts and pores
3. With pharyngotremy (communication from the gut to the exterior is via ciliated pharyngeal gill slits and pores)
4. Well developed, open circulatory system in enteropneusts but simplified in pterobranchs
5. Unique excretory structure, the glomerulus
6. Gonads extracoelic, in metasome
7. Complete gut; deposit or suspension feeders
8. With buccal diverticulum or stomochord as supporting structure for the prosome; stomochord not homologous with the chordate notochord
9. Circular and longitudinal muscles present in body wall of proboscis and collar of enteropneusts; pterobranchs with longitudinal muscles only, as in the trunk of enteropneusts
10. Collagenous skeletal structures in the proboscis and gill bars of enteropneusts derived from basement membrane of adjacent epithelia
11. Short, dorsal, mesosomal, occasionally hollow nerve cord (neurochord), probably homologous with chordate nerve cord
12. Gonochoristic, with external fertilization and indirect development through a unique tornaria larva; some species with direct development; asexual reproduction common
13. Cleavage radial, holoblastic, more or less equal; although blastopore denotes posterior end of body, both mouth and anus forming secondarily, subsequent to closure of the blastopore; mesoderm and body cavities forming by enterocoely
14. Strictly marine and benthic

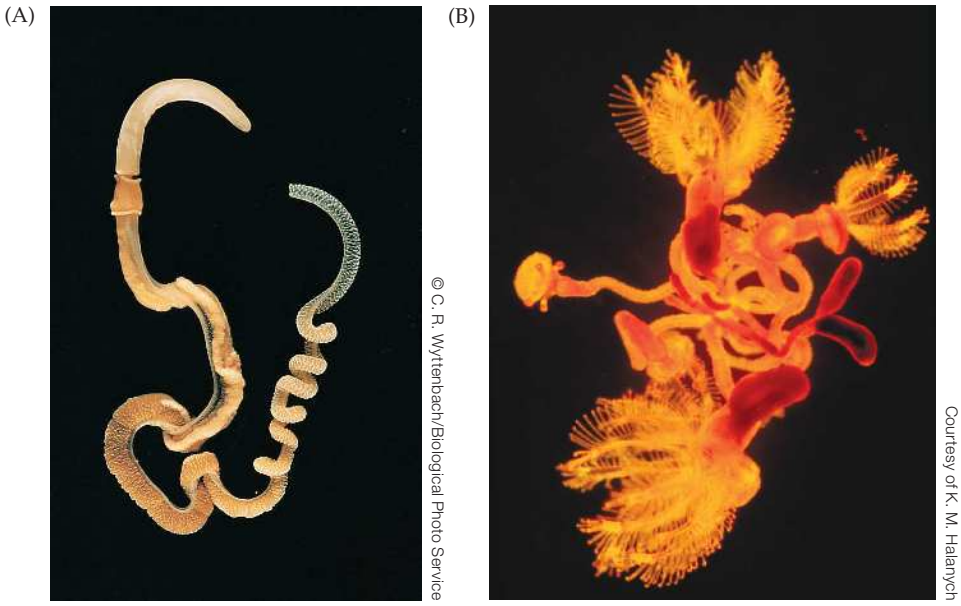

FIGURE 25.2 Representative hemichordates. (A) The acorn worm *Saccoglossus* (class Enteropneusta). (B) Portion of a *Cephalodiscus* colony (class Pterobranchia), showing several individuals at different stages of development.

most (108) of which are benthic burrowers known as acorn worms (or tongue worms) grouped in the class Enteropneusta (Figures 25.2A and 25.3A–D, and chapter opener photo). The remaining species belong to the class Pterobranchia—largely colonial forms of zooids superficially resembling bryozoans (Figures 25.2B and 25.3E–H).

The first known hemichordate, a specimen of *Ptychodera flava* (an enteropneust), was discovered in 1821 and recorded by the Baltic German naturalist Johann Friedrich von Eschscholtz in 1825 as an aberrant holothurian. The German anatomist Johannes Müller discovered in 1850 the first specimen of a tornaria larva, although it was considered to be an echinoderm larva until Metschnikoff recognized it as an enteropneust in 1869. The first pterobranch specimens described were individuals of *Rhabdopleura* dredged by G. O. Sars in 1866, although they were misidentified as bryozoans. Sidney Frederic Harmer later proposed their relationship with *Cephalodiscus* specimens recovered by the *Challenger* expedition and the relation of both with enteropneusts. Harmer also adopted the name Hemichordata for the whole group as proposed by William Bateson in 1885. Most relevant contributions to the knowledge of hemichordate biology in late nineteenth and early twentieth centuries are from J. W. Spengel, C. Dawydoff, and C. van der Horst. Nowadays hemichordates continue to provide exciting discoveries, such as the genus *Saxipendium* from hydrothermal vents, and the bizarre deep-sea enteropneust family Torquaratoridae (Figure 25.3D). Recently, a minute acorn worm, *Meioglossus psammophilus,* has been reported from Belize and Bermuda, living permanently in coral sand as part of meiofauna communities. Developmental biology of hemichordates has played an increasing role in revealing basic organizational principles of the body plan.

Enteropneust worms generally live buried in soft sediments, among algal holdfasts, or under rocks; they have been considered largely intertidal, but recent discoveries point to a substantial and undocumented enteropneust diversity occurring in the deep sea. Of the few deep-water acorn worms known, one species, *Saxipendium coronatum* (the "spaghetti worm"), is a member of hydrothermal vent communities; some other deep-water forms construct highly branched burrow systems, and recent videotaping records confirm that some deep-sea enteropneusts are epibenthic (Figure 25.3D) and use the water column to move between feeding sites. As we have seen in so many other benthic, sessile, and sedentary invertebrates, the hemichordates include a planktonic dispersal phase in their life history strategies. The life cycle of acorn worms includes a free-swimming tornaria larva, although direct development occurs in some species. Tornaria can spend many months in the plankton, whereas direct developers have an abbreviated developmental time course to adult, with a limited planktonic period of hours to days.

Pterobranchs are colonial, tube-dwelling hemichordates that feed with ciliated arms and tentacles (Figure 25.3E–H). Many species have been found in Antarctic waters, although some colonies are found in shallow tropical waters attached to the undersides of rocks, bivalve mollusc shells, or coral rubble. Pterobranchs typically live in colonies formed by extensive aggregations of tubes called **coenecia**, with one individual in each tube. Zooids of *Rhabdopleura* are connected via a stalk or stolon of living tissue, while zooids of *Cephalodiscus* are connected to a basal disk. Colonies of pterobranchs

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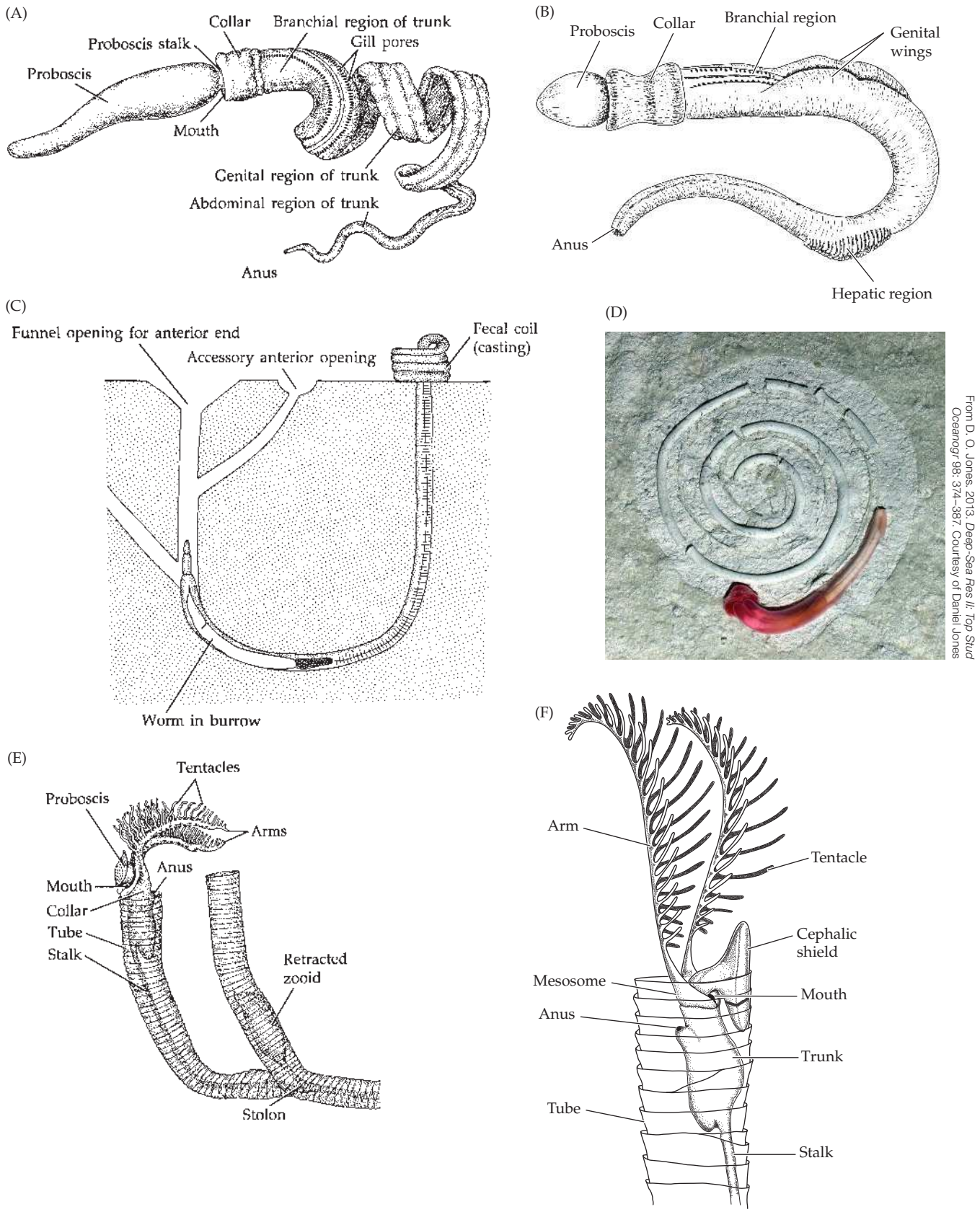

FIGURE 25.3 External anatomy of some representative hemichordates. (A) *Saccoglossus* (Enteropneusta). (B) *Glossobalanus* (Eteropneusta). (C) *Balanoglossus clavigerus* (Enteropneusta) in its burrow system. (D) The epibenthic, deep-sea *Tergivellum cinnabarinum* (Enteropneusta: Torquaratoridae) with its spiral cast. (E) Portion of a colony of *Rhabdopleura* (Pterobranchia). (F) Individual zooid of *Rhabdopleura*.

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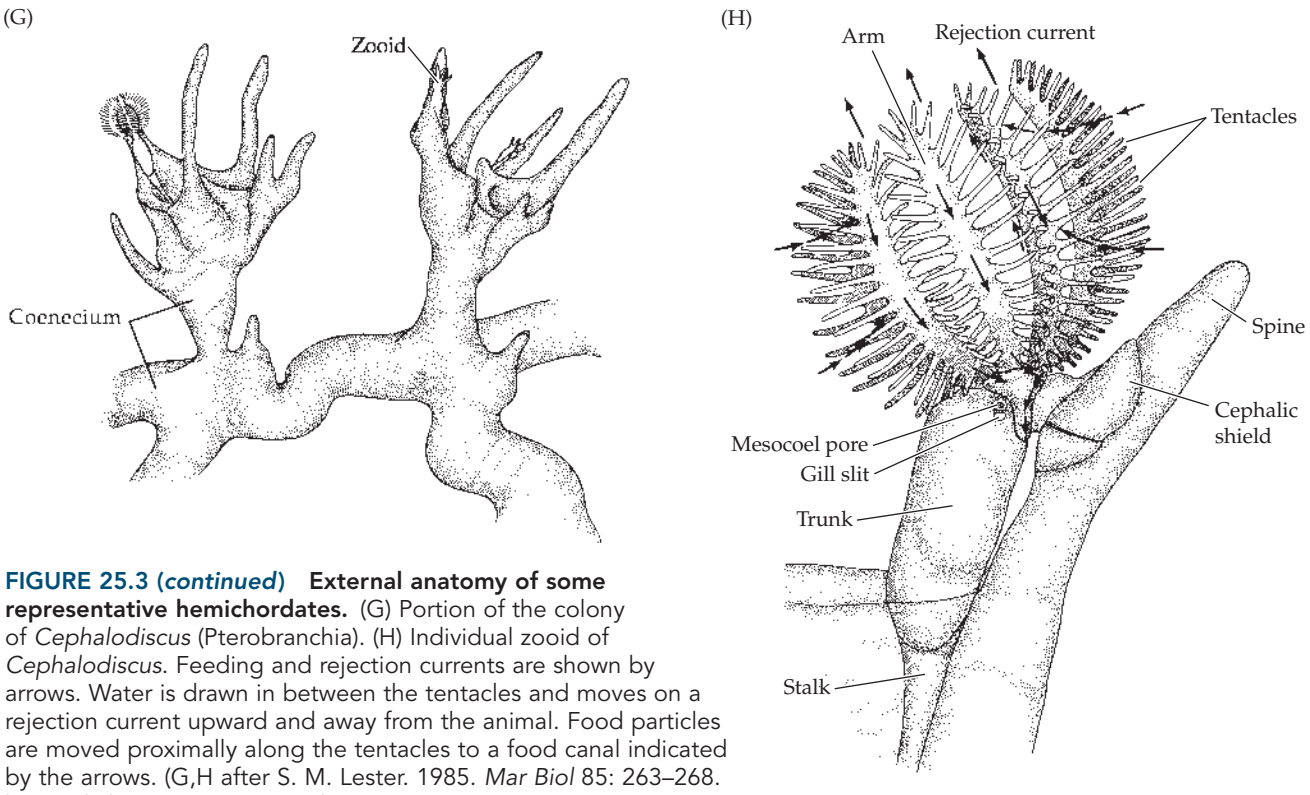

FIGURE 25.3 (*continued*) External anatomy of some representative hemichordates. (G) Portion of the colony of *Cephalodiscus* (Pterobranchia). (H) Individual zooid of *Cephalodiscus*. Feeding and rejection currents are shown by arrows. Water is drawn in between the tentacles and moves on a rejection current upward and away from the animal. Food particles are moved proximally along the tentacles to a food canal indicated by the arrows. (G,H after S. M. Lester. 1985. *Mar Biol* 85: 263–268. https://link.springer.com/article/10.1007/BF00393246)

grow through asexual reproduction by budding. Sexual reproduction involves a swimming, ciliated larva that settles to form a new colony. This pattern is common among small sessile animals, which cannot afford to produce huge numbers of eggs but depend on at least a short-lived dispersal phase.

HEMICHORDATE CLASSIFICATION

The classification presented herein follows the traditional division of the phylum into two classes, Enteropneusta and Pterobranchia.

CLASS ENTEROPNEUSTA Acorn, or tongue worms. Vermiform, with 3 body regions as proboscis, collar, and trunk; coeloms reduced by muscle development; gut elongate, straight; mouth ventral at anterior end of collar; long dorsolateral series of gill slits; dorsal, hollow nerve cord in the collar; anus posterior, terminal; marine, burrow in soft sediments or nestle under rocks or in algal holdfasts; largely intertidal although deep-water species are increasingly being discovered. About 121 described species in 4 families: Harrimaniidae (*Harrimania, Protoglossus, Horstia, Meioglossus, Mesoglossus, Ritteria, Saccoglossus, Saxipendium, Stereobalanus, Xenopleura*); Spengelidae (*Glandiceps, Schizocardium, Spengelia, Willeyia*); Ptychoderidae (*Balanoglossus, Glossobalanus, Ptychodera*); and Torquaratoridae (*Allapasus, Coleodesmium, Tergivellum, Torquarator, Yoda*). The former class Planctosphaeroidea was erected to include *Planctosphaera pelagica*, discovered in 1932, and viewed by most contemporary authorities as the larva of a yet unknown enteropneust.

CLASS PTEROBRANCHIA Pterobranchs. Body sacciform; with 3 body regions as preoral disc (= cephalic shield), tentaculate mesosome, and metasome subdivided as trunk and stalk; neurochord lacking; pharynx with 1 pair of gill slits or none; gut U-shaped; marine; generally small (less than 1 cm), aggregating, or colonial. About 22 species, in 2 families: Rhabdopleuridae (*Rhabdopleura*) and Cephalodiscidae (*Cephalodiscus* and *Atubaria*). The genus *Atubaria* is represented by a single species (*A. heterolopha*), known only from 43 specimens collected in 1935 in Japan. These animals are nearly identical to *Cephalodiscus* but were found as solitary forms, without secreted casings, hence their name. However, they have never been found again, and individuals of *Cephalodiscus* are known to abandon their casing when stressed, making *Atubaria* doubtful as a valid genus and thus currently considered a nomen dubium.

The Hemichordate Body Plan

The two classes of Hemichordata have very different appearances and ways of life: enteropneusts are burrowing, vermiform, solitary animals, whereas pterobranchs are sessile, tube dwelling, and colonial—although both share a common trimeric body plan, attesting to the evolutionary plasticity of their basic deuterostome

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architecture. The hemichordate body is divided into prosome, mesosome, and metasome. The prosome—the enteropneust proboscis and the pterobranch preoral disc or cephalic shield—is joined by a slender peduncle to the mesosome or collar. In pterobranchs, the latter bears two to several arms on which tentacles are located. The metasome or trunk is elongated in enteropneusts and globular to pyriform in pterobranchs, differentiated in the former by the specializations of the gut into branchiogenital, hepatic, and posterior regions, and extended posteriorly in the latter to form a tail or stolon where new individuals form by budding. Diagnostic characters of the phylum also include the presence of a dorsal buccal diverticulum called the **stomochord**; paired gill slits that connect the pharynx to the exterior; a proboscis excretory complex formed by heart vesicle, heart sinus, glomerulus, and proboscis pore; and a dorsal nerve cord in the mesosome. Enteropneusts and pterobranchs look so different and have such different ways of making a living that they are occasionally treated as separated phyla, and we discuss them separately here.

Class Enteropneusta (Acorn Worms)

External Anatomy

Enteropneusts are solitary, elongate, vermiform animals, ranging in length from less than 1 mm to over 2 m. Their bodies are clearly divided into three regions, named **proboscis**, **collar**, and **trunk** (Figure 25.3), homologous with the prosome, mesosome, and metasome of other deuterostomes. The proboscis is short and pyriform to conical. A short, thin proboscis stalk connects the proboscis dorsally to the collar, the latter bearing the ventral mouth at its anterior end. The anus terminates at the posterior end of the long trunk. The trunk bears middorsal and midventral longitudinal ridges that correspond to the locations of certain longitudinal nerves and blood vessels. In addition, the trunk is variably differentiated into regions along its length, mostly by specializations of the gut (Figure 25.3A,B). Most species bear a clear, anterior, branchiogenital region characterized by the presence of two dorsolateral series of gill (= branchial) pores. Gonads also occur along this region, and in species from at least one family (Ptychoderidae) the gonads develop within external longitudinal genital wings (Figure 25.3B). The anterior portion of the intestine shows a dorsolateral series of outpocketings that protrude visibly to the exterior, generally exhibiting a dark greenish color and referred to as the hepatic region. In a number of genera, no clear body subdivisions occur, except for the branchial region.

The epidermis of enteropneusts is formed by tall multiciliated cells, with a basiepithelial nerve plexus. It is usually richly supplied with gland cells, many of which are involved in production of mucus—a very characteristic and abundant secretory product with a distinctive iodine-like odor. Mucus secretion is particularly abundant on the proboscis and collar, where it is involved in trapping food particles for feeding. In some enteropneusts, certain epithelial cells produce noxious mucopolysaccharide compounds that may repel predators.

The epidermis, together with its associated nerve plexus, rests on a well-developed extracellular matrix formed by collagen fibers embedded in a ground substance. The extracellular matrix of the epidermis faces the extracellular matrix of the underlying mesothelium that lines the coelomic cavities. Both extracellular matrices fuse extensively except in places where blood lacunae occur, occupying spaces from blastocoelic origin.

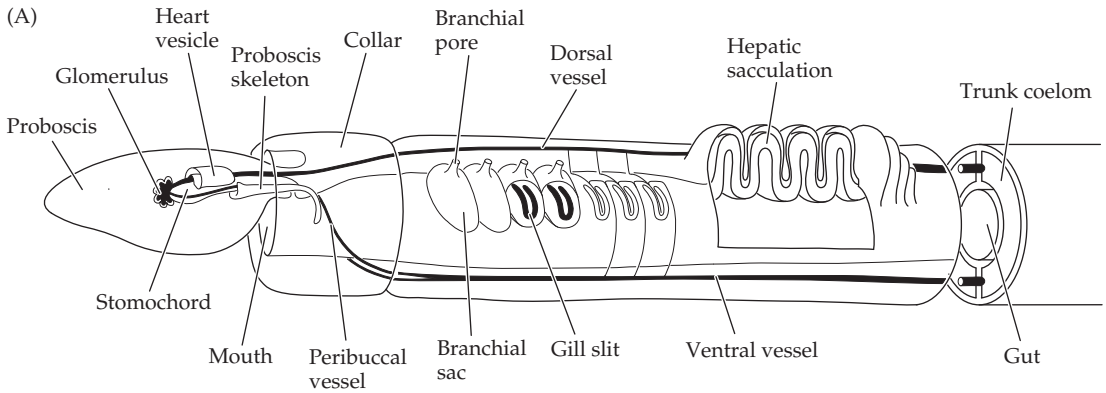
Support Structures

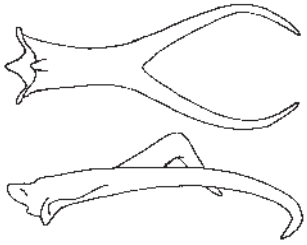
The extracellular matrix is hypertrophied at some locations, forming skeletal supporting structures, namely the **proboscis skeleton** and the **gill bar supporting rods**. The proboscis skeleton is a single piece of cartilage shaped like an inverted *Y*, ventrally juxtaposed to the buccal diverticulum and with the two "horns" or **furcae** directed backward and ventrally to the collar (Figure 25.4A,B). The gill apparatus—bars and slits—are supported by two dorsolateral sets of skeletal, collagenous pieces, each shaped like an elongated trident or *m*. The central rod of the *m* lies inside primary gill bars, while secondary, or "tongue" bars bear two rods from adjacent pieces (Figure 25.4D,E).

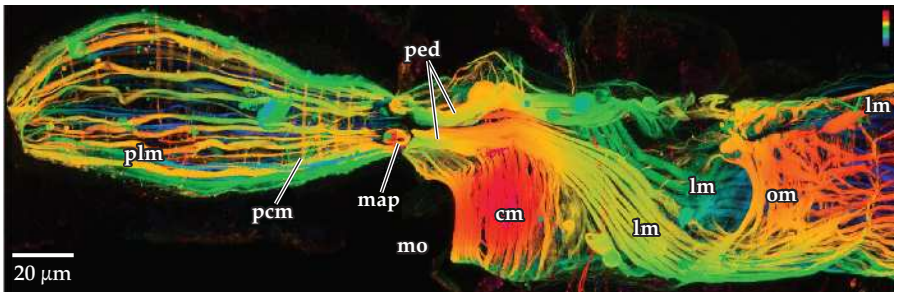
In adult acorn worms, the buccal diverticulum, or stomochord, is a hollow and blind stiff rod formed by a highly vacuolated epithelium. It has a structural, supportive function working to antagonize the contractile pericardium, which pumps blood through the heart and into the glomerulus (Figure 25.4A). Nevertheless, body support is primarily a function of the hydrostatic nature of the body cavities, supplemented by the structural integrity of the body wall, connective tissues, and skeletal structures already described.

Coelomic Cavities

The arrangement of coelomic spaces follows the deuterostome trimeric body plan as a single protocoel in the proboscis and paired mesocoels and metacoels in the collar and trunk. The protocoel is open to the exterior through a single, left pore at the proboscis stalk in most enteropneusts; the mesocoel connects to the first, anterior-most branchial sac through two ciliated ducts, and the metacoel is blind. The metacoel sends two pairs of coelomic extensions with strong musculature into the collar, the so-called **perihemal** and **peribuccal coeloms**, to reinforce support and movement. Contraction of the longitudinal muscle fibers lining these cavities helps to retract the proboscis into the collar, thereby closing the mouth, like inserting a cork in a bottle, and may also help to pump blood into the heart.







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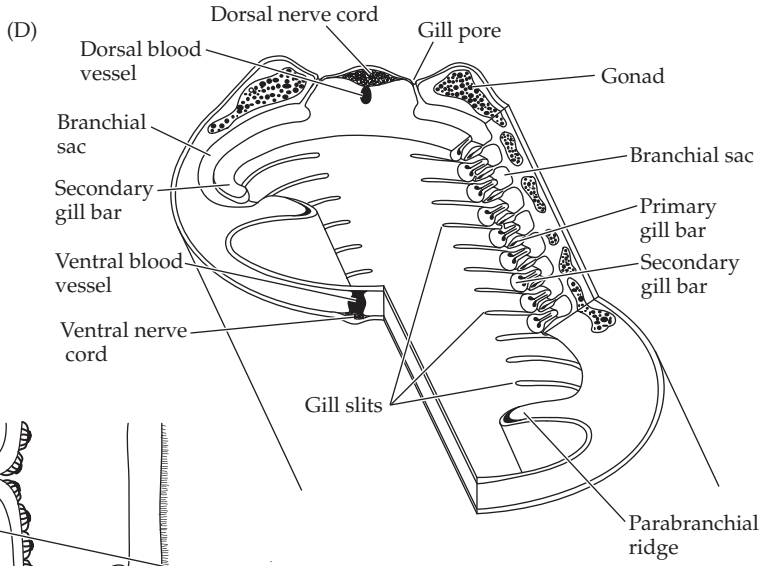

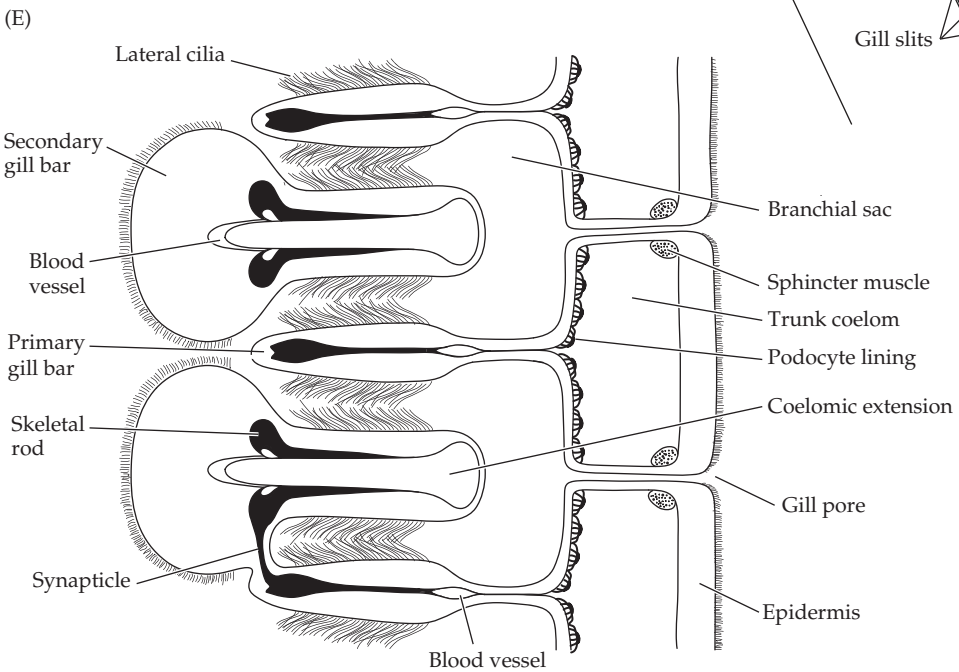

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◀ **FIGURE 25.4 Internal anatomy of enteropneusts.** (A) Internal organization of an idealized acorn worm showing the proboscis complex, gill slits, sacs and pores, hepatic sacculations, and simplified circulatory system. (B) Proboscis skeleton of *Saccoglossus mereschkowskii* in ventral and lateral views. (C) Musculature of proboscis, collar, and anterior trunk of *Meioglossus psammophilus* revealed by confocal laser scanning microscopy (CLSM); phalloidin staining, depth coded. Depth scale follows the colors of spectral light (blue to red); cm: circular muscles; lm: longitudinal muscles; map: muscular anchoring point; mo: mouth opening; om: oblique muscles; pcm: proboscis circular muscles; ped: perihemal diverticula. (D) 3-D reconstruction of the pharynx system of a ptychoderid enteropneust. (E) Detail of the organization of primary and secondary gill bars, branchial sacs, and pores.

Musculature and Locomotion

The musculature of enteropneusts derives from mesothelial linings of coelomic spaces. The arrangement of myofibrils is mostly of the smooth type. Both circular and longitudinal muscles are present in the wall of the proboscis and anterior collar of acorn worms, accounting for peristaltic movements in crawling or burrowing, but elsewhere only longitudinal fibers predominate (Figure 25.4C). Although most enteropneusts are probably strictly benthic and largely sedentary, at least one species (*Glandiceps hacksi*) sometimes swarms at the surface in shallow water, where it feeds on phytoplankton. Recent videotaping of torquaratorid enteropneusts from the deep sea show the animals detaching from the seafloor and entering the water column, presumably to be transported by currents to a new location.

Feeding and Digestion

The digestive tract of enteropneusts is a straight, regionally specialized tube extending from the mouth to the anus. Gut musculature is scant, and the food is moved along largely by cilia. The mouth leads to a buccal cavity inside the collar and can be closed by retraction of the proboscis against the latter. A buccal diverticulum or stomochord projects forward from its roof into the proboscis stalk. The pharynx follows the buccal cavity in the anterior part of the trunk. The pharynx bears two dorsolateral series of gill slits separated by a low, middorsal epibranchial ridge. Two lateral parabranchial ridges divide the pharynx of ptychoderids into a dorsal branchial chamber and a ventral, digestive chamber (Figure 25.4D). The gill slits number from 1 pair (e.g., *Meioglossus*) to over 100 pairs. Each is a U-shaped opening in the wall of the pharynx that leads to a branchial sac and then to a dorsolateral gill pore through which water exits to the outside (Figure 25.4A,D). A septum between adjacent gill slits is a **primary gill bar**, and the partition between the arms of the U of each slit is a **secondary gill bar** or tongue bar. Primary bars are solid, whereas tongue bars contain an extension of the trunk coelom (Figure 25.4E). Both primary and secondary bars are supported by skeletal elements derived from the basement membrane of the gut lining and are supplied with a complex arrangement of blood vessels and sinuses. Short bridges called **synapticles** join the pharyngeal edges of primary and secondary gill bars in the family Ptychoderidae, undoubtedly contributing to the structural stability of the entire gills (Figure 25.4E).

Behind the pharynx is an esophagus, which at least in some (e.g., *Saccoglossus*) bears openings to the outside through the dorsal body wall, probably to eliminate excess water. In most species the wall of the anterior intestine folds deeply, forming two series of dorsolateral outpocketings that protrude visibly to the exterior in *Schizocardium* and the family Ptychoderidae (Figures 25.3B and 25.4A); the gut epithelium is full of dense green or brown inclusions that give a characteristic aspect to this hepatic region of the trunk. The intestine extends, more or less undifferentiated, to a short rectum terminating in the anus. The anus is dorsal in juveniles of harrimaniids, leaving behind it a postanal region.

Enteropneusts are generally assumed to be deposit feeders, in some cases sedimentivorous (ingesting the substratum [*Balanoglossus*]) or detritivorous (trapping food particles from the sediment surface [*Saccoglossus*]). Others tend to be suspension or filter feeders that create ciliary currents to drive water with suspended particles into the gut. In fact, both classical and recent studies show that most species are probably capable of feeding by both methods—deposit and filtering—even simultaneously. Food material, including detritus and live organisms, is trapped in mucus secreted over the surface of the proboscis and moved posteriorly by ciliary currents (Figure 25.5). The sorting occurs at the proximal end of the proboscis, and the stalk passes most large particles over the lip of the collar; these particles are then removed by special rejection currents. Most of the food is moved ventrally around the proboscis stalk, over a horseshoe-shaped structure called the **preoral ciliary organ**, and condensed into a mucous cord that is then passed into the inhalant flow of the mouth. The preoral ciliary organ

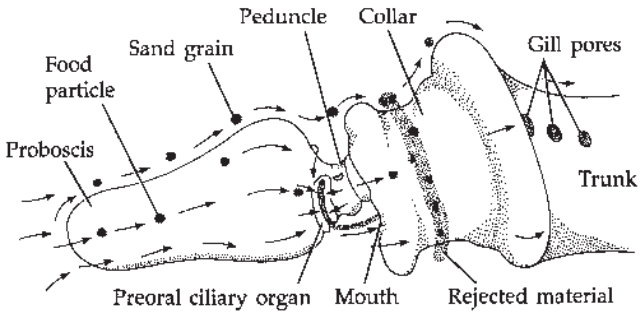

FIGURE 25.5 Food sorting and rejection currents (arrows) on the proboscis and collar region of the enteropneust *Protoglossus koehleri*.

includes a concentration of sensory neurons and probably also functions in chemoreception. The inhalant water current is powered by the long lateral cilia of the gill bars, leaving the body through the branchial sacs and gill pores. Particles of adequate size are retained by pharyngeal mucus and transported ventrally to form a mucus-food cord that is directed posteriorly. The esophagus squeezes excess water from the food. Digestion and absorption of nutrients take place at the hepatic sacculations, first extracellularly in the most anterior diverticuli and then intracellularly in the posterior ones, whose cells store wastes and also transport nutrients to the subjacent blood sinuses. Sedimentivorous species leave characteristic sediment casts outside their U-shaped burrows (Figure 25.3C,D).

Circulatory System

Enteropneusts possess a well-developed, partly open circulatory system of blood vessels and sinuses. The blood is pumped both by contractile cells in the walls of blood spaces by the muscular action of the perihemal coeloms in the collar, and by a contractile heart vesicle located in the proboscis (Figure 25.4A). Two main longitudinal vessels lie in the dorsal and ventral mesenteries along the length of the trunk and in the collar (Figure 25.4A,D). Blood flows anteriorly in the **dorsal vessel** and posteriorly in the **ventral vessel**. The dorsal vessel expands in the collar as the venous sinus, which also receives blood anteriorly from a pair of lateral proboscis veins. The venous sinus leads to a larger, elongate, central sinus or heart in the proboscis, lying between the buccal diverticulum and the dorsal **heart vesicle**. The heart vesicle is a closed cavity of ectodermal origin with myoepithelial walls, whose contraction presses the central sinus against the stomochord below. This sends the blood to the excretory glomerulus in the protocoel with an increased pressure to facilitate ultrafiltration of metabolic waste. The glomerulus, buccal diverticulum, heart, and heart vesicle comprise what is often referred to as the **proboscis complex** of enteropneusts (Figure 25.4A). Blood leaves the glomerulus through two peribuccal vessels that join midventrally to form the ventral longitudinal vessel. Along the trunk, blood passes from the ventral vessel into networks of sinuses supplying both the gut and the body wall. In the pharynx, gut ventral sinuses drain into two lateral parabranchial vessels that send vessels dorsally into primary gill bars. After branching ventrally into secondary bars, these send a vessel dorsally to reach the median trunk dorsal vessel. Enteropneust blood is colorless or pale pink. The pinkish pigment particles are carried in solution and correspond in size to hemoglobin, although that pigment has yet to be confirmed in hemichordates. The blood also contains few amebocyte-like cells.

Excretory System

The main excretory organ in enteropneusts is the **glomerulus**, a structure unique to the hemichordates. It is formed of fingerlike outpocketings of protocoelic mesothelium associated with blood sinuses. Mesothelial cells are differentiated as podocytes, a cell type specialized for ultrafiltration. Pressed by the contraction of the pericardium or heart vesicle, the blood leaving the heart or central sinus is forced to pass through the glomerular sinuses, where metabolic wastes are filtered through the podocyte lining to the protocoel cavity. The primary urine is then presumably evacuated through the protocoel pore, located on the proboscis stalk in most species. Podocyte cells also line the walls of branchial sacs, suggesting a supplemental excretory role for the pharynx.

Gas Exchange

Gill bars have long been thought of as the place of gas exchange, a hypothesis undoubtedly biased by our understanding of chordate gills. However, the epithelial structure of gill bars makes the hypothesis unlikely. Little work has been done on the matter of gas exchange, and it may be that other structures, such as the branchial sacs or the body surface, are also involved in this activity.

Nervous System

Most of the nervous system of hemichordates consists of a netlike, intraepithelial/basiepidermal nerve plexus lying among the bases of the epithelial cells, both of ectodermal (epidermis) and endodermal (gut) origin. In enteropneusts this plexus is thickened, forming longitudinal tracts of neurons along the middorsal and midventral lines of the trunk (hence both dorsal and ventral, intraepithelial/basiepidermal longitudinal nerve cords are present) and at the base of the proboscis. Additionally, a subepidermal (not intraepidermal) dorsal cord, or **collar neurochord**, is present in the mesosome, and its cellular organization and ontogenetic neurulation process have led to comparisons with the chordate neural tube.

Acorn worms possess sensory cells over most of the body, probably serving as touch receptors, chemoreceptors, and photoreceptors that give these cryptic animals some information about their surroundings. As mentioned earlier, they also bear a preoral ciliary organ with a presumptive chemoreception function for feeding.

Reproduction and Development

Asexual reproduction Asexual reproduction in enteropneusts is directly related to their well-known ability to regenerate tissues and body parts that are lost or damaged. They are very fragile worms and easily

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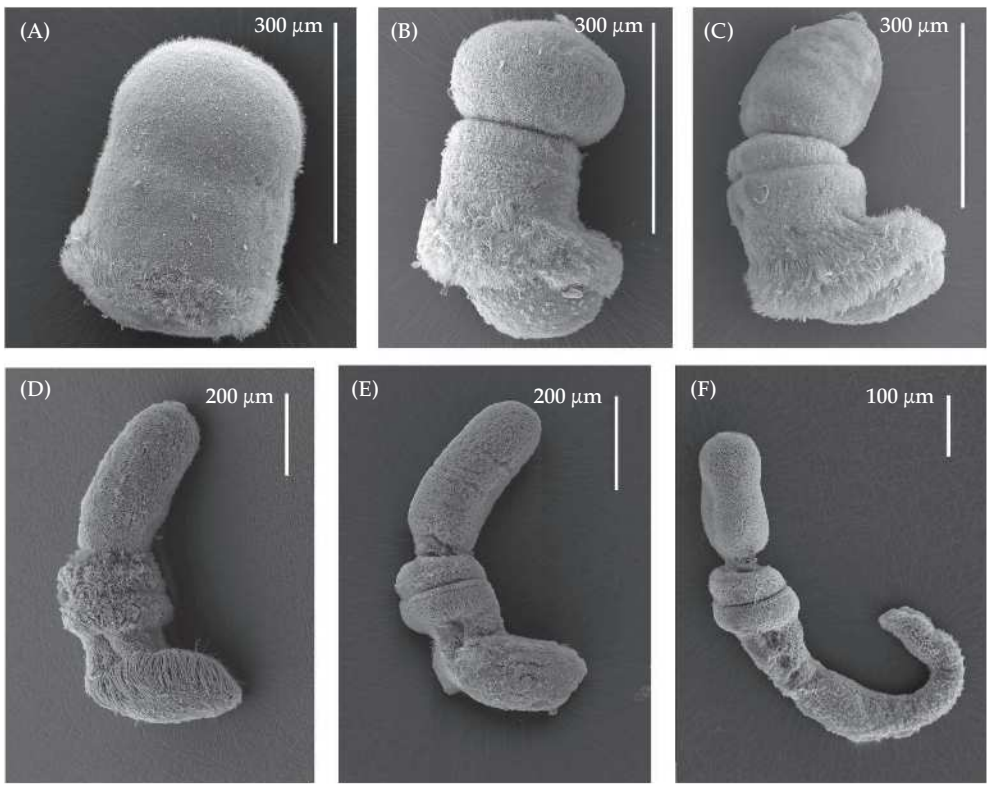
break when handled. Acorn worms have been described to undergo multiple transverse fissions of the body (**architomy**), leading to several regenerating individuals. Recently, **paratomy** has been described in the interstitial species *Meioglossus psammophilus*, in which new individuals develop aligned to the body axis through tissue regeneration and subsequent transverse fission, a process well known in Annelida and Acoela.

Sexual reproduction Acorn worms are gonochoristic but possess no outward evidence of sexual differences. Numerous sacciform gonads lie in the trunk, outside the mesothelium (retroperitoneal), from the branchial region to the hepatic one; they are often very elongate, and in the family Ptychoderidae they occupy two dorsolateral, flaplike extensions of the body called **genital wings** (Figure 25.3B). Each gonadal sac opens to the exterior through a duct and gonopore located dorsolaterally on the anterior trunk.

Fertilization is always external. Spawning in enteropneusts involves the release of mucoid egg masses by the females, followed by shedding of sperm by neighboring males. Once the eggs are fertilized, the mucous coat breaks down, thereby freeing the eggs into the seawater, where all subsequent development occurs. In some direct developers, eggs are shed into the burrow of the female, lining the walls, and all development occurs within the burrow and contained in the vitelline envelope, with hatching releasing competent juvenile worms.

Development Cleavage is holoblastic, radial, and more or less equal, attesting to the deuterostome nature of acorn worms. A coeloblastula forms, which gastrulates by invagination. The blastopore is at the presumptive posterior end, but it closes and the anus and mouth form later. In indirect-developing species, at late gastrula the embryo has acquired cilia and hatches from the vitelline membrane. Coelomic cavities (the single protocoel plus paired meso- and metacoels) derive from the archenteric endoderm as independent pouching through enterocoely. In direct-developing species the coeloms all form during embryogenesis, whereas in indirect developers only the protocoel forms during embryogenesis, and the mesocoels and metacoels form late in larval development before the onset of metamorphosis. Other morphogenetic modes, including schizocoely, have been doubtfully reported in some species.

Some species (Harrimaniidae, e.g., *Saccoglossus*) have direct development from yolky eggs to juvenile worms, without an intervening larval phase (Figure 25.6A–F).



A–C from S. Kaul and T. Stach. 2010. *J Morphol* 271: 1240–1259. © Wiley Periodicals, LLC. Courtesy of Sabrina Kaul-Strehlow

D–F courtesy of Sabrina Kaul-Strehlow

FIGURE 25.6 Enteropneust development. (A–F) Direct development of *Saccoglossus kowalevskii*. (A) Early embryo/larva, 36 hours after fertilization. (B) Differentiation of proboscis and collar, 56 hours after fertilization. (C) Formation of the dorsal neural fold (neurulation), 132 hours after fertilization. (D–F) Juveniles, 156, 340, and 750 hours after fertilization. Note dorsolateral gill pores behind the collar in F.

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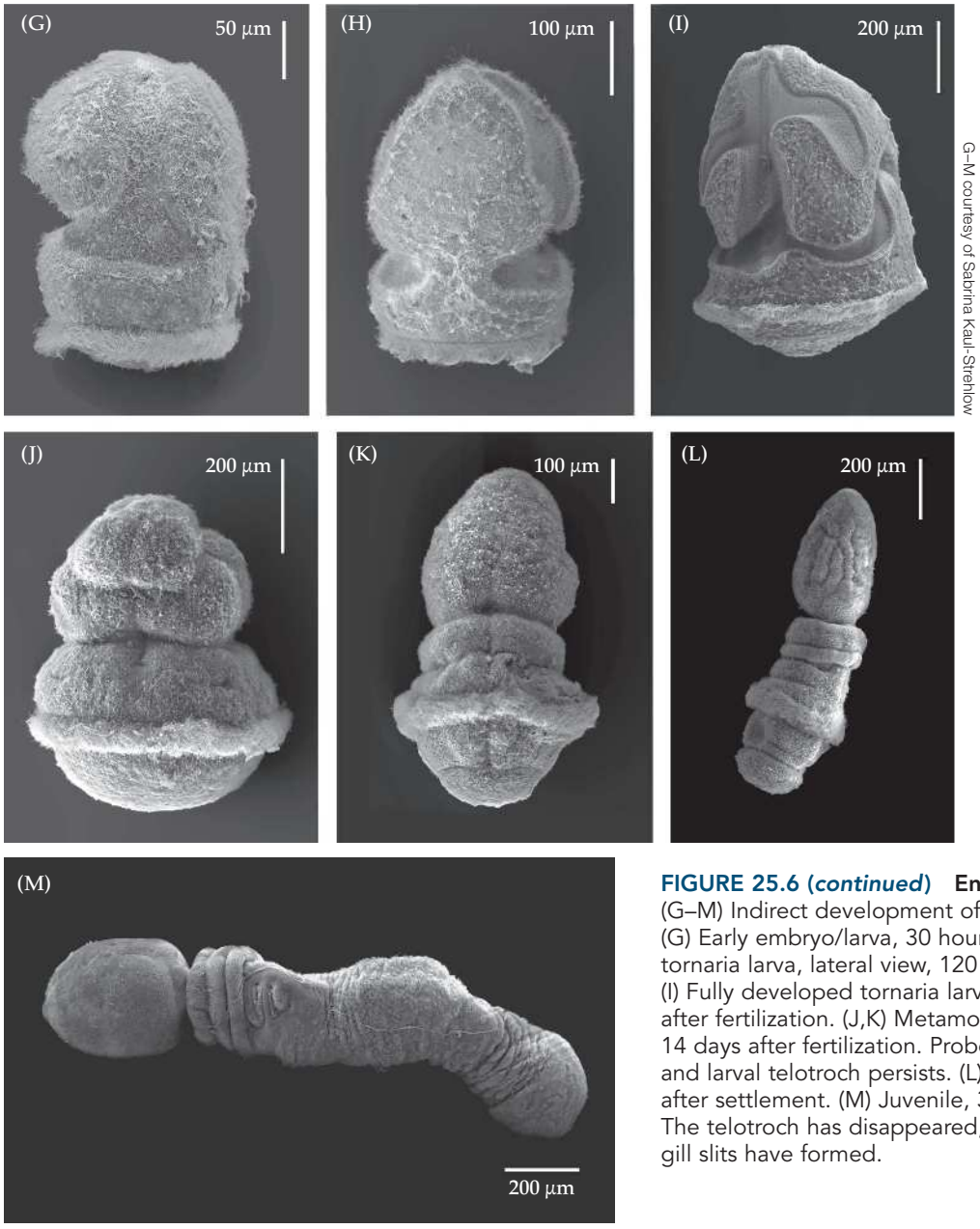

G–M courtesy of Sabrina Kaul-Strehlow

FIGURE 25.6 (*continued*) Enteropneust development. (G–M) Indirect development of *Balanoglossus misakiensis*. (G) Early embryo/larva, 30 hours after fertilization. (H) Early tornaria larva, lateral view, 120 hours after fertilization. (I) Fully developed tornaria larva, ventral view, 10 days after fertilization. (J,K) Metamorphosis of tornaria, 13 and 14 days after fertilization. Proboscis and collar are formed, and larval telotroch persists. (L) Early juvenile, 12 hours after settlement. (M) Juvenile, 3 days after settlement. The telotroch has disappeared, and the first two U-shaped gill slits have formed.

Juvenile worms show a postanal tail that is likely to be homologous not with the chordate postanal tail despite some molecular patterning similarities, but most probably with the pterobranch stalk. In species that shed nonyolky eggs (Ptychoderidae, e.g., *Balanoglossus*), the hatching stage develops quickly to a characteristic, planktotrophic, **tornaria larva** with complex ciliary bands reminiscent of the dipleurula larva of echinoderms (Figure 25.6G–I). This free-swimming tornaria can spend weeks to months in the plankton feeding and growing. By the end of larval development, rudimentary gill pouches in the anterior larval pharynx have formed along with the two posterior coeloms. A radical metamorphosis begins with expansion of the protocoel and migration of the anterior gut posteriorly. Molecular patterning data demonstrate that the larval body plan represents essentially a "swimming head," with no trunk territory. During metamorphosis the posterior of the larva expands to create the trunk of the adult body plan. The elongating larva soon sinks to the benthos and differentiates the three typical body regions and organs (Figure 25.6J–L). Gill slits develop asymmetrically—left side first, from anterior to posterior—as outpocketings of the gut that eventually open to the exterior via dorsolateral gill pores (Figure 25.6M).

Class Pterobranchia (Pterobranchs)

The bodies of pterobranchs are small, usually pyriform or globular, but still retaining the ancestral tripartite regional division. The prosome in these odd creatures, called the **preoral disc** or **cephalic shield**, is a creeping

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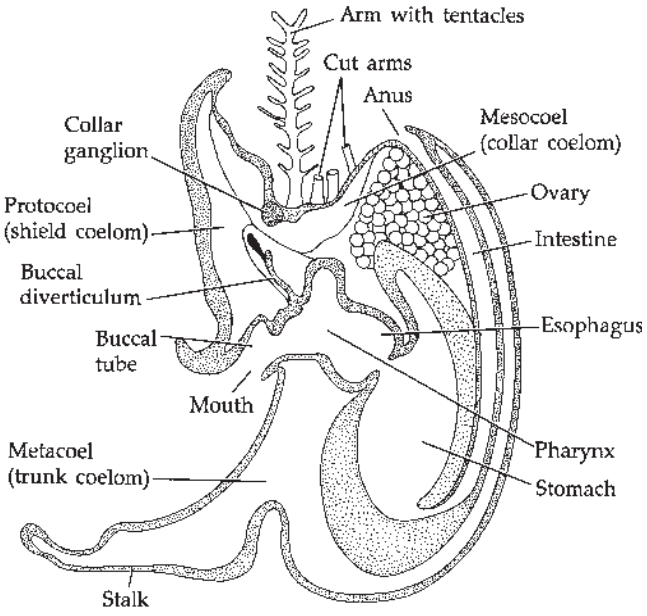

FIGURE 25.7 **Internal anatomy of the pterobranch *Cephalodiscus* (sagittal section).**

sole that folds ventrally over the mouth. The mesosome forms a collar that bears the anteroventral mouth and extends dorsally as one pair to nine pairs of tentaculated arms. The gut is U-shaped, and the anus opens anterodorsally (Figures 25.3G,H and 25.7). The metasome is subdivided into a trunk and posterior stalk.

Pterobranchs live in colonies (*Rhabdopleura*) or aggregations (*Cephalodiscus*) consisting of zooids housed within tubular secreted casings called **coenecia** (Figure 25.3E,G). In colonies of *Rhabdopleura*, the zooids are connected to one another by tissue extensions called **stolons** (Figure 25.3E), but no such interzooidal links occur in *Cephalodiscus*. The overall forms of the aggregations and colonies vary among species. In all cases, the associated zooids are products of asexual reproduction initiated by a single sexually produced individual.

Body Wall and Cavities

The pterobranch epidermis is very simple, composed of squamous cells. Only at the cephalic shield does the epidermis become high and glandular, with several types of secretory cells that produce materials for the coenecium and mucus for gliding. Coelomic spaces follow the trimeric body pattern, with a single protocoel in the cephalic shield, and paired meso- and metacoels in the collar and trunk. The protocoel opens to the exterior via two coelomic ducts and pores at the bases of the arms. The mesocoel penetrates into the arms and tentacles, and in *Cephalodiscus* it sends two collar canals posteriorly that open to the exterior, close to the single gill pore. The metacoel has no openings. No gills or pores have been identified in *Rhabdopleura*.

Support, Muscles, and Movement

The small size of pterobranchs correlates with a dramatic reduction of supporting structures. The proboscis skeleton is lacking, and the single gill opening of *Cephalodiscus* has no supporting rods. Moreover, the pterobranch stomochord is nearly solid and lacks vacuolated cells. Most body support and protection are provided by the secreted outer casing of the colony or aggregation. Pterobranchs possess only longitudinal muscles, in the ventral side of the trunk and stalk and in the cephalic shield, where they are well developed for crawling within their tubes. The protraction and retraction of individuals within their tubular houses are accomplished by hydrostatic pressure and contraction of longitudinal muscles, respectively.

Gut and Feeding

The mouth is located under the anteroventral edge of the collar. The gut is U-shaped, beginning with a buccal tube from which a buccal diverticulum arises dorsally. The pharynx bears one pair of gill slits in *Cephalodiscus*, but none in *Rhabdopleura*. When present, the gill apparatus is much simpler than that of enteropneusts, with no secondary bars nor supporting structures and less defined branchial sacs. The slits open through pores on the exterior. A short esophagus connects the pharynx to a sacciform stomach that occupies most of the space within the trunk (Figure 25.7). The ascending portion of the gut is the intestine, which leads anteriorly to the dorsal anus.

Feeding in pterobranchs is accomplished by the mesosomal arms; two pairs of arms in *Rhabdopleura*, one to five pairs in *Cephalodiscus* (depending on the species) (Figure 25.3F,H). Each arm bears two rows of ciliated tentacles. Pterobranchs are ciliary mucus suspension feeders. During feeding, they assume a position near an opening in the tubular case and extend their arms into the water; *Rhabdopleura* simply spreads its two featherlike arms out into the water current, whereas *Cephalodiscus* forms a so-called "feeding sphere" with its eight to ten arms and interdigitating tentacles (Figure 25.3F,H). Suspended particles and diatoms are trapped in the tentacular mucus and moved to the mouth by the action of cilia on the tentacles and arms. The single pair of gill slits of *Cephalodiscus* eliminates the excess water entering the mouth. Digestion occurs in the stomach and intestine, well supplied by blood sinuses.

Circulation and Gas Exchange

The circulatory system of pterobranchs is a reduced and simplified version of that of enteropneusts. There is a heart or central sinus and a heart vesicle associated with the buccal diverticulum and a glomerular vessel, which

have the same functions as the proboscis complex in enteropneusts. Dorsal and ventral vessels are present in the trunk, continuing into the stalk. Otherwise, the circulatory system is reduced to a net of basiepithelial lacunae.

It is quite improbable that the single pair of gill slits in *Cephalodiscus* actually aids in gas exchange; instead, the small diffusion distances throughout the body probably allow general cutaneous exchange, especially over the high surface areas of the tentacles exposed to water currents.

Nervous System

Little is known about the nervous system of pterobranchs. A neuronal concentration in the mesosome named the **collar ganglion** is the putative homologue of the collar neurochord of enteropneusts, giving off branches to the cephalic shield, gill openings, and tentacular system. Otherwise there is a simple intraepithelial/basiepidermal nerve net all along the body. Eyes are present in tornaria larvae. Touch receptors are presumably present in the tentacles.

Reproduction and Development

As in most colonial invertebrates, asexual reproduction by budding is an integral part of the life history of aggregating and colonial pterobranchs. In *Cephalodiscus*, the buds arise from near the base of stalks of adult individuals and may eventually detach from one another when mature, living as an aggregation of individuals (Figure 25.8). Budding in *Rhabdopleura* occurs along the stolons that grow from the tips of the stalks of adult zooids. However, in this genus, buds never detach from the mother zooids, thereby forming colonies. In both genera, the aggregations or colonies arise by budding after the formation of a single sexually produced individual.

Sexes are usually separate, although hermaphroditism has been reported in *Cephalodiscus*. Gonads are single in *Rhabdopleura* and paired in *Cephalodiscus.* In *Rhabdopleura* a single pore opens on the right side of the trunk; the gonopores of *Cephalodiscus* are at the base of the arms. The eggs are shed into the tubes of the colony or aggregation, where they are fertilized. Developing embryos are brooded within the coenecium. Among the pterobranchs, only *Rhabdopleura* has been studied embryologically, and even here the details are scanty. The large yolky eggs undergo radial, holoblastic, subequal cleavage. There is some argument about the precise nature of gastrulation. Coelom formation is classically reported to occur by archenteric pouching, but the sequence of production is not clear. However, more recent work on pterobranchs has raised the possibility that the meso- and metacoel may arise via schizocoely. The embryos escape the brooding area within the parental tube in a fully ciliated (but unnamed) planula-like larval stage. The swimming larvae settle within 24 hours after being released from the parental tube, although cultured larvae have remained swimming and unmetamorphosed for several months. The settled larva surrounds itself with a translucent, sealed cocoon within which it undergoes metamorphosis. First the oral shield is developed, followed by budding of the arms, posterior stalk, and tentacles. The formation of the gut, the last structure to become functional, begins with invagination of ectoderm to form the pharynx. The larva does not feed during metamorphosis. The metamorphosed juvenile builds a tube at an opening in the cocoon and begins to feed and secrete the coenecium for a new colony.

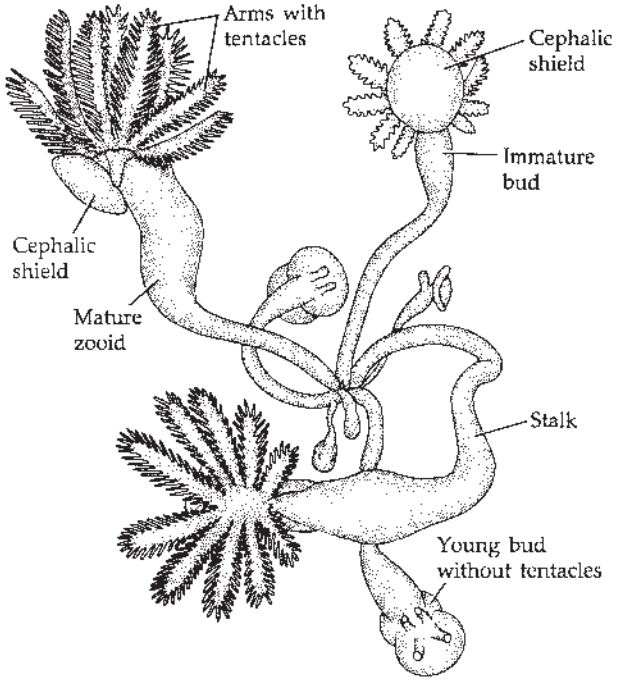

FIGURE 25.8 Budding in the pterobranch *Cephalodiscus*, showing zooids at different stages of development. (After S. M. Lester. 1985. *Mar Biol* 85: 263–268. https://link.springer.com/article/10.1007/BF00393246)

Hemichordate Fossil Record and Phylogeny

The hemichordate fossil record is almost entirely dominated by pterobranchs (notably the graptolites) whose tube skeletons have been well preserved. In fact, a recent study considers *Rhabdopleura* as just an extant graptolite, these being the sister taxon of cephalodiscids. Owing to their low preservational potential, fossil enteropneusts are exceedingly rare, although some fossil genera have been described (*Mazoglossus, Megaderaion, Mesobalanoglossus*), as well as several other genera from putative trace fossils. Recently several fossil taxa have provided important insights into early hemichordate evolution. The fossil enteropneusts

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Spartobranchus tenuis and *Oesia disjuncta* have been described from the middle Cambrian Burgess Shale, surprisingly associated with tubular casings. This finding complements the very recent discovery of deep-sea torquaratorid enteropneusts that build mucous tubes. Even more novel is a very recent finding of *Gyaltsenglossus senis*, another middle Cambrian fossil with characteristic soft-bodied features that define both pterobranchs and enteropneusts: notably, a proboscis and feeding tentacles emanating from the mesosome.

Two very different views have existed for the relationship between enteropneusts and pterobranchs. The classical one, based on morphology and paleontology, considered these taxa sister groups, usually ranked as classes. However, early 18S rRNA analyses suggested that pterobranchs might be an ingroup of the enteropneusts, which would make Enteropneusta paraphyletic and Pterobranchia a sister taxon to the family Harrimaniidae. But subsequent phylogenomic analyses have supported the classical view of the sister-group status of the two classes.

Since their discovery, hemichordates have played a pivotal and controversial role in the attempt to understand relationships among the three major deuterostome phyla (echinoderms, hemichordates, and chordates), as well as attempts to learn the nature of the deuterostome ancestor and to determine the evolutionary origin of chordates. Bateson coined the phylum name Hemichordata after recognizing similarities with chordate embryogeny, and for many years the hemichordates were actually ranked as a subphylum of Chordata. Hemichordate traits such as the presence of stomochord, collar neurochord, and gill slits also reinforced their phylogenetic proximity to chordates. However, current thinking is that the only morphological homology robustly supported by both anatomical and molecular data is the presence of gill slits. Hemichordate pharyngeal gill slits are used for filter feeding in the same way gill slits are used by cephalochordates, and they express the same early patterning genes as all chordates. In addition, a genomic analysis from Simakov and colleagues in 2015 showed that hemichordates and chordates even share the same chromosomal clustering of key pharyngeal patterning genes. These genes have also now been described even in echinoderms, supporting the view that gill slits arose in the stem lineage that gave rise to the Deuterostomia.

On the other hand, a close relationship with echinoderms has also been proposed through characters such as the excretory heart-kidney system and the tornaria-dipleurula larvae. Currently, a sister-group relationship between hemichordates and echinoderms (a clade called Ambulacraria) is generally favored and fairly consistently supported by molecular phylogenetic analyses.

The search for a deuterostome ancestor classically invoked an organism reminiscent of a solitary pterobranch zooid, influenced by the assumed position of pterobranchs as basal hemichordates. However, modern analyses, both morphological and molecular, and in good agreement with fossil findings, suggest that the deuterostome ancestor was a solitary enteropneust-like worm. Considerations of larval forms also agree with this hypothesis. The tornaria-dipleurula larva is shared by echinoderms and the enteropneust ptychoderids. In contrast, harrimaniids and pterobranchs have a very short-lived, nonfeeding larva and are usually considered to be direct developers. Recent findings of miniaturization (*Meioglossus*) and tube dwelling (*Spartobranchus* and Torquaratoridae) in enteropneusts illustrate the evolutionary plasticity of the enteropneust body plan.

Chapter Summary

This chapter introduced you to the bilaterian clade Deuterostomia, which contains just three phyla: Hemichordata, Echinodermata, and Chordata. This clade is defined primarily by molecular phylogenetic evidence, although enterocoelic development leading to a trimeric condition of the coelomic cavities is unique to the deuterostomes and might be a synapomorphy (though it is lacking in Chordata). The small phylum Hemichordata (about 130 described species) is exclusively marine and occurs worldwide at all depths. It contains two classes, Enteropneusta (acorn, or tongue, worms) and Pterobranchia (pterobranchs). Most enteropneusts have radial cleavage and free-swimming, planktonic tornaria larvae; adults are solitary vermiform animals, ranging in length from less than a millimeter to over 2 m. Pterobranchs are colonial, tube-dwelling creatures that also typically have swimming larvae. Adults in both groups have gill slits or gill pores, have an adult body of three regions, and rely on ciliary-mucus feeding, either from the sediment or by capturing particles out of seawater. Although modern phylogenetic analyses strongly suggest the two classes are sister groups, they are so different in appearance that some workers have, in the past, treated them as separate phyla. Owing to their low preservational potential, fossil hemichordates are rare and best represented by the fossilized tubes of certain pterobranchs (notably the graptolites). A sister-group relationship between hemichordates and echinoderms (a clade called Ambulacraria) is generally favored and fairly consistently supported by molecular phylogenetic analyses. Future work on Hemichordata will likely focus on phylogenomics, ecology, and developmental biology.

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CHAPTER 26

Phylum Echinodermata

Starfish, Sea Urchins, Sea Cucumbers, and their Kin

Chapters 8 and 25 introduced the clade Deuterostomia, one of the three great lineages of Bilateria (the others being Protostomia and Xenacoelomorpha). Within the deuterostome clade, molecular, morphological, and paleontological studies now indicate that hemichordates and echinoderms comprise a sister group, a clade called Ambulacraria, and this is the sister group to Chordata. This chapter treats the echinoderms.

Members of the phylum Echinodermata (Greek *echinos*, "spiny"; *derma*, "skin") are familiar to many as iconic sea animals, in part because they are strictly marine and commonly seen along seashores. The phylum contains about 7,300 known living species and includes the sea lilies, feather stars, starfish (or sea stars), brittle stars, sea urchins, sand dollars, heart urchins, and sea cucumbers (Figures 26.1 and 26.2). Another 13,000 to 15,000 or so species are known from a rich fossil record dating back at least to early Cambrian times. Both extant and fossil forms display an enormous breadth of morphological disparity that makes the phylum a particularly interesting group in which to explore the origins of evolutionary novelty.

Echinoderms range in size from minute sea urchins, sea cucumbers, and brittle stars less than 1 cm across, to starfish that exceed 1 m from arm tip to arm tip, and sea cucumbers that exceed 3 m in length. Although some species tolerate brackish water, echinoderms have not evolved excretory, respiratory, or osmoregulatory mechanisms that would allow them to exploit terrestrial or freshwater habitats. However, in the ocean they can be found worldwide at all depths. It is said that echinoderms are largely bottom dwellers (benthic), and it is true that in some regions of the deep sea, the only

This chapter was revised by Rich Mooi.

Classification of The Animal Kingdom (Metazoa)

- PHYLUM PORIFERA
- PHYLUM CTENOPHORA
- PHYLUM PLACOZOA
- PHYLUM CNIDARIA

Bilateria (a.k.a. triploblasts)
- PHYLUM XENACOELOMORPHA

Nephrozoa

PROTOSTOMIA

Spiralia
- PHYLUM DICYEMIDA (=RHOMBOZOA)

GNATHIFERA
- PHYLUM CHAETOGNATHA
- PHYLUM GNATHOSTOMULIDA
- PHYLUM ROTIFERA
- PHYLUM MICROGNATHOZOA

PLATYTROCHOZOA
- PHYLUM ENTOPROCTA
- PHYLUM CYCLIOPHORA

Lophotrochozoa
- PHYLUM MOLLUSCA
- PHYLUM NEMERTEA
- PHYLUM ANNELIDA*

LOPHOPHORATA
- PHYLUM PHORONIDA
- PHYLUM BRYOZOA (=ECTOPROCTA)
- PHYLUM BRACHIOPODA

Rouphozoa
- PHYLUM GASTROTRICHA
- PHYLUM PLATYHELMINTHES

Ecdysozoa

SCALIDOPHORA**
- PHYLUM KINORHYNCHA
- PHYLUM PRIAPULA
- PHYLUM LORICIFERA

NEMATOIDA
- PHYLUM NEMATODA
- PHYLUM NEMATOMORPHA

PANARTHROPODA
- PHYLUM TARDIGRADA
- PHYLUM ONYCHOPHORA
- PHYLUM ARTHROPODA
  - SUBPHYLUM CHELICERATA
  - MANDIBULATA
    - SUBPHYLUM MYRIAPODA
    - PANCRUSTACEA
      - SUBPHYLUM CRUSTACEA***
      - SUBPHYLUM HEXAPODA

DEUTEROSTOMIA
- PHYLUM CHORDATA

AMBULACRARIA
- PHYLUM HEMICHORDATA
- **PHYLUM ECHINODERMATA**

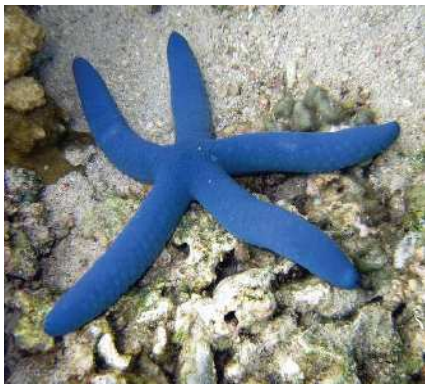
* Annelida includes Sipuncula, Echiura, and Orthonectida

** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent

*** Paraphyletic (excludes Hexapoda)

(A)

Courtesy of R. Mooi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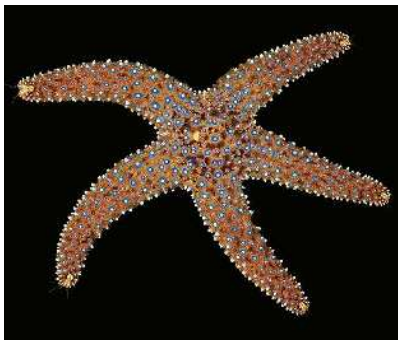
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(D)

Courtesy of P. Fankboner

(E)

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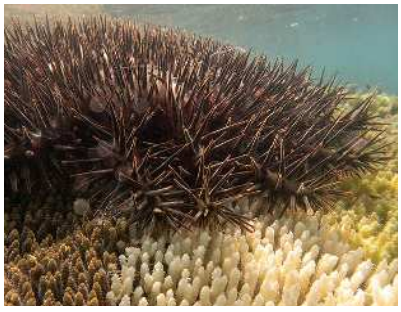

(F)

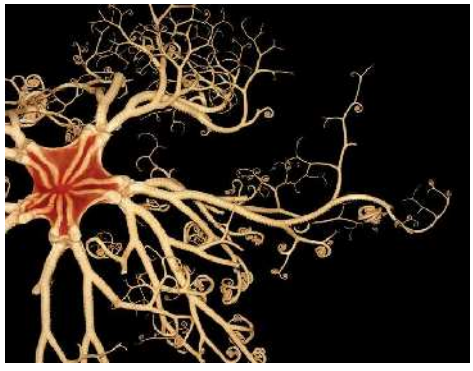
Courtesy of G. Giribet

(G)

Courtesy of T. Gosliner

(H)

Courtesy of P. Fankboner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(J)

Courtesy of A. Kerstitch

(K)

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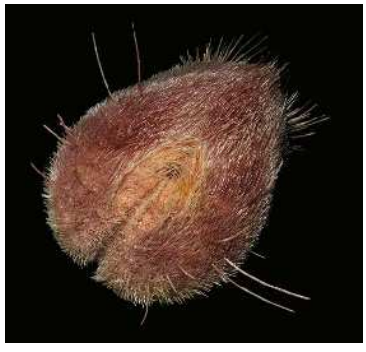
(L)

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identifiable organisms in bottom photos are echinoderms. However, the statement that echinoderms are mostly benthic is true only for the adults (with the exception of a few pelagic and benthopelagic species, see Figure 26.1P,Q), because larval echinoderms are important members of pelagic communities. As larvae, they play important roles in the ecology of planktonic communities, and as adults they perform key roles in benthic marine ecosystems through their deposit and suspension feeding (notably sea cucumbers, sea lilies, and brittle stars), predation (especially certain starfish), herbivorous grazing (many sea urchins), wood eating

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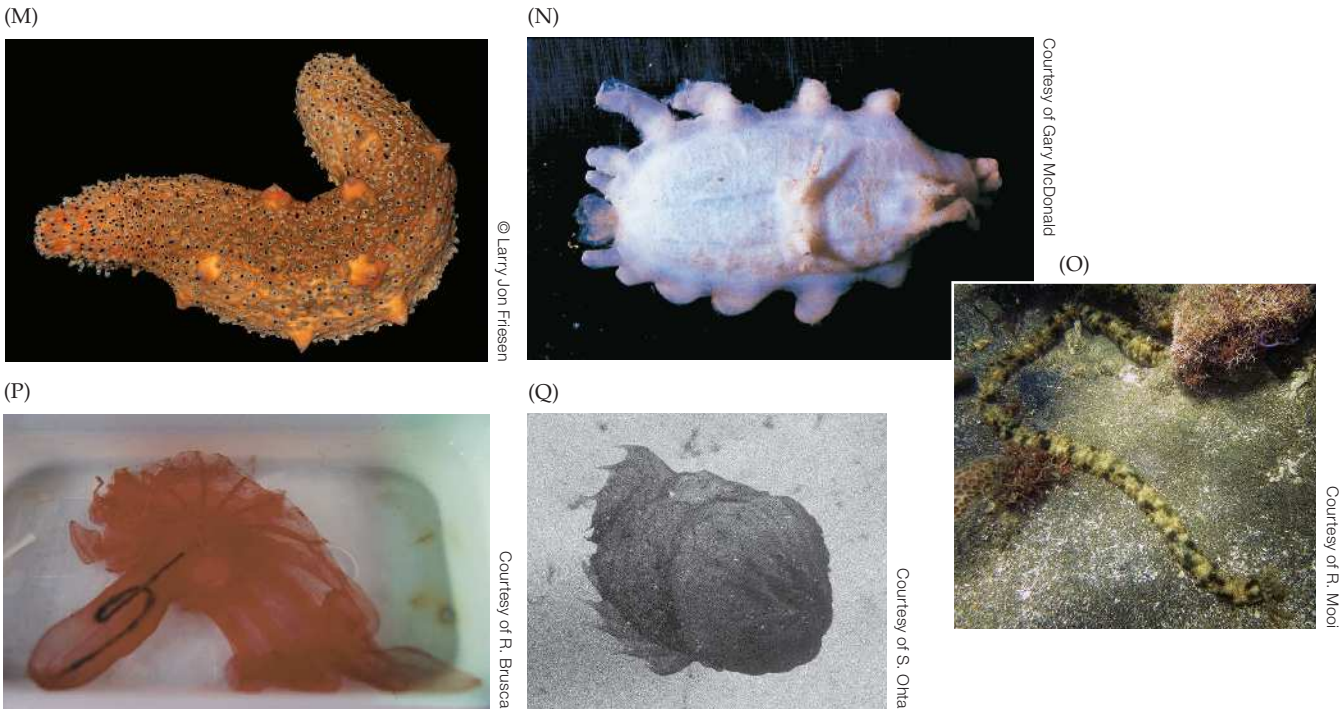


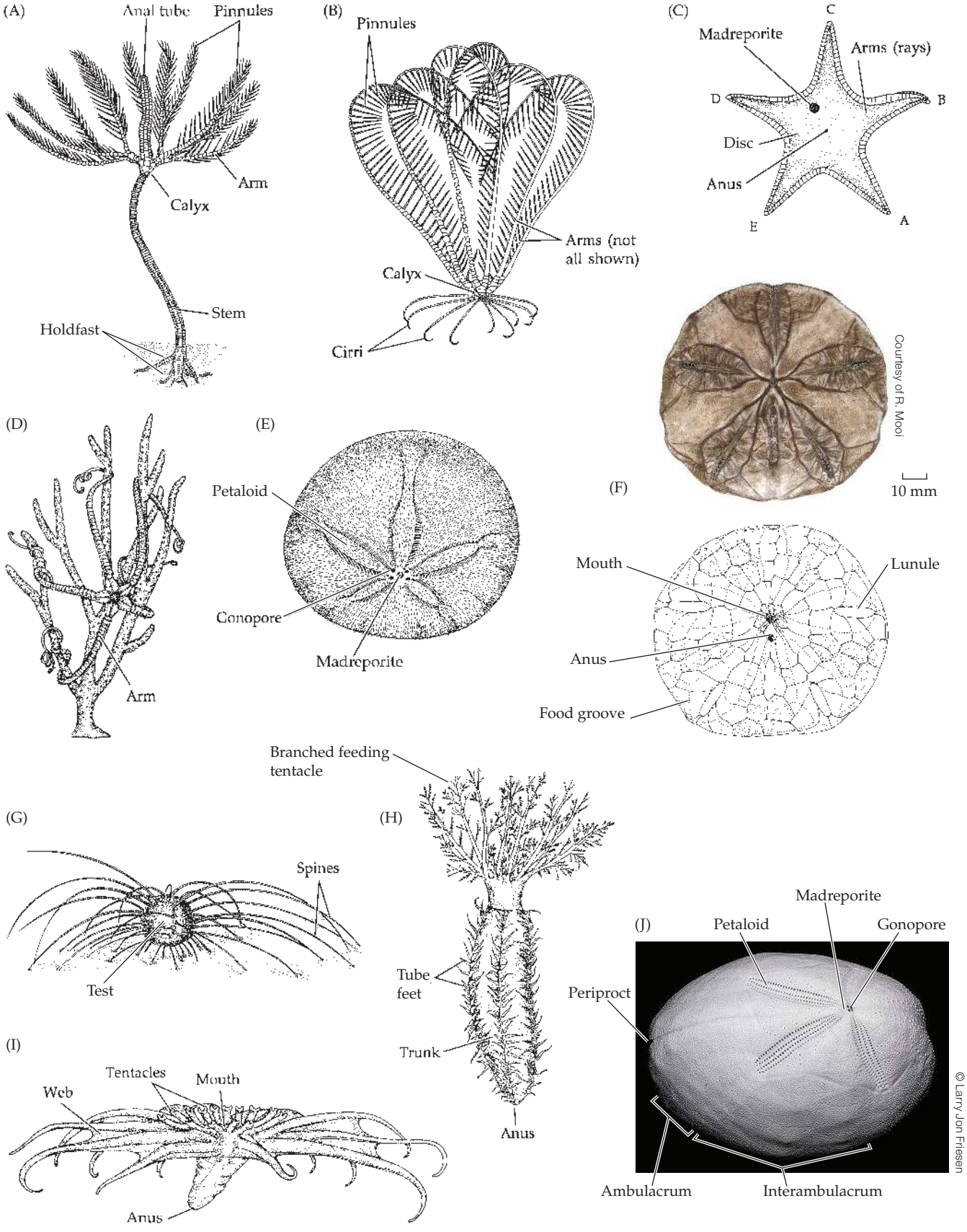
FIGURE 26.1 Representative echinoderms. (A) Feather star (Crinoidea). (B) A tropical starfish, *Linckia laevigata* (Asteroidea). (C) Northeast Pacific starfish, *Pisaster giganteus* (Asteroidea). (D) Northeast Pacific slime star, *Pteraster tesselatus* (Asteroidea) (E) Indo-Pacific cushion starfish, *Culcita novaeguineae* (Asteroidea). (F) Indo-Pacific crown-of-thorns starfish, *Acanthaster planci* (Asteroidea), feeding on coral. Living coral can be seen on the left, the most recent feeding scar is in the middle, and an older feeding scar is on the right. (G) Oral view of caymanostellid "wood star" (Asteroidea). (H) Brittle star, *Ophiopholis aculeata* (Ophiuroidea). (I) Basket star, *Gorgonocephalus* (Ophiuroidea). (J) Purple sea urchin, *Strongylocentrotus purpuratus* (Echinoidea). (K) Indo-Pacific high-intertidal helmet urchin, *Colobocentrotus atratus* (Echinoidea). (L) Heart urchin, *Lovenia elongata* (Echinoidea). (M) Sea cucumber, *Parastichopus* (Holothuroidea). (N) Deep-sea sea cucumber, *Scotoplanes* (Holothuroidea). (O) Apodid sea cucumber, *Synapta* (Holothuroidea). (P) Pelagic holothuroid, *Pelagothuria* (Holothuroidea). (Q) Abyssal swimming holothuroid, *Enypniastes* (Holothuroidea).

(some starfish and sea urchins), and sediment processing and turnover (many sea cucumbers and heart urchins).

Echinoderms are among the most unusual metazoans on Earth. As a body plan, bilateral symmetry is more familiar to us, but the secondarily derived pentaradiality of adult echinoderms challenges our thinking about evolutionary pathways. They have body systems unlike those of any other creatures, and they are missing body parts that it seems they should have. Add in the huge and bizarre fossil catalog, and this phylum can be uniquely challenging to understand. They might seem like mutated leftovers from a Precambrian alien's picnic. In fact, a somewhat complex and unique jargon has evolved just to describe the unlikely anatomy of

BOX 26A Characteristics of the Phylum Echinodermata

1. Calcareous, mesodermally derived endoskeleton composed of separate ossicles and plates made of an open meshwork structure called stereom, with the interstices being filled with living tissue (the stroma)
2. Adults with basic pentaradial symmetry; five rays extending outward from the oral region
3. Embryogeny fundamentally deuterostomous, with radial cleavage, endodermally derived mesoderm, enterocoely, and mouth not derived from the blastopore
4. Body divided into axial, perforate extraxial, and imperforate extraxial regions; axial region expressing radial symmetry derived from the rudiment; extraxial elements derived from the bilateral, larval body
5. With a water vascular system derived from the hydrocoel on left side of larva; composed of complex series of fluid-filled canals expressed externally as tube feet in ambulacra; oldest parts of the ray near the mouth, youngest at ray tips
6. Body wall containing mutable collagenous tissue
7. Gut complete, anus sometimes absent
8. No specialized, distinct excretory organs; excretion through specialized coelomocytes
9. Circulatory structures, when present, consisting of a hemal system derived from coelomic cavities and sinuses
10. Nervous system diffuse, decentralized, consisting of subepithelial nerve net, nerve ring, and radial nerves
11. Mostly gonochoristic; development direct or indirect


(A)
Anal tube
Pinnules
Arm
Calyx
Stem
Holdfast
(B)
Pinnules
Arms (not all shown)
Calyx
Cirri
(C)
C
Madreporite
Arms (rays)
D
B
Disc
Anus
E
A
Courtesy of R. Mooi
10 mm
(D)
Arm
(E)
Petaloid
Conopore
Madreporite
(F)
Mouth
Lunule
Anus
Food groove
Branched feeding tentacle
(G)
Spines
Test
(H)
Tube feet
Trunk
Anus
(I)
Tentacles
Mouth
Web
Anus
(J)
Madreporite
Petaloid
Gonopore
Periproct
Ambulacrum
Interambulacrum
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◀ **FIGURE 26.2 External anatomy of echinoderms.** (A) A fossil crinoid with a stem, *Botryocrinus* (Crinoidea). (B) A feather star, *Neometra* (Crinoidea). (C) Aboral view of *Ctenodiscus* (Asteroidea). Radii labeled according to convention. (D) The brittle star *Asteronyx* (Ophiuroidea) clinging to a gorgonian. (E) Aboral view of the sand dollar *Dendraster* (Echinoidea). (F) Photo and schematic representation of oral view of the sand dollar *Mellita* (Echinoidea). (G) The sea urchin *Plesiodiadema* has extremely long spines for locomotion on sea bottom oozes (Echinoidea). (H) *Cucumaria planci*, a dendrochirotacean sea cucumber (Holothuroidea). (I) A highly modified pelagic sea cucumber, *Pelagothuria* (Holothuroidea). (J) Test of the heart urchin *Brissus latecarinatus* (Echinoidea).

echinoderms, although we will do our best to keep this to a minimum.

All living echinoderms possess some form of a well-developed coelom, a mesodermally derived endoskeleton composed of unique calcareous elements, and five-part radial symmetry (**pentaradiality**). The endoskeleton consists of ossicles and plates formed by microscopic, secreted crystals of calcium carbonate that all orient along the same crystallographic axis. These microcrystals are associated with small amounts of organic tissue and come together to form a unique, porous skeletal material called **stereom**. The stereom consists of anastomosing struts called **trabeculae** that give it a spongelike appearance under high magnification. The hollow spaces in the stereom are occupied by living tissue (the **stroma**). In life, the ossicles and plates are attached to one another by connective tissues. Even earliest fossil echinoderm skeletons have been shown to have this unique form of mineralization in their endoskeleton.

As adults, echinoderms are the only fundamentally five-part, radially symmetrical animals, though this symmetry is modified in some lineages. Because echinoderms are deuterostome bilaterians, their embryology is frequently studied as exemplary of deuterostomy. However, these basic embryological patterns are true only of early, bilaterally symmetrical stages of echinoderm development. The remarkable pentaradial body plan is superimposed on earlier larval bilaterality, and echinoderm adult pentaradiality is evolutionarily and developmentally derived relative to all other animals.

Echinoderm adult pentaradiality is coupled with another unique body feature known as the **water vascular system**, a complex system of tubes and canals derived from a specific part of the coelom. The water vascular system serves a variety of functions, notably in giving rise to **tube feet** (also known as **podia**), which are crucial to nearly every interaction between echinoderms and their environment. These features are described in detail below. Because adult echinoderms are secondarily radially symmetrical, the terms "dorsal" and "ventral" do not have the same anatomical meanings as in other bilaterians, although these terms are still often used for convenience (and refer only to the animal's orientation on the substratum). The mouth is used as a reference point. Features on the mouth side of the adult are said to be on the **oral surface**, whereas those on the side opposite the mouth are **aboral**. For example, in a starfish, the oral region ("bottom" or "ventral") faces the substratum, and the aboral region is therefore at the "top" of the animal ("dorsal").

Taxonomic History and Classification

Echinoderms have been known since ancient times. Early Europeans collected fossil heart urchins and regarded them as divine "thunder stones," burying them with their dead, and likenesses of starfish appear in 4,000-year-old Minoan frescoes. Jacob Klein is credited with coining the name Echinodermata in about 1734 in reference to sea urchins. For nearly a century thereafter, echinoderms were allied with various other groups, including the cnidarians in Lamarck's Radiata. It was not until 1847 that Frey and Leuckart recognized the echinoderms as a distinct taxon. As noted above, recent molecular and embryological evidence place Echinodermata as a sister phylum to the Hemichordata in a clade known as the Ambulacraria. See Box 26A.

The large number of enigmatic echinoderm fossils is a rich source of argument because of varying opinions on the significance of characteristics such as feeding appendages, attachment structures, and even overall symmetry. Some have suggested that certain superficially bilaterally symmetrical fossils can be interpreted as representing the first echinoderms. Others find it more reasonable and congruent with the fossil record to suggest that these oddities exhibit secondary modification of earlier pentaradial morphology. The disparate morphologies of fossil echinoderms have caused some workers to emphasize differences, recognizing upwards of 25 separate classes. Others seek fundamental similarities with overarching homologies and recognize far fewer major clades. Some of the important extinct clades are introduced in the Echinoderm Phylogeny section of this chapter.

CLASSIFICATION OF ECHINODERMATA

SUBPHYLUM CRINOZOA One living class, the Crinoidea, with the mouth (oral surface) facing upward and encircled by branching arms.

CLASS CRINOIDEA Sea lilies and feather stars (Figures 26.1A and 26.2A,B). Arms radiate from central cup (calyx), with mouth directed upward; stem, when present, arising from aboral side of calyx; ambulacra on arms that bear pinnules; arms composed of confluence of axial and extraxial elements; both left and right somatocoels continuing from calyx into arms; ambulacra not calcified, forming soft tissue closure

of the coelomic cavities in arms, with external radial water vessel; each side of ambulacrum with palisade of cover plates; tube feet minute, lacking suckers; ambulacra can branch equally and repeatedly; madreporite, mouth, and anus on oral surface of calyx. About 625 living species.

ORDER COMATULIDA Feather stars and some sea lilies. Stem usually lost following postlarval stage; most proximal stem element in feather stars retained at base of cup to support cirri that act as attachment appendages. (e.g., *Antedon*, *Bourgeticrinus*, *Comatula*, *Mariametra*, *Tropiometra*)

ORDER CYRTOCRINIDA Aberrant, stemless sea lilies. Calyx sometimes elongate to resemble a stem; no cirri; calyx directly attached to bottom, or attached by a disk. (e.g., *Pilocrinus*, *Neogymnocrinus*, *Cyathidium*, *Holopus*)

ORDER HYOCRINIDA Sea lilies with well-developed stem attached to bottom by expanded terminal disk (holdfast); stem lacking cirri and without nodals and internodals, i.e., elements making up stem are identical. (e.g., *Hyocrinus*, *Calamocrinus*, *Ptilocrinus*, *Laubiericrinus*, *Thalassocrinus*)

ORDER ISOCRINIDA Sea lilies with calyx of very thick stereom elements; with well-developed stem composed of internodals (without cirri) and nodals (with cirri). (e.g., *Isocrinus*, *Hypalocrinus*, *Neocrinus*, *Teliocrinus*, *Endoxocrinus*, *Metacrinus*, *Saracrinus*)

SUBPHYLUM ASTEROZOA Contains the stellate forms, Asteroidea and Ophiuroidea, in which the mouth (oral surface) faces the substratum.

CLASS ASTEROIDEA Starfish (Figures 26.1B–G and 26.2C). Body stellate with five or more arms; arms not sharply demarcated from central disk by distinct articulations; arms have coelomic extensions enclosed by both axial and extraxial body wall; anus (when present) on aboral surface; ambulacral grooves with external radial water vessel; tube feet with internal ampullae, with or without suckers; madreporite aboral on CD interambulacrum. About 1,900 extant species.

ORDER PERIPODIDA Circular, lacking arms; tube feet with suckers; anus absent; mouth very large; young retained in brood chambers on oral surface. Deep-sea wood-dwelling starfish. Three species in a single genus, *Xyloplax*. (Formerly regarded as a separate echinoderm class or sometimes treated as an infraclass of Asteroidea.)

ORDER FORCIPULATIDA With 5–50 arms; tube feet with suckers; anus present; with pincerlike pedicellariae. Widely distributed, including most familiar intertidal species; several hundred species. (e.g., *Asterias*, *Pisaster*, *Heliaster*, *Labidiaster*, *Pedicellaster*, *Pycnopodia*, *Stichaster*, *Zoroaster, Stylasterias*)

ORDER BRISINGIDA With 6–20 long, attenuated arms; fused ring of disk plates; crossed, pincer-like pedicellariae. Most are deep-sea suspension feeders. (e.g., *Brisinga*, *Odinia*, *Freyella*, *Astrocles, Novodinia*)

ORDER SPINULOSIDA With 5–18 arms; tube feet with suckers; anus present; generally lacking pedicellariae. With a few hundred species. (e.g., *Echinaster*, *Henricia*, *Acanthaster*, *Mithrodia*)

ORDER NOTOMYOTIDA Usually five long, straight-sided arms; small disk; prominent muscle bands running inside arm coeloms from disk to arm tip. (e.g., *Benthopecten, Cheiraster*)

ORDER PAXILLOSIDA Upper surface with umbrella-like clusters of ossicles (paxillae); tube feet without suckers; anus present or absent. Epibenthic or shallow burrowers. (e.g., *Astropecten*, *Luidia*, *Platasterias*, *Ctenodiscus*)

ORDER VALVATIDA Tube feet with suckers; anus present; some possess paxillae; some possess clamplike pedicellariae recessed into plates. Widely distributed, with several hundred species. (e.g., *Archaster*, *Asterina*, *Patiria*, *Goniaster*, *Fromia*, *Linckia*, *Solaster*, *Ophidiaster*, *Odontaster*, *Oreaster, Valvaster, Culcita, Dermasterias, and Porania*)

ORDER VELATIDA Usually 5–15 arms; body relatively thick; disk large; stereom ossicles sometimes poorly developed, particularly aborally. Primarily cold-water, deep-sea forms. (e.g., *Pteraster*, *Hymenaster*, *Korethraster*, *Myxaster*, *Caymanostella*)

CLASS OPHIUROIDEA Brittle stars and basket stars (Figures 26.1H,I and 26.2D). Body with five unbranched or branched, thin, articulated arms, clearly demarcated from a central disk; oral arm plates cover ambulacral groove; coelom in arms greatly reduced; tube feet without internal ampullae or suckers; anus lacking; madreporite on CD interambulacral plate on oral surface, often reduced. About 2,000 extant species in six orders.

ORDER EURYALIDA Arms often highly branched (branching extensively in basket stars) and capable of coiling vertically (in the oral-aboral plane) as well as horizontally; "dorsal" arm plates absent; central disk often covered with thick dermis. Many use outstretched arms to form basketlike filter for suspension feeding; others live with arms tightly coiled around coral branches. (e.g., *Asteronyx*, *Gorgonocephalus*, *Euryale*, *Asteroschema*)

The following five orders contain similar forms: Unbranched arms capable of horizontal coiling, but only limited vertical movement; aboral and oral arm plates present and usually well developed.

ORDER OPHIURIDA (e.g., *Ophiura, Ophiomusium, Ophiosphalma*)

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ORDER AMPHILEPIDIDA The most speciose group of brittle stars. (e.g., *Amphilepis, Amphiura, Ophiactis, Ophiolepis, Ophiothrix, Ophiophragmus*)

ORDER OPHIACANTHIDA (e.g., *Ophiacantha, Ophiocanops, Ophiopteris, Ophiocoma, Ophioderma*)

ORDER OPHIOLEUCIDA (e.g., *Ophioleuce, Ophiernus, Ophiopallas*)

ORDER OPHIOSCOLECIDA (e.g., *Ophiomyces, Ophiotholia, Ophioscolex, Ophiolycus, Ophiogeron*)

SUBPHYLUM ECHINOZOA The Echinoidea and Holothuroidea. Species in this subphylum lack distinct arms but possess a specialized subdivision of the left somatocoel, which in echinoids develops into a jaw apparatus.

CLASS ECHINOIDEA Sea urchins, pencil urchins, heart urchins, and sand dollars (Figures 26.1J–L and 26.2E–G,J). Body globose to flattened and discoidal, often secondarily bilateral; stereom plates sutured together by connective tissue and calcite interdigitations to form a usually rigid test; pedicellariae of varying types always present; movable spines mounted on tubercles; radial water vessels wholly enclosed within test; internal jaw apparatus (Aristotle's lantern) present in most groups. About 1,000 extant species in two subclasses.

SUBCLASS CIDAROIDEA Pencil urchins. Test high and globular, ambulacral plates not compound, each with a pore pair supporting a single tube foot; primary spines large, pencil-like, without epidermal covering; anus at aboral pole; ambulacral plates continuing onto peristomial membrane. About 150 living species in one order (Cidaroida). (e.g., *Cidaris*, *Histocidaris*, *Stylocidaris*, *Eucidaris*, *Phyllacanthus*, *Psychocidaris*)

SUBCLASS EUECHINOIDEA Sea urchins, heart urchins, lamp urchins, sea biscuits, sand dollars. Test globular to discoidal, with pronounced bilateral symmetry in some forms (the Irregularia); numbers of tube feet and spines per plate vary; anal position varies from aboral to "posterior." Aristotle's lantern absent in heart and lamp urchins. About 850 living species.

INFRACLASS AULODONTA Includes five orders. Echinothurioida are among largest of echinoids, with test up to 30 cm in diameter, flexible, collapsing upon removal from water; plates usually small and thin, joined with large amounts of collagen; anus aboral; subset of spines with poison glands; usually deep-water (1,000–4,000 m); some species with club-shaped spines for walking on ooze (e.g., *Araeosoma*, *Asthenosoma*, *Phormosoma*, *Sperosoma*). Pedinoida are a less well known deep-water group (e.g., *Caenopedina*). Diadematoida have thin poison-tipped spines below a canopy of longer nonpoisonous spines, and a rigid test; shallow or deep-water (e.g., *Diadema*, *Astropyga*, *Echinothrix*). Aspidodiadematoida are deep-water with a small, almost spherical rigid body held up above the sea bottom by extremely long curved spines (e.g., *Aspidodiadema*, *Plesiodiadema*). Micropygoida are similar to diadematoids but with greatly enlarged aboral tube feet ending in umbrella-shaped, sticky expansions (e.g., *Micropyga*).

INFRACLASS ECHINACEA Globose sea urchins with keeled teeth and large spines. Includes the orders Salenioida (e.g., *Salenia*, *Bathysalenia*), Arbacioida (e.g., *Arbacia*, *Coelopleurus*, *Podocidaris*), Stomopneustoida (e.g., *Stomopneustes*), and Camarodonta (e.g., *Echinometra*, *Echinus*, *Heterocentrotus*, *Paracentrotus*, *Strongylocentrotus*, *Toxopneustes*, *Tripneustes, Lytechinus*).

INFRACLASS IRREGULARIA Heart urchins, lamp urchins, sea biscuits, sand dollars. Body globular or discoidal, always with some bilateral symmetry; anus never wholly within apical system and shifted to "posterior" (even oral) position; spines small, forming dense covering; Aristotle's lantern absent or present. Seven extant orders: Echinoneoida, lantern absent in adults (e.g., *Echinoneus*, *Koehleraster*); Holasteroida, deep-sea heart urchins, lantern always absent (e.g., *Urechinus*, *Pourtalesia*); Spatangoida, "true" heart urchins, lantern always absent (e.g., *Spatangus*, *Echinocardium*, *Maretia*, *Meoma*, *Metalia*, *Lovenia*); Cassiduloida, lamp urchins, lantern absent in adults (e.g., *Cassidulus, Rhyncholampas, Oligopodia*); Clypeasteroida, sea biscuits, lantern always present (e.g., *Clypeaster*, *Arachnoides*); Echinolampadoida, lamp urchins that form a sister group to Scutelloida, lantern absent in adults (e.g., *Echinolampas*, *Conolampas*); Scutelloida, "true" sand dollars, lantern always present (e.g., *Laganum*, *Echinocyamus*, *Echinarachnius*, *Dendraster*, *Mellita*).

CLASS HOLOTHUROIDEA Sea cucumbers, or holothuroids (Figures 26.1M–Q and 26.2H,I). Body fleshy and elongated along oral-aboral axis, even wormlike; skeleton usually reduced to isolated ossicles embedded in body wall; pentaradial symmetry manifested in circumoral feeding tentacles, which are derived directly from radial vessel; feeding tentacles can be highly branched; tube feet along body variably expressed, derived from embryologically interradial longitudinal canals that are not homologous with radial canals of other echinoderms (Figure 26.3A); madreporite suspended from stone canal within coelom; with circle of feeding tentacles around mouth. About 1,700 extant species in five orders.

ORDER APODIDA Body wormlike or snake-like, often very elongate, contractile; lacking tube feet along body; distinctive and abundant wheel or anchor ossicles in body wall; 10–25 branched

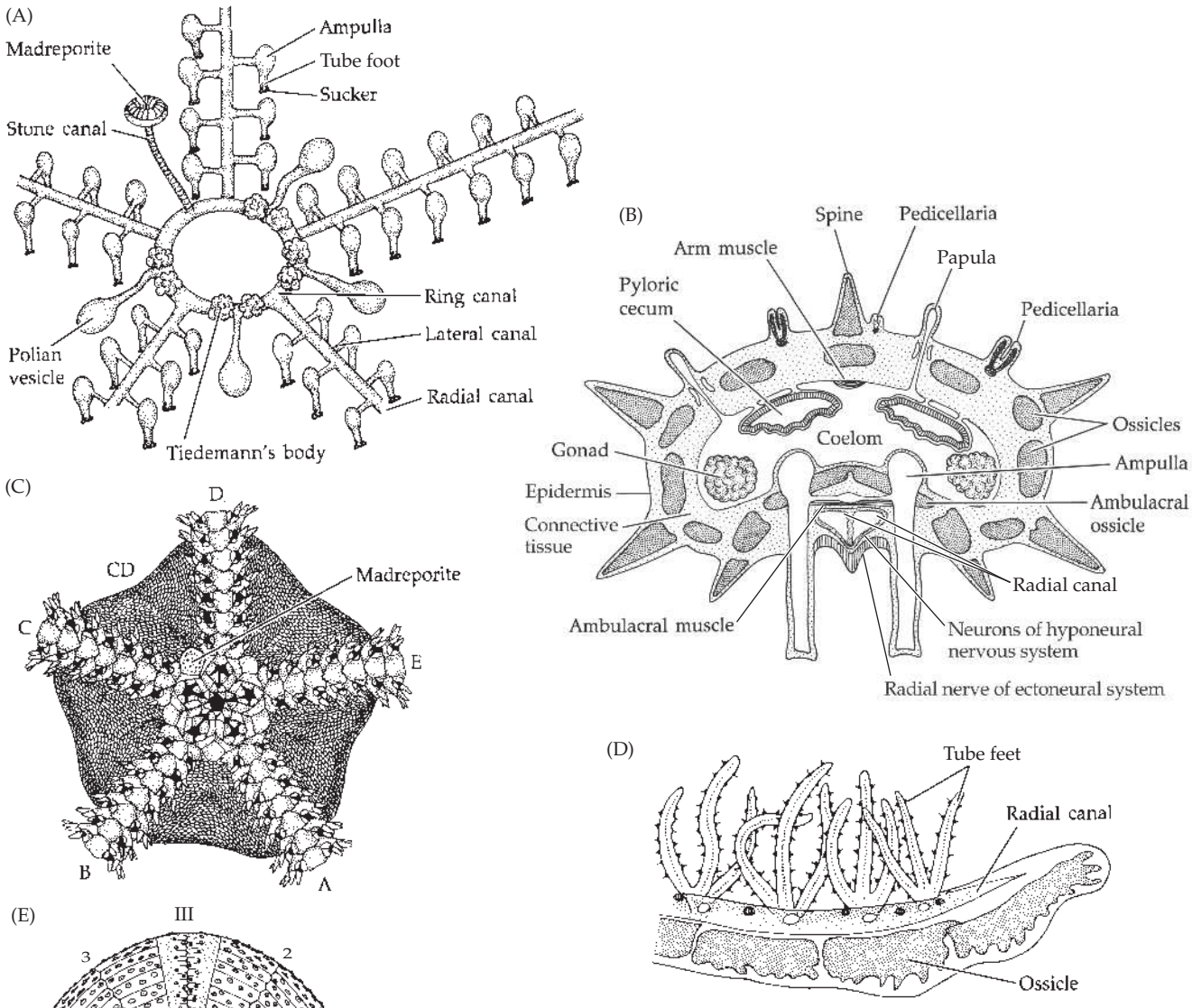

FIGURE 26.3 The water vascular system and related structures. (A) General structure of the water vascular system in a starfish (Asteroidea). (B) A starfish arm (cross section). (C) The central disk (oral view) of a brittle star, *Amphiura* (Ophiuroidea). The madreporite is on the CD interambulacrum. (D) The end of a crinoid pinnule (longitudinal section). The tube feet occur in groups of three. (E) The test (aboral view) of the sea urchin *Echinus* labeled according to Lovén's rule. (F) The periproct and surrounding plates of *Strongylocentrotus*.

feeding tentacles; respiratory trees absent. Some burrow through peristaltic action of body wall muscles, others are epifaunal at varying depths. (e.g., *Chirodota*, *Myriotrochus*, *Synapta*, *Euapta*, *Leptosynapta*)

ORDER ASPIDOCHIROTIDA Body sausage-like; tube feet present along body, often arranged to make solelike flattened area on lower surface; oral tentacles flattened, even leaflike; oral region lacks retractor muscles; respiratory trees present. Includes the largest holothuroids and many familiar, shallow-water forms. (e.g., *Holothuria*, *Stichopus*, *Parastichopus*, *Thelenota*, *Actinopyga*, *Bohadschia*, *Mesothuria*, *Bathyplotes*, *Synallactes*, *Apostichopus*)

ORDER DENDROCHIROTIDA Body sausage-like, sometimes U-shaped; body wall with small ossicles but partially enclosed in plates in certain genera (e.g., *Psolus*); feeding tentacles typically branched; retractor muscles present in tentacles

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and oral region; tube feet present along body. Includes many common intertidal sea cucumbers; most are suspension feeders. (e.g., *Cucumaria*, *Eupentacta*, *Phyllophorus*, *Psolus*, *Thyone*, *Ypsilothuria*, *Vaneyella*)

ORDER ELASIPODIDA Body wall often thin with elongated papillae, sails or fins; respiratory trees absent. Typically deep-sea cucumbers, some with strange body forms adapted for swimming (some are benthopelagic, and at least one species is fully pelagic). (e.g., *Deima*, *Elpidia*, *Peniagone*, *Scotoplanes*, *Laetmogone*, *Enypniastes*, *Pelagothuria*, *Benthodytes*)

ORDER MOLPADIDA Body stout, narrowed posteriorly to a distinct tail; with 10 or 15 digitate tentacles; lacking tube feet along body. Found from shallow water to over 5,000 m. (e.g., *Caudina*, *Molpadia*, *Gephyrothuria*)

The Echinoderm Body Plan

Radial symmetry is usually linked to sessile or planktonic habits of animals that face their environments on all sides as suspension feeders (e.g., feeding structures of tube-dwelling polychaetes, bryozoans, phoronids, and others) or as passive predators (e.g., cnidarians). However, echinoderms have managed to combine motility with radial symmetry in their adult form, and they display many different feeding strategies and lifestyles. Much of the biology of echinoderms is associated with their unique **water vascular system** (Figure 26.3A), a complex of fluid-filled canals and reservoirs that supports the function of the tube feet (or podia). These are hydraulically operated, fleshy projections that serve in locomotion, gas exchange, feeding, attachment, and sensory perception. Much of the evolution of echinoderms is associated with elaboration of the **ambulacra**, that is, the region along the rays in which the water vascular system and skeletal plates that support the tube feet are situated.

The water vascular system is derived relatively late in development, in the bilaterally symmetrical larva. The coelomic cavities of adult echinoderms are not expressed in the typical three body regions usually associated with deuterostomes. All the elements of the water vascular system come from a specialized part of the left mesocoelic portion of the embryonic tripartite coelom, called the **hydrocoel** (see below). The interaction of the hydrocoel with the left somatocoel leads to formation of a region on the left side of the echinoderm larva called the **rudiment**—and the rudiment represents the first glimmerings of pentaradial symmetry. In fact, it represents the first glimmerings of the adult animal itself because the adult form is produced by elaboration of the rudiment, with accompanying loss or incorporation of the bilateral parts of the old larva into the newly emerging adult. This patterning, an extreme case of maximal indirect development, is the key to understanding the uniqueness of echinoderm anatomy and almost all the morphologies seen throughout the phylum—even the most bizarre of the Paleozoic forms.

Developmental Roots of the Echinoderm Body Plan

Axial and extraxial body regions Echinoderms look like nothing else in the animal kingdom. What is more, the echinoderm classes look nothing like one another. How has this strange anatomy come about? Part of the explanation lies in the unique transformation of the echinoderm's bilaterally symmetrical larva into a pentaradial adult. A theory that describes this complex process and body plan is called the **extraxial/axial theory**, or **EAT**. The theory draws from embryology, larval development and metamorphosis, and body wall morphology. The EAT describes adult body regions and homologies in the various echinoderm lineages based on how different larval regions develop into adult body regions.

There are two main body wall regions in larval echinoderms, called the **axial** and the **extraxial regions** (Figure 26.4A). These two regions produce very different parts of the adult echinoderm, which is thus also composed of axial and extraxial regions. Each region produces skeletal material but develops following different patterns.

During the gastrula stage, echinoderms form the three right and left pairs of coelomic compartments that characterize archimeric deuterostomes—protocoel, mesocoel, and metacoel. However, the mesocoel comes to be dominated by the left compartment, called the **hydrocoel**. The compartments of the metacoel are called the **left and right somatocoels**. One of the most unusual features of echinoderms is the expansion of the left side of the larva as the adult begins to form. During larval development, the hydrocoel and left somatocoel become a single functional unit called the **rudiment**. The rudiment contains the axial region, and it develops a ring around the larval esophagus. From this ring are sent out the five radial canals that characterize adult echinoderms. The adult axial region thus includes the mouth, water vascular system, tube feet, and ambulacral skeleton (which grows according to the ocular plate rule, described below).

In contrast, the extraxial region derives from the non-rudiment part of the larva, and it makes up most of the central body of adult echinoderms (except in echinoids, in which the extraxial region is almost entirely lost). The extraxial region consists of two parts, known as the **perforate** and **imperforate extraxial regions**. In adult echinoderms, the skeletal components of the perforate extraxial region are pierced by various orifices (hence the name), such as the anus, genital pores,

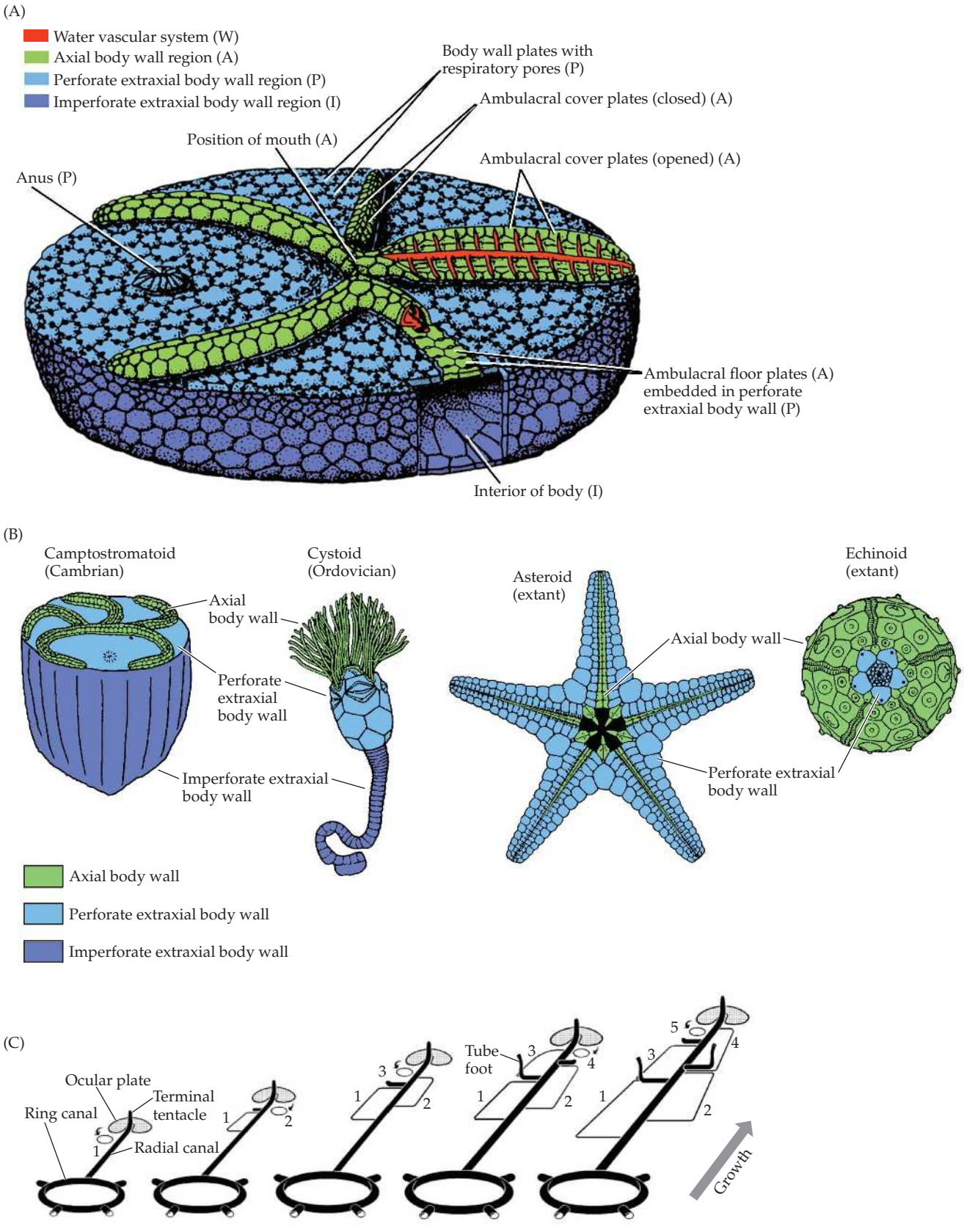

FIGURE 26.4 Body wall regions in echinoderms. (A) Axial and extraxial body wall regions mapped onto a generalized reconstruction of an early echinoderm, such as the disk-shaped *Stromatocystites*. (B) Differential expression of axial and extraxial body wall regions in selected echinoderm groups. (C) The ocular plate rule.

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and specialized openings to the water vascular system. Skeletal components of the extraxial region are not added by any organized "law," but can be generated anywhere needed in the body wall.

During evolution in the Echinodermata, alterations in relative amounts of each of the major body regions (axial and extraxial) gave rise to the diverse forms seen throughout the phylum's half-billion year history (Figure 26.4B). Most significantly, in the living classes Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea, the imperforate body wall region is greatly reduced and contributes very little to the adult body wall (Figure 26.4B). In crinoids, on the other hand, much of the main body wall below the arms and the stem is made up of imperforate extraxial body wall. Regulatory genes that help control timing and rate of development of major regions of echinoderms, and their associated coelomic structures also have distinctive expression patterns in these regions. From these patterns, researchers are starting to gain insights into the mechanisms by which the unique pentaradial symmetry of echinoderms evolved.

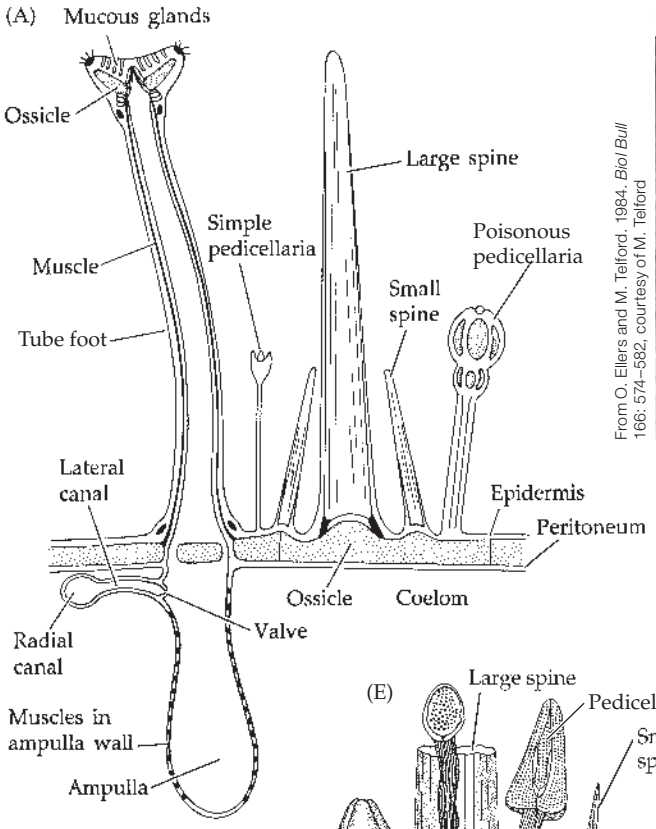
During development, as the axial region gives rise to the ambulacral plates and their accompanying tube feet, growth tightly adheres to a set of empirical "rules." Within the axial region, the tip of the growing hydrocoel farthest from the mouth is expressed as a terminal "tentacle" (similar to a tube foot) in starfish. In sea urchins, for which the dynamics of this system were first understood, this small terminal extension protrudes through a distinctive plate known as the **ocular plate**. The term "ocular" derives from an old idea that the pore through which the terminal tentacle pierces the plate in echinoids was a kind of eye. Although light sensitive tissues can be associated with the terminal tentacle itself, there are no known true eyes among echinoderms. The ontogenetic pattern by which new tube feet are laid down in the axial region is known as the **ocular plate rule (OPR)**, whether or not the ocular plate itself (Figure 26.4C) is actually calcified. In all echinoderms, as the **radial canals** (hydrocoelar extensions) of the developing rudiment expand outward along the rays from the **ring canal** (the hydrocoelar ring that encircles the esophagus), new tube feet appear just proximal to the ocular tentacle (the **terminal tentacle**). A new tube foot appears first on one side of the radial canal, and then on the other, to form a zigzag pattern of tube foot additions along the growing biserial ambulacrum (Figure 26.4C). In most echinoderms, as each new tube foot appears, so does a new ambulacral plate. Therefore, a basic property of the OPR is that the oldest plates and tube feet in the ambulacrum are near the mouth, and the youngest are at the tip of the ambulacrum, just proximal to the terminal tentacle.

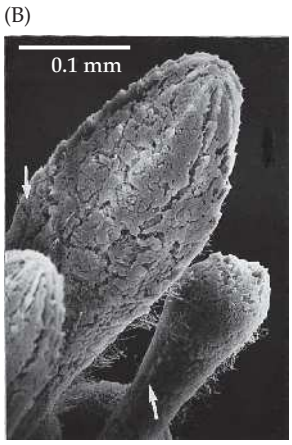
Ray homologies Although it is not always obvious, each ray of an echinoderm can be homologized to those of any other in terms of reference to particular radii. For example, the position of the opening to the water vascular system is marked by one or more **hydropores**. These minute pores, which are often borne on a special plate called the **madreporite**, lead via an internal canal to the water vascular system (Figure 26.3A). The madreporite gives a clue to body orientation because it lies between specific rays. A system of lettering has been developed in which the ambulacrum opposite the madreporite is coded A; the others are then coded B through E in a counterclockwise fashion as viewed from the aboral surface (Figure 26.2C). The madreporite (or hydropore, in forms lacking a madreporite) always lies between ambulacra C and D (i.e., on the CD interradius). Ambulacra C and D comprise the **bivium**, while radii A, B, and E comprise the **trivium**.

Body Wall and Coelom

An epidermis covers the body of all echinoderms and overlies a mesodermally derived dermis that contains stereom skeletal elements referred to as **ossicles** and **plates**, as noted earlier (Figure 26.5A–D). Internal to the dermis and ossicles are muscle fibers and the peritoneum of the coelom. The degree of development of the skeleton and muscles varies greatly among groups. In echinoids, the ossicles are firmly attached to one another to form a rigid test, and body wall musculature is weakly developed. In sea cucumbers, ossicles are seldom contiguous and are usually scattered within the fleshy dermis (Figure 26.5D), in which distinct muscle layers are present. Between these two extremes are cases in which adjacent skeletal plates articulate to varying degrees. In the arms of starfish and brittle stars, the body wall muscles are arranged in bands between the plates, providing various degrees of arm motion. In some groups, skeletal plates are developed to such a degree that they nearly obliterate internal cavities. In brittle stars, for example, each arm is made up of a column of tightly interlocked pairs of ambulacral plates called **vertebrae** (see Figure 26.9A,B), and the arm coeloms are reduced to small channels. Similarly, the arm coeloms in crinoids are relatively small canals within skeletal plates.

The endoskeleton is calcareous, mostly $CaCO_3$ in the form of calcite, with small amounts of $MgCO_3$ added to increase hardness through "dolomitization." Each ossicle begins as a separate spicule-like element to which additional material is added in precise patterns to make specific elements in the skeleton. Within each ossicle, an anastomosing network of minute struts (the trabeculae) forms, creating labyrinth-like spaces (Figure 26.5D) so that the ossicle is made of porous, spongelike stereom. The spaces contain dermal cells and fibers (the stroma). Although each plate behaves as a single crystal, the stereom is polycrystalline, with aligned microcrystals intermixed with small amounts of organic matrix.





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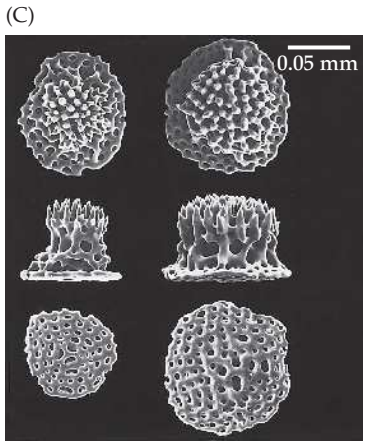

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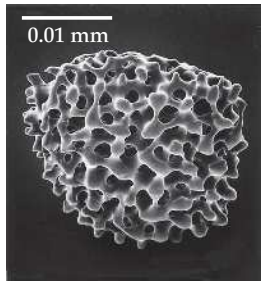

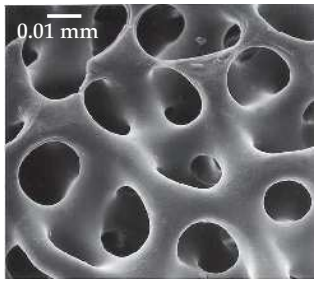

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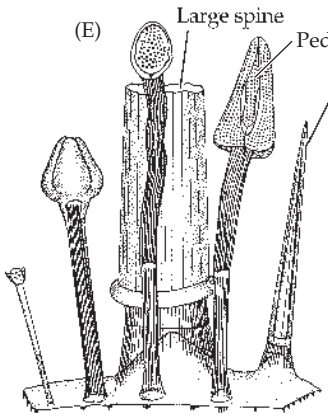

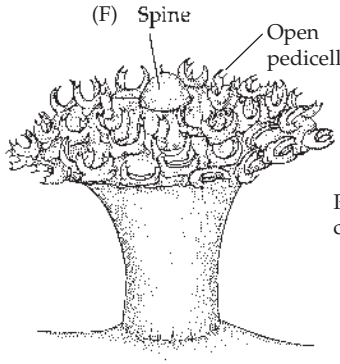

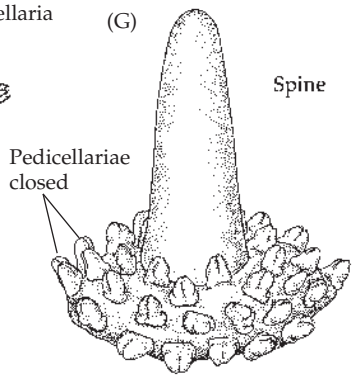

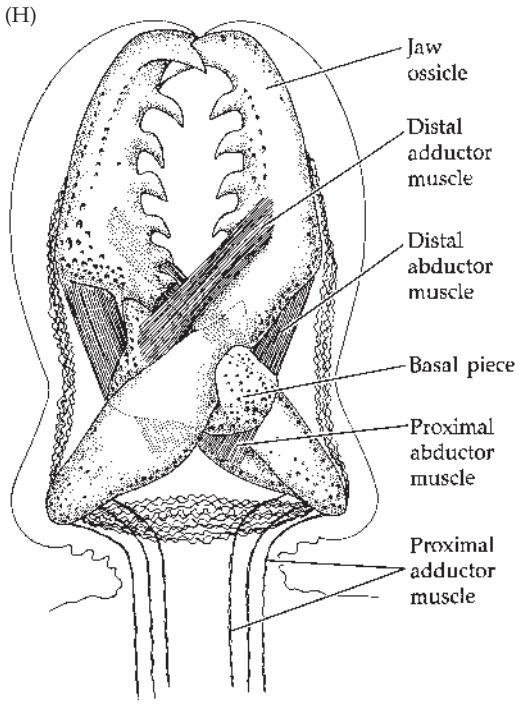

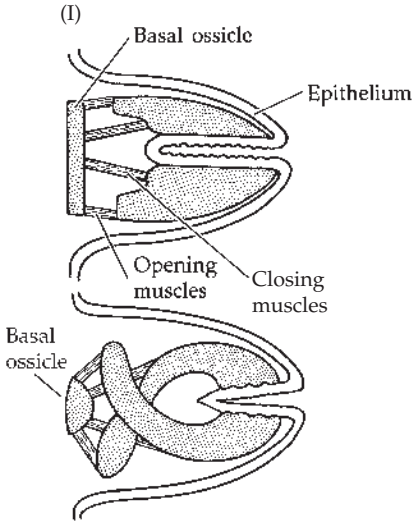

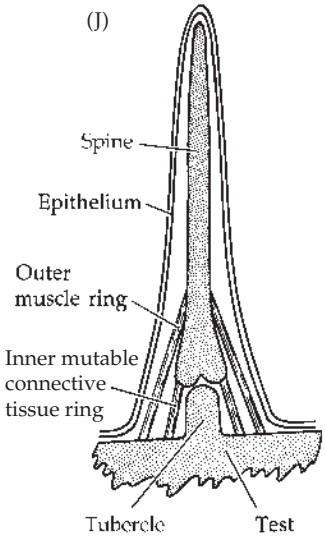

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◀ **FIGURE 26.5 Echinoderm body wall and some skeletal elements.** (A) Composite section of a sea urchin's body wall. (B) Scanning electron micrograph (SEM) scans of spines on the sand dollar *Echinarachnius parma* (Echinoidea). Arrows point to ciliary tracts. (C) SEM of skeletal ossicles from the central disks of ophiuroids, shown in top, side, and basal views. (D) SEM of skeletal ossicles from the sea cucumber *Psolus chitinoides* (Holothuroidea), with detail of stereom. (E) Diversity of echinoid pedicellariae surrounding the base of a large spine. (F,G) Prey-catching pedicellariae of the starfish *Stylasterias forreri* (Asteroidea). (F) Pedicellariae open and extended; (G) Pedicellariae retracted and closed. (H) Details of a generalized starfish pedicellaria. (I) Muscle systems in starfish pedicellariae. (J) A movable echinoid spine (section). Note the position of muscles relative to the body wall layers.

Plates can remain single (simple plates) or, more rarely, fuse to form compound plates. External plates can have bumps and knobs called tubercles, some of which support a variety of articulated, external projections such as spines (Figure 26.5A,E). In asteroids, echinoids, and euryalid ophiuroids, unique pincerlike structures called **pedicellariae** (Figure 26.5E–I) can also be mounted on these tubercles. Movable spines and pedicellariae respond to external stimuli independently of the main nervous system, and they possess their own neuromuscular reflex components. Pedicellariae were discovered in 1778 by O. F. Müller, who described them as parasitic polyps and gave them the genus name "*Pedicellaria*." He recorded three species of these "parasites" (*P. globifera*, *P. triphylla*, and *P. tridens*); variations on these names are still used to describe different types of pedicellariae. Nearly a century later, it was realized that pedicellariae are produced by the echinoderms themselves, but their exact nature remained elusive. Louis Agassiz even believed they were attached young! It is now known that pedicellariae are functional appendages of the animals that produce them. Pedicellariae vary in morphology, size, and distribution on the body. In echinoids, most are elevated on stalks, but on asteroids, they usually lie nestled directly on the body surface, sometimes in clusters. Some help keep debris and settling larvae of other invertebrates off the body, and others are used in defense. Some echinoid pedicellariae are venomous to discourage predators, and others are pincers that grasp and hold objects for camouflage and protection. A few starfish even use their pedicellariae to capture prey (Figure 26.5F,G).

Spines, pedicellariae, and the epidermis contain tissues isolated from the coelom and digestive system because they are external to the main body wall (Figure 26.5H–J). Being isolated from the gut and coelom, in which nutrient supply is aided by circulation and hemal systems, external appendages and epidermal structures have their nutritional needs met by nutrients absorbed directly from the water or by small trapped organic particulates or organisms that are absorbed.

As in all deuterostomes (except Chordata), the coelomic system of echinoderms typically develops as a tripartite series, originating as paired **proto-**, **meso-**, and **somatocoels** that are thought to be homologous to the tripartite coeloms seen in other deuterostomes. As noted above, in adult echinoderms, these coelomic cavities do not form the usual three body regions typically associated with deuterostomes. Recall that the main body coeloms of adult echinoderms are derived from the left and right somatocoels, and they are usually well developed. However, the water vascular system forms from the left mesocoel—called the hydrocoel (as described earlier). Other coelom derivatives include gonadal linings and certain neural sinuses. The main body cavities, or **perivisceral coeloms**, are lined with ciliated peritoneum, and their coelomic fluid plays major circulatory roles. A variety of coelomocytes, many phagocytic, are present in the body fluid and water vascular system. Hemoglobins occur in the coelomocytes of certain holothuroids and brittle stars. Echinoderm coelomic fluid is isotonic with ambient seawater, and no mechanisms have evolved to control osmolarity of these fluids—a major reason that there are no terrestrial or freshwater echinoderms.

Mutable Collagenous Tissue

Between many of their skeletal ossicles, and in the body wall itself, echinoderms have a uniquely elaborated system of connective tissue. The material properties of this tissue are mutable on short time scales and are under neuronal control. This **mutable collagenous tissue (MCT)** is normally rigid, but it can be temporarily softened, allowing echinoderms to maintain fixed postures with zero muscular effort and energy expenditure. Long viewed as a curiosity, MCT is crucial to understanding how echinoderms maintain relatively low metabolic budgets in situations causing nutritional challenges to other phyla. In holothuroids, much of the body wall is constructed of MCT, allowing them to quickly change turgidity. In echinoids, muscular rings around the bases of the spines position them within a rocky crevice, then a similarly positioned ring of MCT (so-called "catch collagen") "freezes" the spine into position to wedge the animal into place. During crawling, starfish soften their body, then use MCT in their body wall to adopt a new posture, securing their position over uneven substrata, making them virtually impossible to dislodge by predators or wave action.

Water Vascular System

The water vascular system is so critical to all aspects of echinoderm biology that a discussion of its anatomy is a necessary preface to other considerations, starting with starfish and then comparing their system to other echinoderms.

Asteroidea Figure 26.3A is a schematic representation of the starfish water vascular system. The system opens to the exterior through a skeletal plate, the madreporite (or sieve plate) located off-center on the aboral surface on the CD interambulacrum (Figure 26.2C). The madreporite is perforated by hydropores set in deep furrows. The overlying epidermis is ciliated, even where it lines the pores. The traditional view of madreporite function is that it permits seawater to enter the system to replace water lost through the thin walls of the tube feet, as demonstrated by using radioactive tracers.

Internally, the madreporite forms a cuplike lumen called the ampulla (distinct from the tube foot ampulla) that communicates with other coelomic derivatives of the water vascular and hemal systems. The lower end of the ampulla connects with the **stone canal**, so named because of hard skeletal deposits in its wall. A portion of the hemal system called the **axial sinus** is often intimately associated with the stone canal. The stone canal proceeds orally to join with a circular ring canal encircling the esophagus. The ring canal gives rise to radial canals extending into each arm. Interradial blind pouches called **Tiedemann's bodies** and **Polian vesicles** are attached to the ring canal (Figure 26.3A,B). There is uncertainty about the function of these pouches, but the former are suspected to produce certain coelomocytes, and the latter to help regulate internal pressure within the water vascular system.

The liquid in the water vascular system consists of ambient seawater to which the animal adds specific components such as coelomocytes, organic compounds such as proteins, and a relatively high concentration of potassium ions. The fluid is moved through the system largely by cilia that line the internal epithelia of the canals, some of which, especially the stone and ring canals, contain partition-like inner extensions that could help direct the flow. The stone canal, at least in some starfish, has been described as a "ciliary pump" that draws fluid into the water vascular system from both the madreporite and the axial sinus of the hemal system.

In each arm, the radial canal gives rise to numerous **lateral canals**, each of which terminates in a tube foot–ampulla system. All tube feet form according to the ocular plate rule (Figure 26.4C), with oldest ones near the mouth, and youngest at the arm tips. The tube foot is a contractile, muscular tube typically ending in a sucker; it extends externally from a bulblike, internal ampulla (Figure 26.3B). Longitudinal and circular muscles attach to a collagenous sheath surrounding a coelomic lumen, and the tip and shaft are well supplied with nerves. Tube feet function as primary tactile, locomotory, attachment, and food-manipulating organs. Each radial canal ends in an unsuckered, tentacle-like, terminal tube foot that is most likely photoreceptive.

The system of tube feet and ampullae comprise a sophisticated hydrostatic system. Two sets of muscles operate around the fluid in the lumens of tube feet and ampullae. A valve in the lateral canal can effectively isolate the tube foot and ampulla from the rest of the canal. With the valve closed, muscles in the ampullar wall contract, forcing fluid into the lumen of the extending tube foot, in which the longitudinal muscles are relaxed. The sucker is then pressed against the substratum and held there by adhesive secretions of the epidermis and by the contraction of tip muscles that raise the center of the sucker and create a suction-cup-like vacuum. When the longitudinal muscles of the tube foot contract, it shortens, decreasing the lumen volume and forcing fluid back into the now relaxed ampulla. When the tip muscles relax, the suction is broken. Chemicals secreted by cells in the sucker reverse the adhesive action of substances secreted by the tube foot. Tube feet bend by differential contraction of the longitudinal muscles.

Ophiuroidea The water vascular system of brittle stars is similar to that of asteroids. However, the madreporite is on the oral surface of the central disk (Figure 26.3C), and the internal plumbing is modified accordingly. In some ophiuroids the madreporite is reduced to just two hydropores.

The ring canal bears Polian vesicles, but apparently lacks Tiedemann's bodies. The ring canal gives off the usual five radial canals and also bears a wreath of buccal tube feet around the mouth. In basket stars (order Euryalida) the arms and the radial canals are branched. The suckerless tube feet are highly flexible, being fingerlike structures that can secrete copious amounts of sticky mucus. They function in feeding, digging, locomotion, and sensation.

Crinoidea The water vascular system of crinoids operates entirely on coelomic fluid. There is no centralized madreporite in modern forms. Multiple stone canals arise from the ring canal and open to coelomic channels. There can be hundreds of such canals. The main perivisceral coeloms bear ciliated funnels to the exterior through which water enters the body cavities, perhaps to regulate hydraulic pressure in the water vascular system.

From the ring canal, radial canals bifurcate into all the branches of each arm, which can have as many as 200 termini. Crinoid arms also bear side branches called **pinnules** (Figure 26.2B), into which extensions of the radial canals also reach. Topologically with respect to the coeloms, radial canals are positioned just as they are in starfish. However, ambulacral ossicles are lacking, and the canals are embedded in a soft tissue shelf, reducing weight and metabolic expense otherwise needed to produce a skeleton in the long arms. The arms are well supported by brachial ossicles, relatively large, articulated stereom elements that form the aboral surface of all arms and pinnules (see Figure 26.7A,B). Suckerless tube feet

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occur along pinnules, often in clusters of three (Figure 26.3D), and each cluster is served by a branch from the radial canal. Equipped with adhesive papillae, the tube feet are highly mobile, functioning primarily as feeding and sensory organs.

Echinoidea Echinoids bear a special set of skeletal plates, called the **apical system**, around the aboral pole, one of these plates being a madreporite (Figure 26.3E,F) that leads to an ampulla–axial gland complex. A stone canal extends to a ring canal atop the jaw apparatus (Aristotle's lantern, see below). The ring canal gives rise to a radial canal beneath each ambulacrum, as well as to Tiedemann's bodies and Polian vesicles. Each radial canal gives off lateral canals leading to tube feet and ends with a terminal tentacle protruding through an ocular plate in the apical system. The tube feet of echinoids may be suckered or unsuckered. They serve a variety of functions including attachment, locomotion, feeding, and gas exchange.

To understand the water vascular system of sea urchins, picture a starfish in which the aboral region (the perforate extraxial region) has been reduced to a tiny button (the apical system). The result is a "pulling" of the tips of the radial canals together to converge on the apical system, leaving the rows of tube feet extending around the sides of the body like five lines of longitude on a globe (Figures 26.3E and 26.4B). However, unlike any other echinoderm, stereom plates of the test are laid down external to the water vascular components, rendering the radial canals truly internal. Pores through the plates forming the ambulacra allow communication between the tube feet and ampullae. This is very different from ophiuroids, in which the radial canal is usually covered by ventral arm plates and not truly internal, and from the holothuroids in which the longitudinal canals are not homologous to radial canals of other echinoderms (see below).

Holothuroidea The story of the holothuroid water vascular system is one of reduction, or truncation of growth probably through pronounced paedomorphosis. In a sense, holothuroids can be viewed as "giant larvae"—metamorphosis is suppressed, producing an adult animal in whose construction the rudiment plays only a small part.

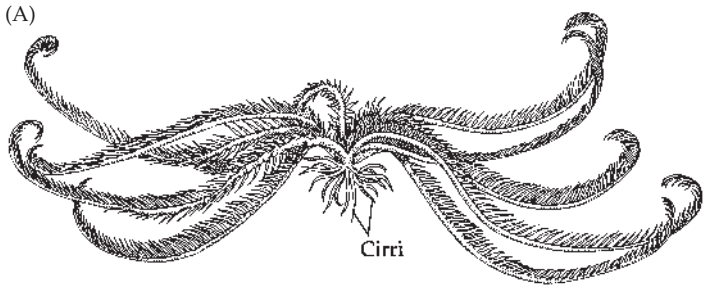
In the Holothuroidea, the stone canal usually extends from beneath the pharynx in an interradial position, giving rise to a madreporite opening to the coelom. A ring canal encircles the esophagus and bears from 1 to 50 Polian vesicles. Five radial canals arise from the ring canal to give off extensions to the **oral tentacles**, which are actually highly modified terminal tentacles and the first few tube feet. These represent the only elaborations of that part of the radial canal homologous to the radial canal in other echinoderms. In the least derived holothuroids, such as the Apodida, these tentacles, restricted to the circumoral region, are all that exists of the water vascular system, there being no canals or tube feet along the vermiform body. Early in postlarval growth of more derived forms, thin interradial extensions from the ring canal form to produce interradial, **longitudinal canals** that are later twisted in a kind of "torsion" that pulls them into alignment with the radial canals leading to the feeding tentacles. The longitudinal canals lie along the inside of the larval body wall, inducing formation of tube-foot-like structures without respect for the ocular plate rule. These tube-foot-like extensions can be scattered over the body wall, restricted to ambulacrum-like lines, or missing in certain radii entirely, usually along the "dorsal" or upper surface. The tube feet around the mouth serve in food gathering, whereas the tube-foot-like appendages along the body assist in locomotion, attachment, and touch.

Support and Locomotion

Except in holothuroids, structural support in echinoderms is maintained primarily by skeletal elements and the mutable collagenous tissue. Tube feet and gill-like extensions of the body wall (such as papulae) are supported mostly by hydrostatic pressure. Most sea cucumbers lack skeletal plates, which are reduced to minute, separated ossicles, but body wall muscles form thick sheets, adding integrity to the body and working antagonistically on coelomic fluids to function in a hydrostatic skeleton. The mutable collagenous tissue of echinoderms also contributes to overall support and aspects of locomotion.

Apart from sessile sea lilies (e.g., *Ptilocrinus*), most extant crinoids are capable of crawling and even swimming. Aboral cirri of feather stars (and along the stem of isocrinids) are used for temporary attachment (Figure 26.6A). During isocrinid crawling, the animal lies prone and with the stem trailing, and the arms pull the main body region, the **calyx** or **theca** (the central cup at which the arms converge), along the bottom (Figure 26.6B) to reposition the animal. Isocrinids also "run away" from deep-sea cidaroid echinoids while casting off a piece of the stem to preoccupy the echinoid predator. Swimming among the Crinoidea is accomplished by up-and-down sweeps of the arms, which are divided into functional sets that can move alternately.

Asteroids exemplify locomotion using suckered tube feet. Starfish arms are held more or less stationary relative to the central disk, even in species with a flexible skeletal framework (e.g., *Pycnopodia*). Movement is accomplished by upwards of thousands of tube feet on the oral surface. The starfish appears to glide smoothly because of the large number of tube feet, though at any given instant they are in different phases of the power and recovery strokes (Figure 26.6C). Although control of tube foot action is



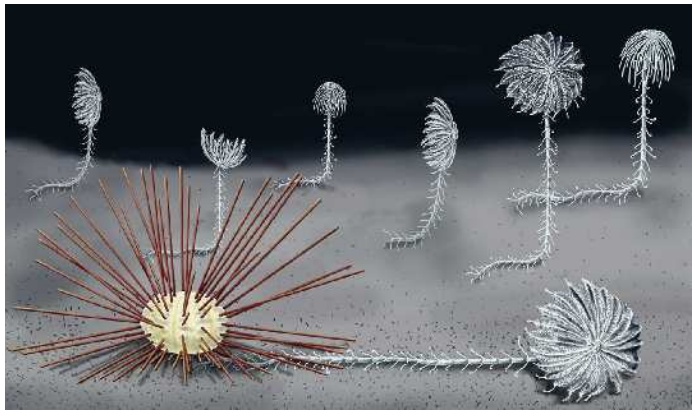
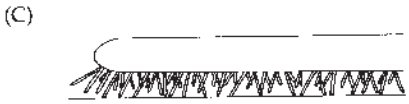
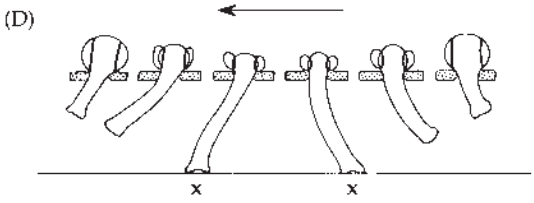


Illustration by Laura Garrison





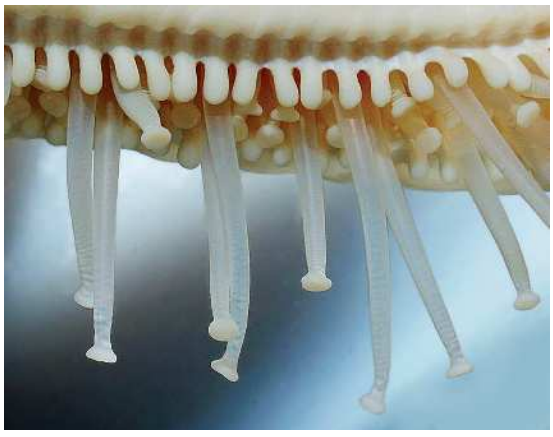


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FIGURE 26.6 Locomotion in echinoderms. (A) A feather star, *Antedon* (Crinoidea), at rest. (B) Depiction of an isocrinid sea lily (Crinoidea) escaping from a cidaroid sea urchin (Echinoidea) predator by crawling on its arms, dragging the stem. Note numerous other, erect sea lilies in the background, living in groups sometimes referred to as "gardens" of crinoids. (C) Starfish arm (side view) with tube feet in motion. (D) Tube foot movements as a starfish moves in the direction of the arrow. Power stroke occurs with sucker in contact with the substratum (x), recovery stroke while lifting. Note changes in tube foot length and corresponding changes in volume of the ampulla. (E) Tube feet of a crawling starfish *Dermasterias imbricata*.

not fully understood (even isolated arms crawl about normally), tube feet are coordinated to produce movement in a particular direction. There are no metachronal waves of motion as seen in many other multi-legged creatures. Most starfish move slowly, but a few (e.g., *Pycnopodia*) are relative speedsters, and otherwise sedentary asteroids become rapid "runners" upon encountering a potential predator. Species that cannot "run" have other defense mechanisms. The slow-moving Pacific cushion star, *Pteraster tesselatus* (Figure 26.1D), secretes copious amounts of mucus that discourages predators such as *Solaster* and *Pycnopodia*. Starfish on sandy bottoms (e.g., *Astropecten*) can burrow rapidly by using tube feet to move sand from below to on top of themselves.

Following the action of a single tube foot during movement reveals the sources of the locomotory forces (Figure 26.6D). At the end of a recovery stroke, the tube foot extends in the direction of movement and attaches to the substratum. The sucker remains attached during the power stroke as the longitudinal muscles in the wall of the tube foot shaft contract, shortening the tube foot and pulling the body forward. At the end of the power stroke, the tube foot detaches and swings forward again. The great number of tube feet and the general flexibility of the body allow starfish to move easily over even the most irregular surfaces (Figure 26.6E).

Ophiuroids primarily use their flexible, articulated arms for crawling or clinging (Figure 26.2D). In most forms, the skeletal arrangement within the arms allows for rapid lateral, snakelike movements on a plane parallel to the disk (hence the Greek prefix *ophio*, "snake"). Only in taxa such as basket stars do the arms have full range of movement in all planes. In most species, the articulated arms are fragile and break easily when seized (hence "brittle stars"). The tube feet lack suckers and ampullae, but a well-developed lattice of muscles in their wall allows protraction, retraction, and swinging motions. Combined action of arms and tube feet allows some ophiuroids to burrow into sediments, or move swiftly when escaping from predators or chasing prey.

Sea urchins move by the use of tube feet and movable spines. Strong, suckered podia are capable of a wide range of extension and motion, while spines provide stiltlike support and movement. Some urchins can excavate stone by scraping with their spines and

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chewing with their teeth. Some populations of *Strongylocentrotus purpuratus*, a common northeast Pacific urchin, form pockets in intertidal rocks, and *Echinometra vanbrunti* also does this on tropical eastern Pacific shores. Individuals are sometimes trapped in their self-made homes, but they are protected from predation and wave action. The common Indo-Pacific reef urchin, *Echinometra mathaei*, excavates elongate channels in rock largely by the action of teeth in the jaw apparatus; in these species the test is slightly elongated to allow movement of the urchin along the channel as it harvests a "garden" of algae growing there. Some irregular urchins burrow below the sediment surface. Sedentary species (e.g., *Echinocardium*) maintain an open chimney to the overlying water (see Figure 26.11G). Soft-sediment burrowers often have specialized spatulate spines along the body that aid in locomotion and digging. Clypeasteroid sand dollars live on sandy bottoms, and all species lie flat with the oral surface toward the bottom except *Dendraster excentricus*, an abundant North American west coast species that lives embedded upright in the substratum (see Figure 26.11F). Clypeasteroid burrowing and crawling are accomplished by the action of spines that move in metachronal waves. Sand dollar morphology is strongly tied to hydrodynamic forces. Deep marginal notches and holes (**lunules**) in the tests of some sand dollars (Figure 26.2F) are not for feeding, but act as lift spoilers to help the animals maintain stability in strong currents characterizing their coastal environments. Lift forces are also mitigated by flow along **pressure drainage channels** from the center of the body to the lunules.

Holothuroids inhabit various substrata, coral crevices, spaces under rocks, or soft sediments. They crawl or burrow in sand or mud using tube feet or peristaltic actions of body wall muscles. In epibenthic species that lodge themselves in rock crevices, the tube feet can be used for anchorage and to hold bits of shell and stone for camouflage and protection. In deep-sea forms such as *Scotoplanes* (Figure 26.1N), some tube feet are elongated for walking like small mammals, hence the nickname "sea pig." In psolids, the lower surface is modified into a footlike sole upon which the animal creeps. Among the apodids are the bizarre synaptids, with unique anchor ossicles in densities up to 1,500 per cm^2 of body wall. In lieu of tube feet, these provide a grip akin to Velcro by protruding and retracting into the skin in peristaltic waves along the body wall. Some holothuroids live completely buried, whereas others form U-shaped burrows. A few holothuroids are truly pelagic and capable of swimming (Figure 26.1P,Q).

Feeding and Digestion

Crinoidea Sea lilies and feather stars sit with their oral sides up and suspension feed, usually clinging to elevated areas exposed to currents (see the yellow feather star *Comaster* at the chapter opener). The arms and pinnules are held outstretched into ambient water flow, presenting a large food-trapping surface. Some forms emerge from concealment to feed only at night. Deep-water species hold their arms upward and outward, forming a funnel with which they capture detrital rain, and stalked forms raise a crown of arms like an umbrella into the current; the stalk is bent with the current flowing into the underside of the umbrella, and particle capture occurs downstream, on the oral surfaces of the arms.

Food particles, including plankton and organic particulates, contact tube feet along the ambulacral grooves in arms and pinnules (Figure 26.7B). These tube feet flick the food into the grooves, which are lined with cilia that beat toward the calyx, driving food to the mouth, where it is ingested. This use of the tube feet and ambulacral grooves for feeding likely represents an original function of the early water vascular system in Echinodermata.

The mouth opens to a short esophagus leading to a long intestine (Figure 26.7A,C) that loops inside the calyx, then straightens to a short rectum terminating at the anus, which is borne on an anal cone near the arm bases. The intestine can bear diverticula, some of which are branched. The histology of the crinoid gut has been described, but little is known about the digestive physiology of these animals.

Asteroidea Most starfish are opportunistic deposit feeders, scavengers, or predators, feeding on nearly any organic matter or small prey. Many species are generalists in terms of food preference and play important roles as high-level benthic predators in intertidal and subtidal communities. Others, such as *Solaster stimpsoni* from the northeastern Pacific, are specialists feeding on holothuroids, while a related species (*S. dawsoni*) preys almost exclusively on *S. stimpsoni*! Tropical crown-of-thorns starfish (species of *Acanthaster*) feed on coral polyps, receiving great notoriety because of their implied destruction of coral reefs. There remains disagreement concerning causes for increases in *Acanthaster* populations, and even the level of harm they actually perpetrate on the reefs, but most agree that human interference in predator-prey balance in reef communities is more to blame than *Acanthaster* itself. A major predator of *Acanthaster* is the giant triton snail *Charonia tritonis*, which is collected in high numbers for its handsome shell. In undisturbed environments, *Acanthaster* likely plays a role in maintaining coral diversity by acting as forest fires often do, opening new habitats in climax ecosystems for the establishment of other species.

Except for a few suspension feeders, starfish use an eversible portion of the stomach to obtain food. Some forms, including *Culcita* (a cushion star, Figure 26.1E), *Acanthaster* (Figure 26.1F), and *Patiria* (a bat star; see Figure 26.8D), spread their stomach over the surface of a food source, secrete digestive enzymes, and suck in the partially digested soup.

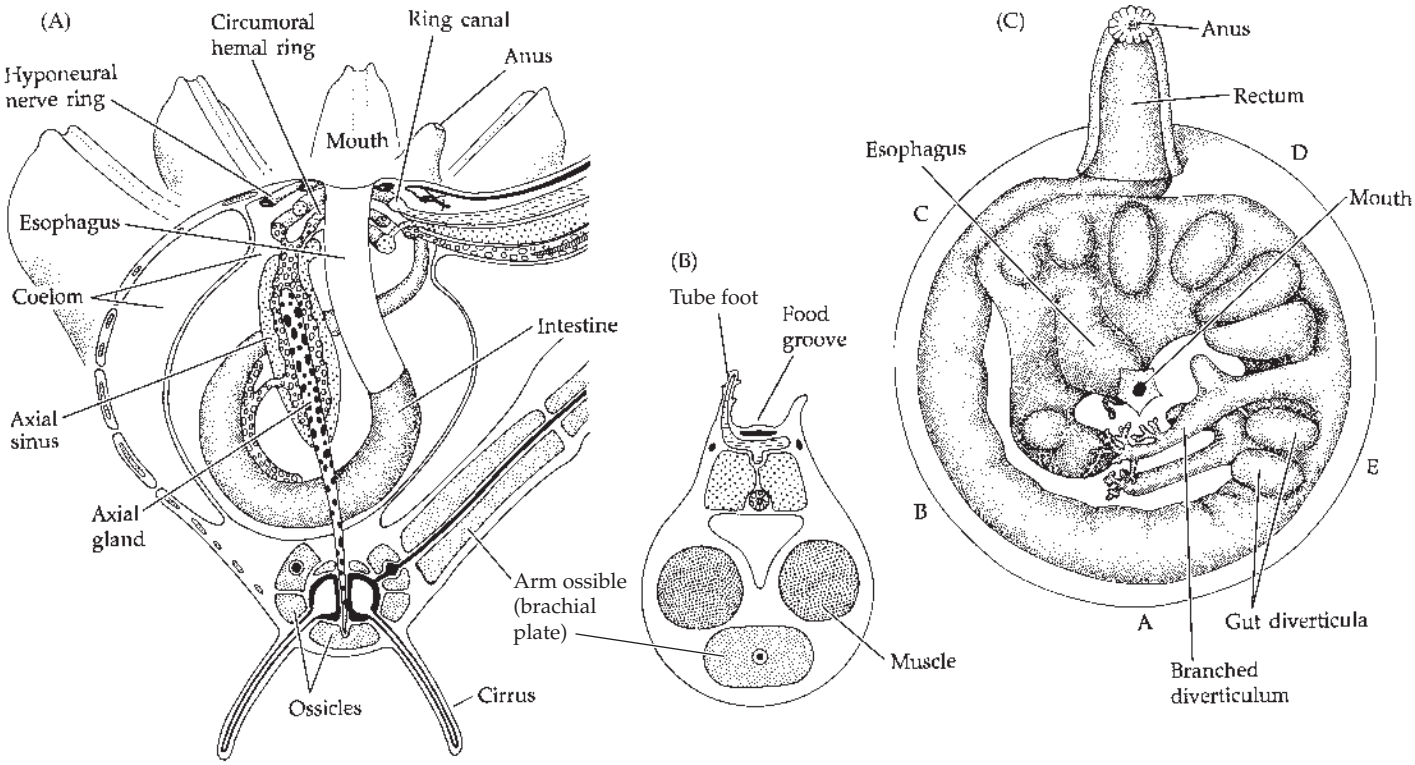

FIGURE 26.7 Internal anatomy of sea lilies and feather stars (Crinoidea). (A) Central disk and base of one arm (vertical section). (B) Arm with open ambulacral groove (cross section). (C) Oral surface of the feather star *Antedon* (cutaway view). Positions of radii indicated by letters.

For *Culcita* and *Patiria*, food can include encrusting sponges, algal mats, or accumulated organic detritus over which the starfish crawls. *Oreaster*, also a cushion star, feeds similarly but switches to a predatory or scavenging mode when appropriate food sources are encountered. Sedentary or sessile prey, such as gastropods, bivalves, and barnacles, are eaten by asteroid predators, especially members of the Forcipulatida. The voracious Pacific ochre star *Pisaster ochraceus* hunches over its prey with the oral area pressed against the potential victim, holding itself in position with its tube feet. The stomach is very thin and flexible and can be slid between even the tightly clamped valves of mussels and clams to liquefy the prey's body inside its own shell so that nutrients are drawn in with the retracting stomach.

Some starfish are suspension feeders, consuming plankton and organic detritus. *Henricia*, *Porania*, and a few others are typically full-time suspension feeders, and some predators, such as *Astropecten*, are facultative suspension feeders to supplement their usual diet. Usually, particulate food material that contacts the body surface is trapped by mucus and moved by ciliary action to the ambulacral grooves and ultimately to the mouth. *Novodinia* extends its arms upward into water currents. The dozen or so arms form a large feeding surface used to capture planktonic crustaceans; the prey are grasped by clusters of pincerlike pedicellariae. A few forms, including *Stylasterias*, *Pycnopodia*, and *Labidiaster*, possess wreathlike circlets of pedicellariae (Figure 26.5F,G) used to capture a variety of animals, even fishes.

The starfish gut typically extends from the mouth at the junction of the arms to the aboral anus (Figure 26.8A). The mouth is surrounded by a leathery **peristomial membrane**, which is flexible to allow eversion of the stomach, and contains a sphincter muscle that closes the mouth orifice. Internal to the mouth is a very short esophagus leading to the **cardiac stomach**—the portion that is everted during feeding. Radially arranged retractor muscles retract the stomach. Aboral to the cardiac stomach is a flat **pyloric stomach**, from which arises a pair of pyloric ducts extending into each arm and leading to paired digestive glands (**pyloric ceca**) (Figure 26.8A,C). A short intestine, often bearing outpocketings (rectal glands or rectal sacs) leads from the pyloric stomach to the anus. The pyloric ceca and cardiac stomach are the main producers of enzymes (mostly proteases) carried by ciliary action through the everted stomach and released onto the food material. Digestion is completed internally, but extracellularly, after ingestion of the liquefied food. Digested products are moved through the pyloric ducts to the pyloric ceca, where they are absorbed and stored. The intestine does not seem to function in actual digestion, but the rectal sacs are known to absorb nutrients.

Many starfish harbor commensals that derive nutrition from their host's leftovers. A polynoid scale worm, *Arctonoe vittata*, is an obligate symbiont living

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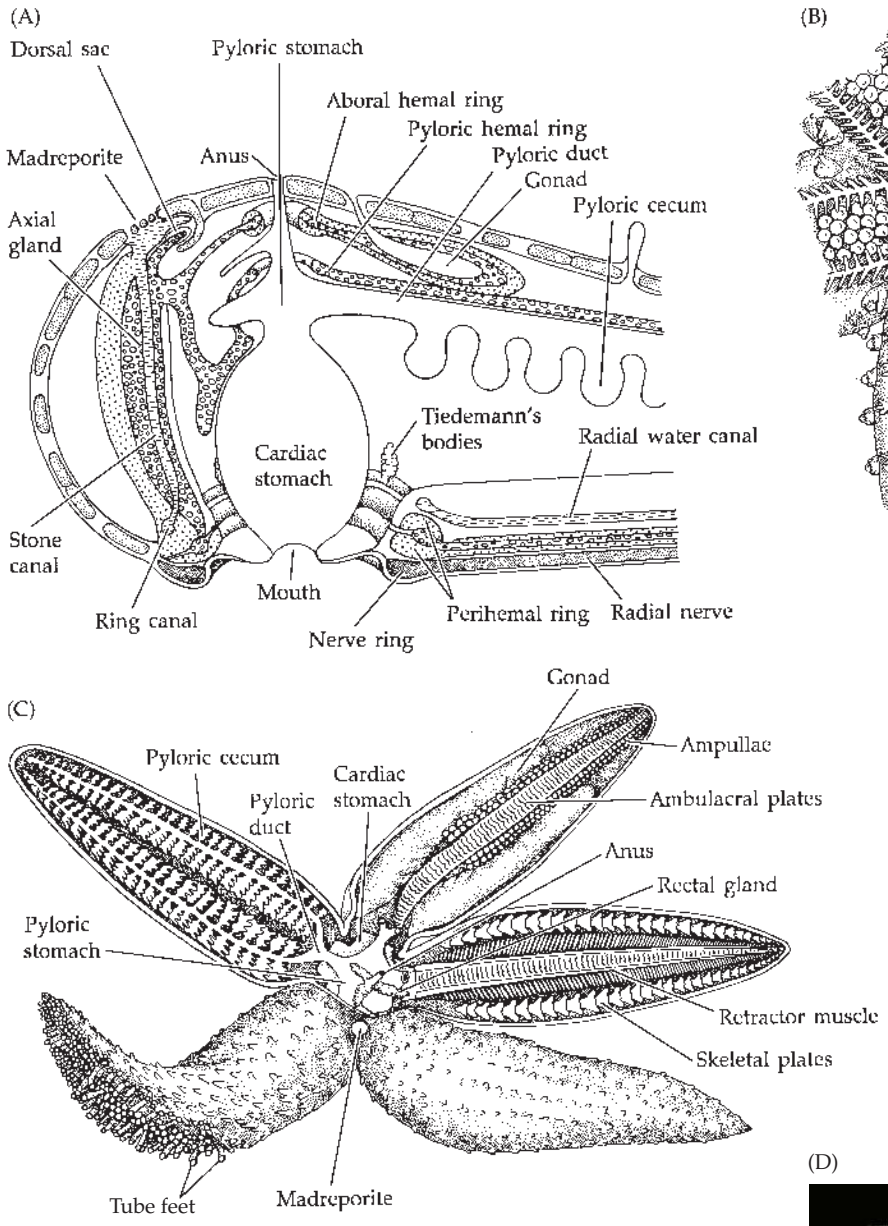

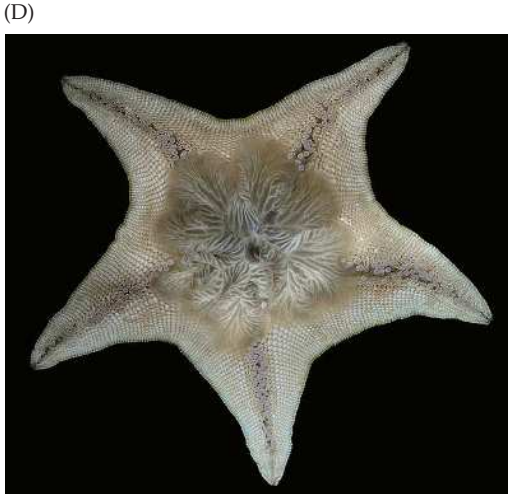

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FIGURE 26.8 Feeding and internal anatomy of starfish (Asteroidea). (A) The central disk and base of one arm of a starfish (vertical section). (B) *Asterias* (oral view). The mouth is ringed by oral spines and tube feet. (C) Internal organs in the disk and arms of the trivium of *Asterias*. Each dissected arm has various organs removed. (D) Protruded stomach of a deposit-feeding asteroid, *Patiria miniata*.

with several species of asteroids, including the Pacific leather star, *Dermasterias*. The worm spends most of its life cruising and feeding in the host's ambulacral grooves. Not only is the polychaete chemically attracted to its host, but studies indicate that *Dermasterias* is also attracted to *A. vittata*, suggesting that the starfish might also derive benefit from the association. Another polynoid from the northeast Pacific coast, *Arctonoe pulchra*, is commensal on several echinoderm species, including the sea cucumber *Apostichopus parvimensis*. Forms such as *Xyloplax* and caymanostellid "wood stars" (Figure 26.1G) that live only on sunken wood seem to be **xylophagous**, harboring cellulose-digesting gut bacteria that help the starfish derive nutrients from wood that starfish are otherwise incapable of digesting.

Ophiuroidea Brittle stars exhibit predation, deposit feeding, scavenging, and suspension feeding, and some species are capable of more than one feeding method. Basket stars (Figure 26.1I) are actually predators that utilize suspension-feeding behaviors to capture relatively large swimming prey (up to about 3 cm long).

Selective deposit feeding is accomplished in ophiuroids by tube feet and sometimes by spines along the arms. The arm spines and tube feet produce mucus to which organic material adheres. The tube feet roll the mucus and food into a bolus. Near the base of each tube foot is a flaplike projection called a **tentacle scale** (Figure 26.9B,D). The bolus is transferred from a tube foot

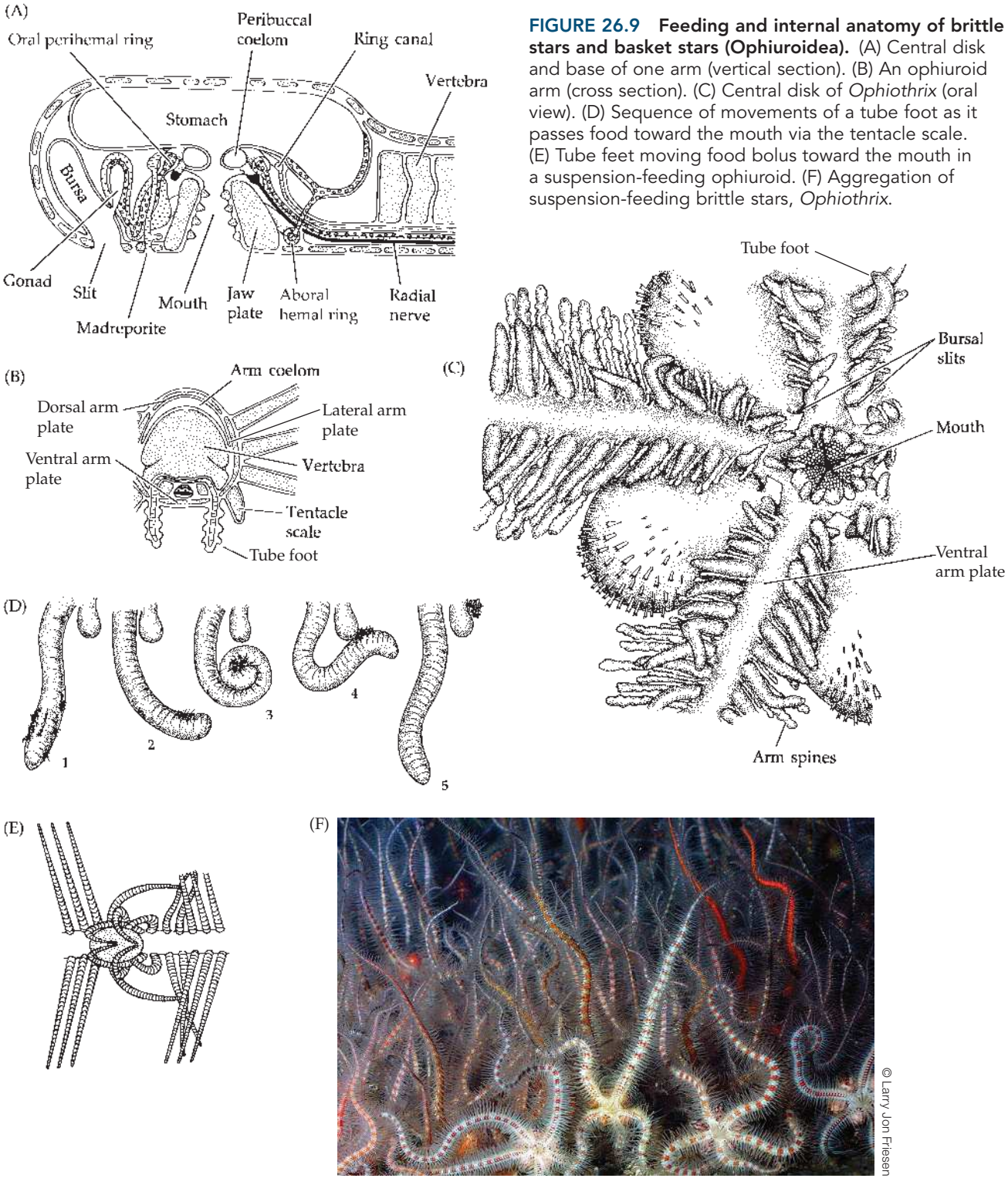

FIGURE 26.9 Feeding and internal anatomy of brittle stars and basket stars (Ophiuroidea). (A) Central disk and base of one arm (vertical section). (B) An ophiuroid arm (cross section). (C) Central disk of *Ophiothrix* (oral view). (D) Sequence of movements of a tube foot as it passes food toward the mouth via the tentacle scale. (E) Tube feet moving food bolus toward the mouth in a suspension-feeding ophiuroid. (F) Aggregation of suspension-feeding brittle stars, *Ophiothrix*.

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onto its adjacent scale, picked up by the next tube foot, and so on, transporting the food along the arm to the mouth. Suspension feeding usually involves a similar method of transport once food is trapped. Food capture is sometimes aided by secretion of mucous threads among the arm spines and holding the arms within currents to trap plankton and organic detritus. Brittle stars using this technique typically have very long arm spines (e.g., *Ophiocoma*, *Ophiothrix*). *Astrotoma* (a euryalid with unbranched arms) extends its arms (each up to 70 cm long) into the overlying water to capture planktonic copepods. Other brittle stars suspension feed by using extended tube feet to form a trap, passing clumps of food to the mouth (Figure 26.9E). Several species burrow to form semipermanent, mucus-lined burrows. The arms extend to the surface and help maintain ventilation currents within the burrows. Such species are able to extract food from the sediment, the substratum surface, and the overlying water. The commensal brittle star *Ophiothrix lineata* lives in the atrium of the large sponge *Callyspongia aculeata*, emerging to feed on detritus adhering to its host's outer surface. While keeping the sponge clean, the ophiuroid is supplied with food and afforded protection from predators.

Predatory suspension feeding by basket stars occurs mostly at night. At dusk the animals emerge from their hiding places and unfold and hold their branched arms fanlike, in a manner similar to that of feeding crinoids. *Astrophyton* changes position with the tidal direction, always orienting its arms into the current; it stops feeding at slack tide. When a small animal contacts an arm, the appendage curls to capture it by impaling it on microscopic hooks along the arm. Ingestion is often postponed until darkness has passed; the prey is then transferred to the mouth by the flexible arm. Basket stars feed on a variety of small invertebrates, such as swimming crustaceans and demersal polychaetes.

Some brittle stars are active predators, capturing benthic organisms by curling an arm into a loop around the prey, then pulling it to the mouth. Species that feed this way usually have short arm spines that lie flat against the arm (e.g., *Ophioderma*). *Ophiura sarsii*, an ophiuroid from northern temperate seas, acts in groups to subdue and tear apart active swimming prey, such as fishes and crustaceans.

In ophiuroids, the intestine and anus have been lost, and the digestive system is confined entirely to the central disk (Figure 26.9A). The mouth, surrounded by a jawlike set of modified ambulacral ossicles, leads to a short esophagus and large stomach in which digestion and absorption occur. Digested waste material is ejected back through the mouth. The stomach fills most of the interior of the disk, reducing the coelom to a thin chamber.

Echinoidea Echinoids engage in various kinds of herbivory, suspension feeding, detritivory, and rarely, predation and xylophagy. In typical globose urchins, feeding is facilitated by an intricate masticatory apparatus, the **Aristotle's lantern**, that lies just inside the mouth and bears five calcareous protractible teeth (Figure 26.10). It is an impressive example of evolutionary engineering: a complex of hard stereom elements and muscles that control protraction, retraction, and grasping movements of the teeth. Usually, the entire apparatus can be rocked so that the teeth protrude at different angles. There is great variation in lantern structure among echinoids, but the following applies to most conditions in which it is well developed.

The main structural part of the lantern (Figure 26.10) consists of five pairs of vertically oriented, calcareous, trapezoidal elements connected to form five triangular pyramids, each of which supports a single tooth in a groove called the tooth slide. The interambulacrally positioned pyramids are attached to one another by muscles that pull the pyramids (and the teeth) together to close the jaws. Along the aboral edge of each pyramid is a thickened bar, the epiphysis. Tooth honing occurs by the manner in which small platelets that make up the tooth are worn off, like a self-sharpening chisel. The tooth grows at the proximal end through the constant addition of new platelets where the tooth emerges from the top of the pyramid. This region is covered by a soft dental sac of coelomic origin that encloses the unhardened proximal end of each tooth. With normal wear, the teeth usually grow about 1 mm each week. Atop the main structure of the lantern are five, small, Y-shaped skeletal ossicles known as **compasses**, one along each ambulacral radius. The compasses and associated muscles appear to regulate hydrostatic pressure within the peripharyngeal coelom.

Protractor muscles originate from an interambulacral "lantern girdle" around the mouth and insert small skeletal elements (**rotules**) on the **epiphyses** that are attached to the proximal (upper) end of each pyramid. Contraction of these protractors pulls the entire lantern orally through the mouth, spreading the teeth apart (Figure 26.10A). Retractor muscles originate on thick ambulacral girdle extensions (auricles), inserting on the distal end of the lantern. Additional muscles associated with the pyramids and the rotules produce a variety of tooth movements.

Most urchins with well-developed lanterns use their teeth to scrape algae from the substratum and to bite off chunks of macroalgae. Some species feed on animal matter by similar actions. Some tiny, deep-water urchins nip pieces from sunken wood so that symbiotic microbes in their gut can digest the cellulose and release nutrients into the urchin's gut. Urchins that excavate burrows in hard substrata feed on the algal film that develops on the burrow wall. Others ingest suspended particles or drift algae that enter the chamber, or organic material trapped by spines, tube feet, and pedicellariae. Some irregular urchins

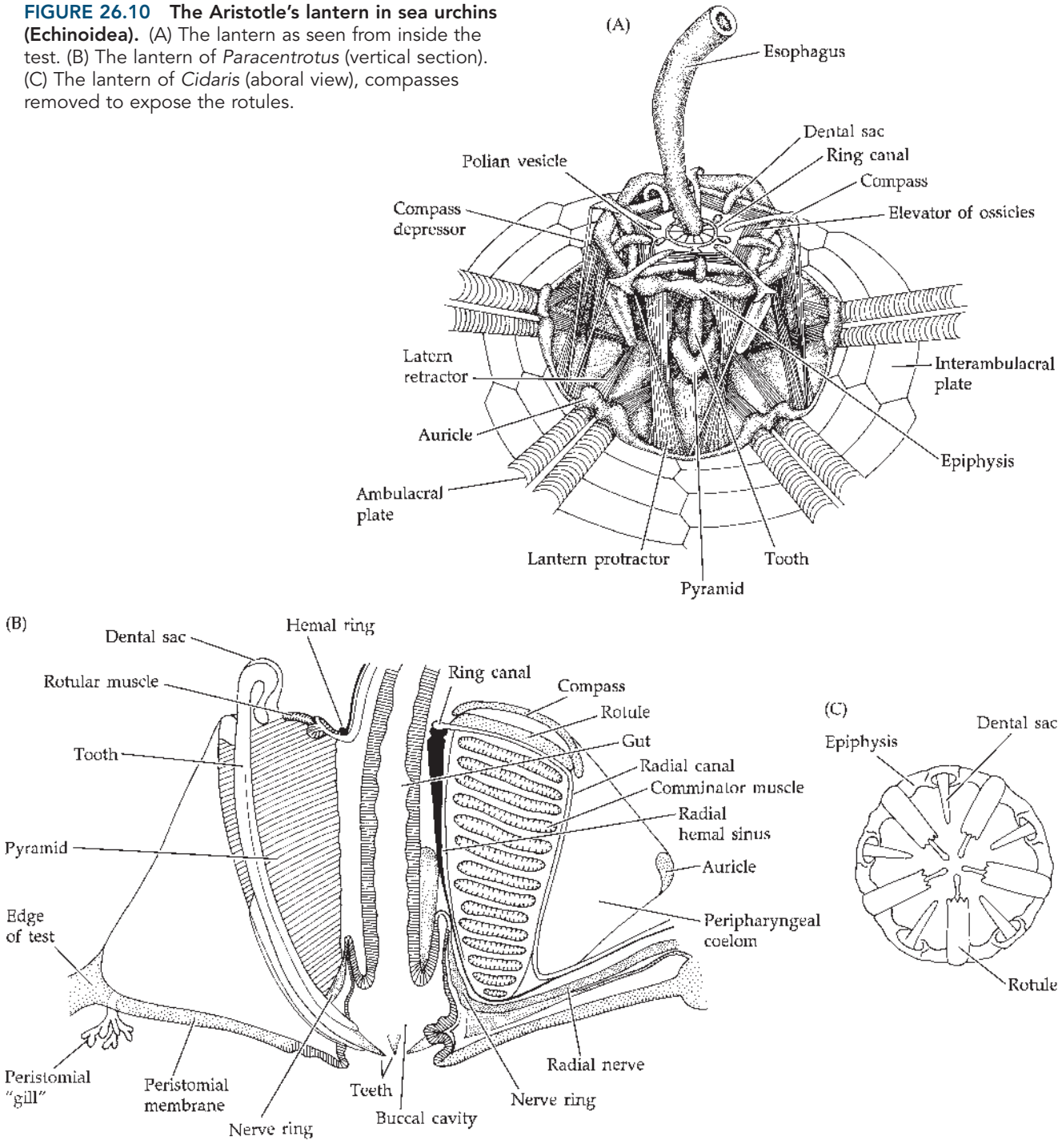

FIGURE 26.10 The Aristotle's lantern in sea urchins (Echinoidea). (A) The lantern as seen from inside the test. (B) The lantern of *Paracentrotus* (vertical section). (C) The lantern of *Cidaris* (aboral view), compasses removed to expose the rotules.

(e.g., cassiduloids and echinoneoids) lose the lantern before adulthood, and spatangoid heart urchins never develop one. Spatangoids burrow and swallow the sediment to digest the contained organic material (Figure 26.11G). Tube feet can be used to sort food material from the mud or sand and pass it to the mouth. The superimposed bilateral symmetry derived from evolutionary movement of the anus from the apical system to a functional "posterior" in irregular echinoids is an adaptation to sediment-swallowing habits, much as in an earthworm.

Most sand dollars are "podial particle pickers," possessing a highly modified lantern with nonprotractable teeth that act as a crushing mill. As they move over the sediment, sand dollars select organic-rich material using thousands of miniaturized tube feet distributed in fields over the oral surface, add mucus to the particles, and pass them into food grooves. Specialized tube feet act as a "bucket brigade" to shunt mucus-coated particle trains to the mouth (Figure 26.11E). Related to the sand dollars, sea biscuits feed on larger particles, including bits of seagrass.

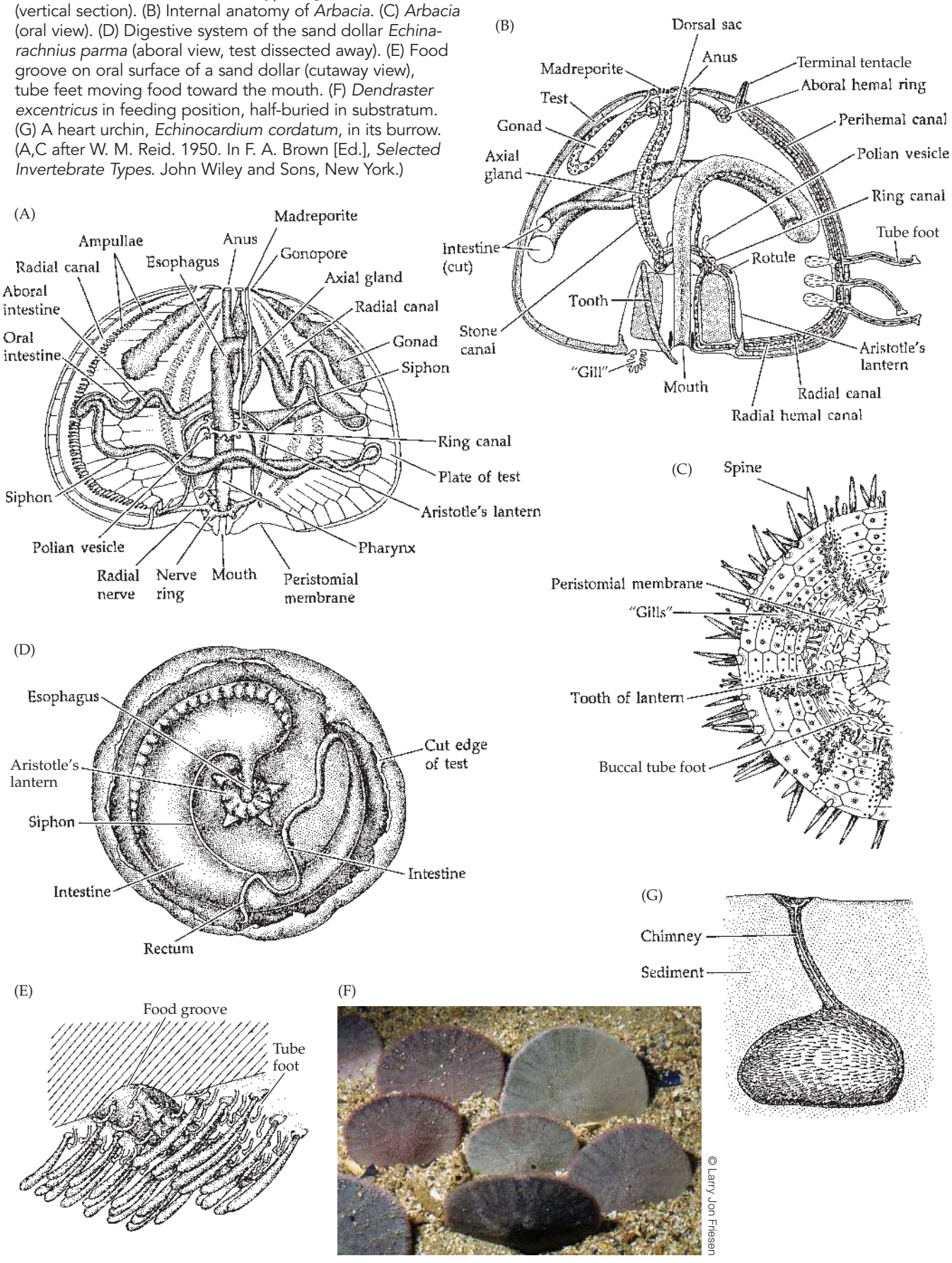

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FIGURE 26.11 Feeding and internal anatomy of sea urchins (Echinoidea). (A) A typical globose sea urchin (vertical section). (B) Internal anatomy of *Arbacia*. (C) *Arbacia* (oral view). (D) Digestive system of the sand dollar *Echinarachnius parma* (aboral view, test dissected away). (E) Food groove on oral surface of a sand dollar (cutaway view), tube feet moving food toward the mouth. (F) *Dendraster excentricus* in feeding position, half-buried in substratum. (G) A heart urchin, *Echinocardium cordatum*, in its burrow. (A,C after W. M. Reid. 1950. In F. A. Brown [Ed.], *Selected Invertebrate Types*. John Wiley and Sons, New York.)

Dendraster excentricus buries the anterior portion of its body in the sand so that the posterior part extends upwards above the sediment (Figure 26.11F), trapping diatoms and other particulate food in the water with its tube feet and ingesting it as described above. Tiny crustaceans can be captured by the pedicellariae. Members of most populations of *Dendraster* position themselves in groups oriented edgewise into the current, exploiting hydrodynamic properties of ambient flow to enhance each other's food collection process. Some sand dollars have high-density sand grains (especially those containing iron oxides) stored in a diverticulum of the gut as ballast to help stabilize their position on the sea bottom. Microechinoids (e.g., *Echinocyamus*) nestle among coarse sand grains, which are brought to the mouth by tube feet, then rotated by the peristomial membrane and tube feet as the teeth scrape off attached diatoms and organic detritus.

The digestive system of echinoids is essentially a simple tube from mouth to anus. The mouth is at the center of the oral surface, or it is shifted slightly anteriorly in some irregular urchins; the anus is on the aboral surface, located centrally or shifted posteriorly. An esophagus extends through the vertical axis of the lantern (when present) to join an elongate stomach-intestine (Figure 26.11A,B,D). In most echinoids, a narrow duct (the **siphon**) parallels the intestinal tract for part of its length. Both ends of this siphon open to the intestine, possibly providing a shunt for excess water taken in with the food. In many species, blind ceca of uncertain function arise from the gut near the junction of the esophagus and stomach-intestine. The intestine narrows into a short rectum leading to the anus, located either centrally in the apical system or at various points along the posterior interambulacrum. Digestive enzymes are produced by the intestinal and cecal walls, and breakdown is largely extracellular.

Holothuroidea Most sea cucumbers are suspension or deposit feeders. Many of the sedentary epibenthic or nestling forms (e.g., *Eupentacta, Psolus, Cucumaria*) extend their branched, mucus-covered tentacles (Figure 26.12D,E) into the water to trap suspended material, including live plankton and organic detritus. The tentacles are then pushed into the mouth one at a time and the food ingested (Figure 26.12F). A supply of mucus is provided by secretory cells in papillae on the tentacles and gland cells of the foregut.

More active epibenthic types (e.g., *Stichopus*) crawl across the substratum and use their tentacles to collect and ingest sediment and organic detritus (Figure 26.12C). Studies indicate that some holothuroids (e.g., *Stichopus*, *Holothuria*) are highly selective deposit feeders, preferentially collecting sediments rich in organic content. Many apodid holothuroids ingest sediment as they burrow through the substratum by peristaltic movements.

The anterior mouth is surrounded by a whorl of buccal tentacles. The esophagus (or pharynx) leads inward and passes through a ring of calcareous plates supporting the foregut and ring canal of the water vascular system. The esophagus joins an elongate intestine, the anterior of which is often enlarged as a stomach. The intestine, along which digestion and nutrient absorption occurs, extends posteriorly, loops forward, and then posteriorly again, sometimes in coils (Figure 26.12A,B). The intestine terminates in an expanded rectum leading to the posterior anus. The rectal area is attached to the body wall by a series of suspensor muscles and often bears highly branched outgrowths, the **respiratory trees**, that extend anteriorly within the body cavity. Water is pumped via the anus into the trees for gas exchange (Figure 26.12A,B,H).

The digestive system of sea cucumbers exhibits two fascinating phenomena: (1) auto-evisceration and (2) the discharge of structures called Cuvierian tubules (Figure 26.12H,I). Evisceration is the expulsion by autotomy and muscular action of part or all of the muscles, digestive tract, and sometimes other organs, including the respiratory trees and gonads. These lost parts are usually regenerated. In some forms, these structures are expelled following rupture of the hindgut region. In others, rupture occurs anteriorly and the feeding tentacles and foregut are lost. Evisceration can be induced in the lab by chemical stress, physical manipulation, and crowding, but it also occurs in nature in some species, although its significance remains unclear. It is viewed by some as a seasonal event associated with adverse conditions, and by others as a defense mechanism wherein eviscerated parts serve as sacrificed decoys.

Cuvierian tubules are clusters of sticky, blind tubules arising from the base of the respiratory trees in certain genera (e.g., *Actinopyga*, *Holothuria*) (Figure 26.12A,H,I). When threatened, these holothuroids aim the anus at the potential predator and contract the body wall to discharge the tubules by rupturing the hindgut, everting the tubules onto the predator and entangling it in a mass made extremely sticky by secretions from the tubules. The Cuvierian tubules are regenerated. Such elaborate defense mechanisms are important, since holothuroids can fall prey to various fishes, starfish, gastropods, crustaceans, and even humans.

Circulation and Gas Exchange

Circulation Internal transport in echinoderms is accomplished largely by the main perivisceral coeloms, variously augmented by hemal and water vascular systems (Figure 26.13), both of which are derived from the coelom. Fluids move through these systems primarily by ciliary action and in some cases by muscular pumping. In at least one species of sea urchin (*Lytechinus variegatus*), coelomic fluid is known to be driven by movements of Aristotle's lantern.

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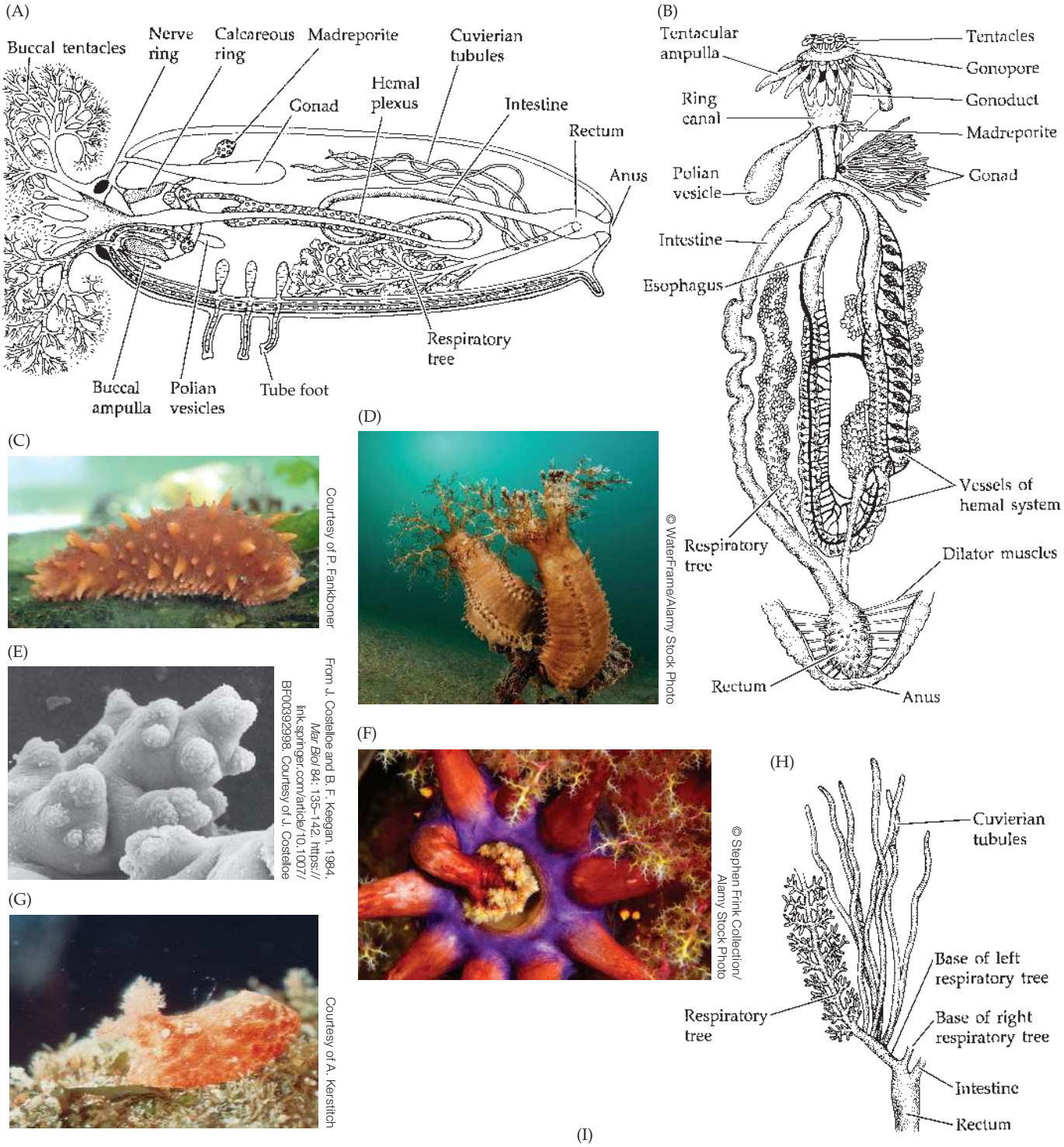

FIGURE 26.12 Feeding and internal anatomy of sea cucumbers (Holothuroidea). (A) Feeding and digestive structures in a sea cucumber (longitudinal section). (B) Major internal organs of *Holothuria tubulosa*. (C) *Parastichopus*, a deposit feeder. (D) Feeding tentacles of *Cucumaria*, tentacles extended. (E) Scanning electron micrograph of mucus-secreting papillae on tentacles of *Aslia lefevrei*. (F) Feeding tentacles of *Pseudocolochirus violaceus*. (G) *Psolidium*, a suspension-feeding holothuroid with buccal tentacles directed upward. (H) Respiratory tree and Cuvierian tubules of *Holothuria impatiens*. (I) Release of Cuvierian tubules by *Holothuria*.

The hemal system is a complex array of canals and spaces, mostly enclosed within coelomic channels called **perihemal sinuses**. The system is best developed in holothuroids, in which it is bilaterally arranged, and in crinoids, in which the channels can form netlike plexi. In other groups the system is radially arranged and generally parallels the elements of the water vascular system consisting of oral and aboral **hemal rings**, each with radial extensions. The two rings are connected by an axial sinus (Figure 26.13A) that lies against the stone canal. Within the axial sinus there is a core of spongy tissue called the **axial gland**, thought to be responsible for producing certain coelomocytes. Radial hemal channels extend from the aboral ring to the gonads. Other radial channels arise from the oral hemal ring and are associated with the rows of tube feet; these channels are housed within a perihemal space called the hyponeural sinus (Figures 26.3B and 26.13A). A third hemal ring, the gastric ring, occurs in many echinoderms, including most asteroids, and is associated with the digestive system.

Cilia move fluid through the hemal system. In asteroids and most echinoids the axial sinus bears a **dorsal sac** near its junction with the aboral hemal ring. This sac pulsates, likely to aid fluid movement within hemal spaces. The hemal system of holothuroids includes an elaborate set of vessels intimately associated with the digestive tract (Figure 26.13B) and, when present, the respiratory trees. In many holothuroids the hemal system can include a multitude of "hearts" or circulatory pumps.

The function of the hemal system is not fully understood, but it probably helps distribute nutrients absorbed from the digestive tract. Experiments on the starfish *Echinaster graminicola* show that absorbed nutrients appear in the hemal system within a few hours after feeding and eventually concentrate in gonads and tube feet. In sea cucumbers the hemal system probably also plays a role in gas exchange because some of the vessels are in contact with the respiratory trees.

Gas exchange Most echinoderms rely on thin-walled external processes as gas exchange surfaces. Crinoids apparently exchange oxygen and carbon dioxide between the coeloms and the ambient seawater across all exposed thin parts of the body wall, especially the tube feet. Only ophiuroids and holothuroids have specific internal organs for respiration. Given the relatively large coelomic volumes of many echinoderms, and the lack of circulatory connections from the inside to the outside of the body wall, coelomic fluid transport mechanisms figure prominently in internal gas exchange, whereas external tissues exchange directly with the ambient seawater.

Gas exchange in asteroids occurs across tube feet and special outpocketings of the body wall called **papulae** (Figure 26.14A,B), which are evaginations of the epidermis and peritoneum. Both tissues are ciliated to produce currents in both the coelomic fluid and the overlying water. The two currents move in opposite directions, setting up countercurrents that maximize concentration gradients across the surfaces of papulae.

Ophiuroids possess ten invaginations of the body wall, called **bursae**, that open to the outside via ciliated slits (Figure 26.9A,C). Water circulates through the bursae by cilia and, in some species, by muscular pumping of the bursal walls. Gases are exchanged between flowing water and body fluids. Hemoglobin occurs in the coelomocytes of a few species of ophiuroids.

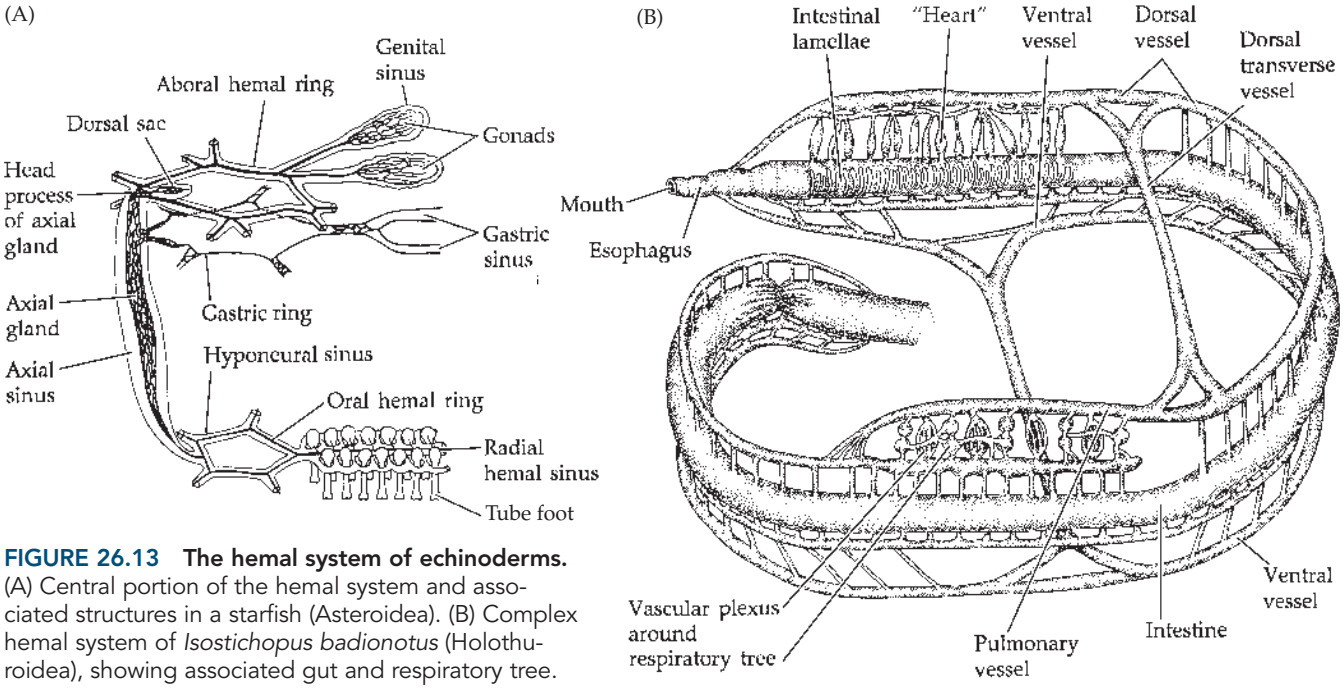

FIGURE 26.13 The hemal system of echinoderms. (A) Central portion of the hemal system and associated structures in a starfish (Asteroidea). (B) Complex hemal system of *Isostichopus badionotus* (Holothuroidea), showing associated gut and respiratory tree.

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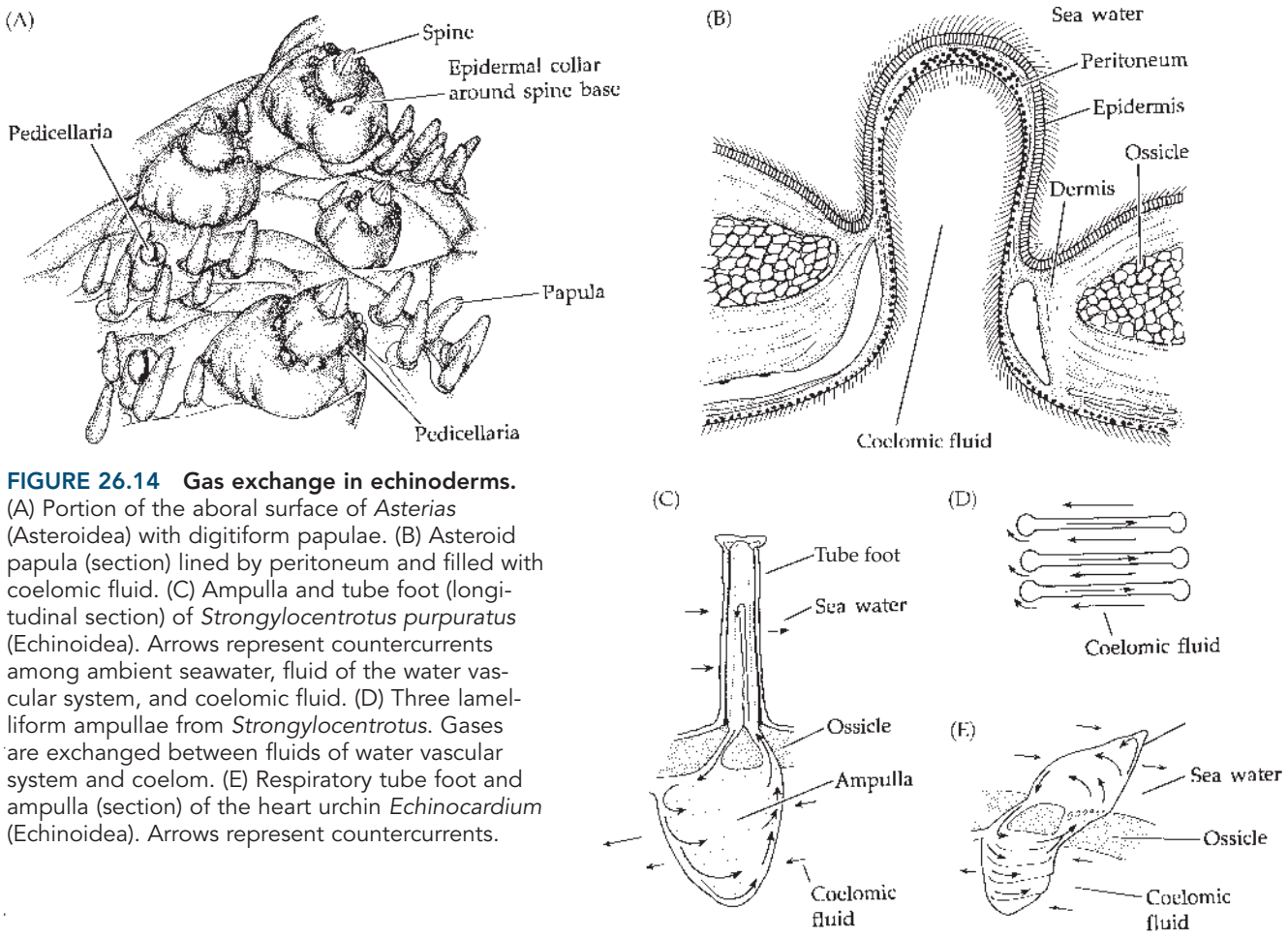

FIGURE 26.14 Gas exchange in echinoderms. (A) Portion of the aboral surface of *Asterias* (Asteroidea) with digitiform papulae. (B) Asteroid papula (section) lined by peritoneum and filled with coelomic fluid. (C) Ampulla and tube foot (longitudinal section) of *Strongylocentrotus purpuratus* (Echinoidea). Arrows represent countercurrents among ambient seawater, fluid of the water vascular system, and coelomic fluid. (D) Three lamelliform ampullae from *Strongylocentrotus*. Gases are exchanged between fluids of water vascular system and coelom. (E) Respiratory tube foot and ampulla (section) of the heart urchin *Echinocardium* (Echinoidea). Arrows represent countercurrents.

Typical sea urchins possess five pairs of lobate gills around the **peristome**, or the opening in an echinoid test surrounding the mouth (Figure 26.11B,C). These were long viewed as important gas exchange organs. However, various authors have provided evidence of a different function. The pressure within these gills changes by manipulation of the compasses of Aristotle's lantern, so gills probably function to accommodate pressure changes in the peripharyngeal coelom during movements of the lantern and perhaps to enhance oxygen supply to associated muscles. The main gas exchange structures in urchins are thin-walled tube feet that operate on a countercurrent system similar to that associated with the papulae of asteroids (Figure 26.14C,D). Irregular urchins such as heart urchins and sand dollars bear highly modified respiratory tube feet arranged in modified aboral ambulacral regions of the test called **petaloids** (Figure 26.2E,J). Respiratory tube feet are leaflike and thin walled to serve as gas exchange surfaces. A countercurrent flow occurs between water vascular system fluid in the tube foot and seawater, and between water vascular system fluid in the internal ampullae and coelomic fluid.

In the respiratory trees of certain holothuroids, water is pumped in and out of the hindgut and branches of the respiratory trees, and gases are exchanged between the water and the coelomic and hemal systems. This process is augmented by exchange across the tube feet, which is facilitated by a countercurrent system. Hemoglobin occurs in the coelomocytes of many holothuroids.

Excretion and Osmoregulation

Excretion In most echinoderms, dissolved nitrogenous wastes (ammonia) diffuse across body surfaces to the outside. This type of excretion occurs across the tube feet and papulae in asteroids and is suspected to occur across the paired respiratory trees in holothuroids.

Precipitated nitrogenous material and other particulate wastes are phagocytized by specialized coelomocytes in body fluids and then discharged by various methods. In asteroids, waste-laden coelomocytes can accumulate in papulae, which then pinch off their distal ends, expelling the cells and waste material. Some studies suggest that rectal glands might also be involved in excretion. In ophiuroids it is suspected that coelomocytes deliver wastes to the bursae, where they are released. Phagocytic coelomocytes in echinoids accumulate wastes and transport them to the tube feet and gills for release. In holothuroids, particulate wastes are carried by coelomocytes to the respiratory trees,

gut, and even the gonads, and released to the outside. Crinoid coelomocytes deposit wastes in tiny pockets along the sides of the ambulacral grooves.

Osmoregulation Echinoderms are generally strictly marine stenohaline creatures that do not have to deal with severe osmotic and ionic regulation. However, some species have been reported from brackish water. For example, *Asterias rubens* (Asteroidea) has been collected from the Baltic Sea (8% salinity), *Ophiophragmus filograneus* (Ophiuroidea) from Cedar Key, Florida (7.7% salinity), and various holothuroids from the Black Sea (18% salinity). Some mechanism must allow these taxa to survive in such low salinities, but it is, as yet, unknown. Evidence suggests that echinoderms are osmoconformers. Both water and ions pass relatively freely across thin body surfaces, and the tonicity of the body fluids varies with environmental fluctuations. There appears to be some ionic regulation through active transport, but it is minimal.

Nervous System and Sense Organs

The derived pentaradiality of echinoderms is clearly reflected in the anatomy of their nervous systems and the distribution of their sense organs. The nervous system is decentralized, somewhat diffuse, and without significant ganglia. There are three main neuronal "systems," integrated with one another and developed to varying degrees among the clades: ectoneural (oral), hyponeural (deep oral), and entoneural (aboral). The **ectoneural system** is predominately sensory, although motor fibers do occur; the **hyponeural system** is largely motor in function. The **entoneural system** is absent from holothuroids and reduced to different degrees in other groups—except the crinoids, in which it is the primary nervous system, serving both motor and sensory functions. Note that these terms refer only to the *position* of the neuronal systems, not to their embryological origins.

The three systems are interconnected by a nerve net derived primarily from ectoneural and entoneural components. The net is described as a subepidermal plexus, but it gives rise to intraepidermal neurons and clearly has an intimate association with the epithelium both internal and external to the body wall. Except for crinoids, in which the entoneural component predominates, the most obvious nerves in echinoderms are derived from the ectoneural system. A circumoral nerve ring just beneath the oral epithelium encircles the esophagus. From this ring arise radial nerves extending along each ambulacrum. In starfish, these radial nerves appear as a distinct V-shaped, epidermal thickening in each ambulacral groove (Figure 26.3B). The entoneural nerve plexus also produces radial cords, such as those along the margins of asteroid arms. The hyponeural system generally parallels the nerves of the ectoneural system. Hyponeural neurons are subepidermal and lie near the hyponeural sinus of each ambulacral area (Figure 26.3B), giving rise to motor fibers and ganglia in the tube feet.

Sensory receptors are largely restricted to relatively simple epithelial structures innervated by a plexus of the ectoneural system. Frequently associated with outgrowths of the body wall, such as spines and pedicellariae, sensory neurons in the epidermis respond to touch, dissolved chemicals, water currents, and light. Photoreceptors occur in asteroids as light-sensitive regions comprising pigment-cup ocelli at the tips of the arms. Some brittle stars (e.g., *Ophiocoma*) have a comprehensive network connecting opsin-containing cells across the body surface. Statocysts are known in some holothuroids, while in certain echinoids there are structures called **sphaeridia** that are thought to function in georeception. Chemoreception is understudied in echinoderms, but some evidence suggests that buccal tentacles of holothuroids and oral tube feet of echinoids are sensitive to dissolved chemicals. Chemoreception in asteroids appears to depend largely on direct contact, although distance chemoreception is reported in some species. Larvae are reported to respond to pheromones in the water column in order to metamorphose.

In spite of their rather simple nervous system and lack of specialized sense organs, many echinoderms engage in complex behaviors. Time-lapse videos of echinoderms reveal that they have complex interactions similar to any invertebrate—they just do nearly everything at such a slow pace that it is difficult to notice. There is still much to be learned about functional mediation between circuitry of the nervous system and observed behavioral responses, as in coordination of tube feet and spines during locomotion. Most echinoderms exhibit distinct righting behaviors when overturned—actions involving touch, georeception, and perhaps photoreception. Orientation to currents is known in some sand dollars and in many ophiuroids and crinoids, and responses to potential predators often include coordination of spine movements, pedicellariae, and locomotion.

Reproduction and Development

Regeneration and asexual reproduction Echinoderms have remarkable powers of regeneration. Tide pool observers often encounter starfish regenerating a new arm, or notice tube foot suckers left on a rock from which a starfish or urchin has been pulled free. Lost suckers are quickly replaced by regeneration. During the processes of evisceration and expulsion of Cuvierian tubules, multiple lost organs are replaced. Damage to the test of echinoids, even perforation and loss of plates, is usually followed by healing and regeneration of the plates and associated appendages. Studies have put to rest tales of oystermen claiming

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that chopping starfish into small pieces resulted in regeneration of an entire new animal from each part. Although a damaged animal can grow new arms if a substantial portion of the central disk remains intact, an isolated arm soon dies. However, an exception to this is *Linckia*, which can regenerate an entire individual from a single arm, the regenerating stage being appropriately called a **comet** (Figure 26.15). Ophiuroids and crinoids frequently cast off arms or arm fragments when disturbed, then regenerate the lost part. Such autotomy is also documented for certain asteroids. The Pacific coast ochre star, *Pisaster ochraceus*, autotomizes arms at their junction with the central disk when confronted by predators. Deep-sea isocrinid sea lilies autotomize distal portions of their stems to distract echinoid predators.

Asexual reproduction occurs in some asteroids, ophiuroids, and holothuroids by **fissiparity**. In the stellate forms the central disk divides in two, and each half forms a complete animal by regeneration. When forms such as certain species of the small six-rayed brittle star *Ophiactis* divide, each half retains three arms. Asexual fission also occurs in some holothuroids, but the process is not well understood.

Sexual reproduction The majority of echinoderms are gonochoristic, but hermaphroditic species are known among asteroids, holothuroids, and especially ophiuroids. The reproductive system is relatively simple and intimately associated with derivatives of the coelom. Gonads are usually housed within genital sinuses lined with peritoneum. Holothuroids are unique among extant echinoderms in possessing a single gonad, which lies "dorsally" (Figure 26.12A,B). A single gonoduct opens between the bases of two "dorsal" buccal tentacles or just posterior to the tentacular whorl, and this is why they often raise the oral end when spawning.

Crinoids lack distinct gonads. Gametes arise from the peritoneum of special coelomic extensions, called genital canals, in the pinnules extending from the proximal portion of each arm. There are no gonoducts; gametes are released by rupture of pinnule walls. Ophiuroids possess from one to many gonads attached to the peritoneal side of each bursa adjacent to the bursal slits (Figure 26.9A). Gametes are released into the bursae and expelled through the slits.

Asteroids and echinoids possess multiple gonads (Figures 26.8C and 26.11B) with gonoducts leading to interambulacral gonopores (Figure 26.8A). Typical sea urchins contain five gonads, one in each interradius. Gonopores are located on the five interambulacral genital plates of the apical system (Figures 26.3F and 26.11A). The **periproct** (the opening of an echinoid test surrounding the anus) and anus have migrated posteriorly in irregular urchins, but the genital plates remain more or less centrally located on the aboral surface. In most irregular echinoids there are only four (and sometimes fewer) gonads, one being lost along the line of migration of the anus, with corresponding reduction in number of gonopores. In urchins typically one of the genital plates is perforated and functions as a madreporite.

Echinoderm life history strategies vary, from free spawning followed by external fertilization and indirect development, to various forms of direct development and brooding. Studies indicate that spawning is mostly a nocturnal event, wherein the animals assume characteristic postures with their bodies elevated off the substratum, especially holothuroids, asteroids, and ophiuroids. In at least some asteroids and echinoids, gametogenesis is regulated by photoperiod, which ensures more or less synchronous spawning among members of the same population. In some species of free-spawning asteroids, females release pheromones that stimulate sperm release from nearby conspecific males, and many species aggregate before spawning to enhance fertilization success.

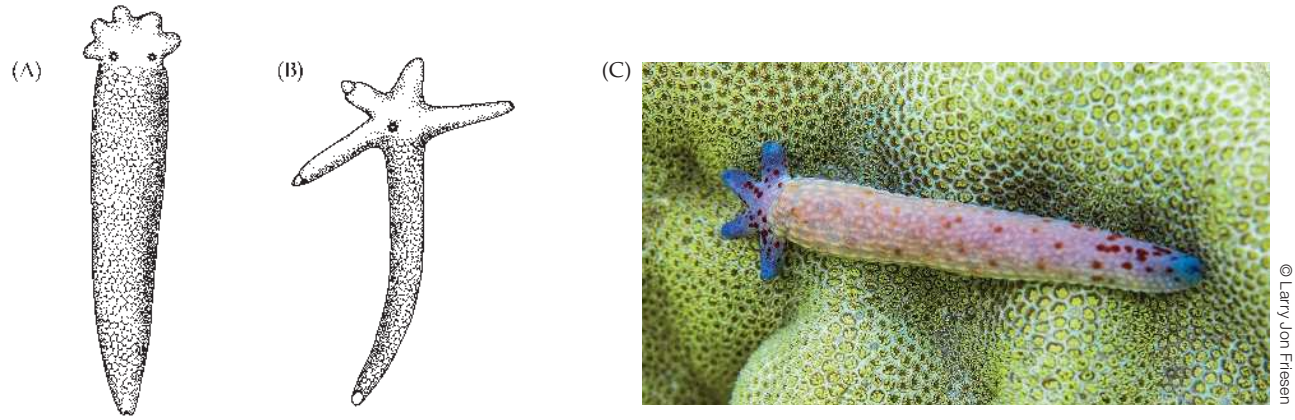

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FIGURE 26.15 Regeneration in the starfish *Linckia* (Asteroidea). (A) Initial regeneration from a single arm, yielding a central disk with dual madreporites and five new rays. (B) Later stage, with a single madreporite and normal number of rays. (C) Comet stage of *Linckia multiflora*.

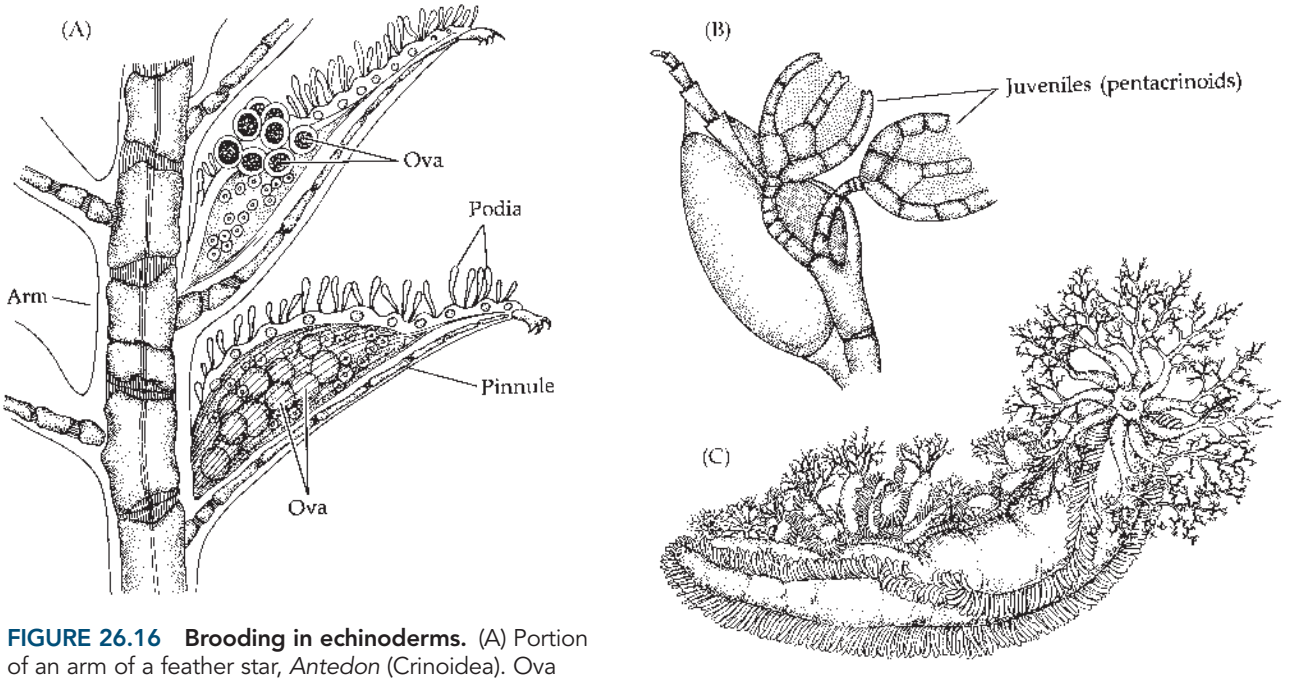

FIGURE 26.16 Brooding in echinoderms. (A) Portion of an arm of a feather star, *Antedon* (Crinoidea). Ova are housed within a pinnule and released to exterior. (B) Part of a pinnule of the crinoid *Phrixometra* (Crinoidea) with developing young. (C) *Cucumaria crocea* (Holothuroidea), brooding young. (D) Antarctic asteroid *Diplasterias* with brood of young around mouth.

Courtesy of G. Giribet

Brooding is especially common among boreal and polar species (in all groups of echinoderms) (Figure 26.16C) and in certain deep-sea asteroids, whose environments might be unfavorable for larval life. Brooding species produce fewer but larger and yolkier eggs than do their free-spawning counterparts. Among the crinoids, *Antedon* and a few others cement their eggs to the epidermis of the pinnules from which they emerge (Figure 26.16A,B); once eggs are fertilized by free sperm, embryos are held by the parent until hatching. Most brooding asteroids hold embryos on the body surface. One species from the northeastern Atlantic and Mediterranean (*Asterina gibbosa*) cements its eggs to the substratum, and another from the northwestern Atlantic (*Leptasterias tenera*) broods its early embryos in the pyloric stomach before moving them to the outer body surface. The deep-sea *Xyloplax* and caymanostellid wood stars (Figure 26.1G) seem to brood within the gonads, releasing juveniles that drift or crawl away. Brooding is common among ophiuroids. Sperm enter the bursae and fertilize the eggs, and embryos are held within these sacs during development. Some echinoids brood embryos and young urchins among clusters of spines on the body, around the peristome, in depressions caused by the sunken petaloids of females or, remarkably, in body wall invaginations at the apical system through which the urchins are "born." Brooding holothuroids usually carry their embryos externally (Figure 26.16C), but some species of *Thyone* and *Leptosynapta* brood inside the coelom.

Development The tremendous numbers of eggs produced by many echinoderms, and the ease with which they can be reared in the laboratory, have made many of these animals embryological model organisms, from studying the original characterization of the dynamic changes of transcription during embryogenesis to analyses of gene regulatory networks. Much of our information about biology of animal fertilization and early development comes from over a century of work on urchins and starfish, and early ontogeny of some echinoderms serves as a model of deuterostome development. Except in brooding species, in which development is modified by large amounts of yolk, the sequence of ontogenetic events is remarkably similar throughout the phylum.

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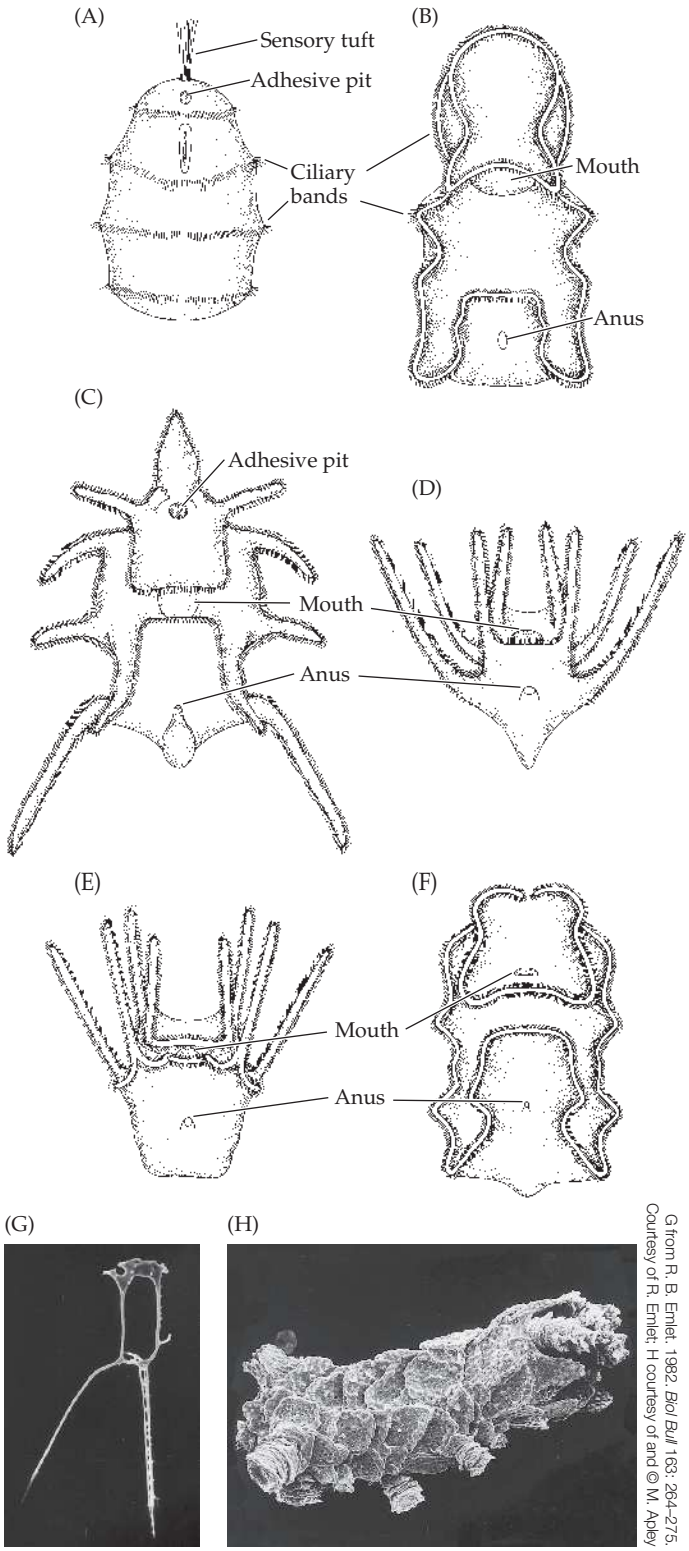
It is impossible to completely cover the vast amount of information on this subject; what is provided here is only a brief overview of indirect development based largely on urchins and asteroids, including some comparative comments on other taxa. As you read this section, keep in mind the fact that echinoderm development produces two very different body organizations in succession: first a bilaterally symmetrical larva and later a radially symmetrical adult.

In free-spawning echinoderms, after sperm enters the vitelline layer on the egg, a fertilization membrane forms (which facilitates recognition of which eggs have been fertilized). The ova are usually isolecithal with relatively small amounts of yolk. Cleavage is radial, holoblastic, and initially equal or subequal, leading to a spacious coeloblastula. In groups such as echinoids, cleavage preceding the blastula becomes unequal, resulting in blastomere tiers of animal pole **mesomeres** underlain by slightly larger **macromeres** and a cluster of **micromeres** at the vegetal pole. (These terms refer only to the relative sizes of the cells and are not to be confused with the same terms used in describing spiral cleavage.) The coeloblastula usually becomes ciliated and breaks free of the fertilization membrane as a swimming embryo. As in many other phyla, this stage of development is known as the **primary larva**, characterized in part by the **apical organ**—a cluster of ciliated cells with sensory ability thought to aid in orientation of the larva during settlement. Although there is evidence that the apical organ is homologous across many invertebrate phyla, the number of cells in, and the overall shape of the apical organ varies among the five echinoderm classes.

The blastula flattens slightly at the vegetal pole, forming the gastral plate from which some cells proliferate into the blastocoel as primary or larval mesoderm (sometimes called "mesenchyme"), which is destined to become larval muscles, skeletal elements (Figure 26.17G), and coelomic pouches. In most echinoids these cells are micromeres. The surrounding macromeres are presumptive endoderm and adult mesoderm; the vegetal mesomeres are presumptive ectoderm. A coelogastrula is produced by invagination of the vegetal pole cells. The blastopore typically forms the anus; the archenteron grows to connect with a stomodeal inpocketing that forms the mouth. Before the gut is complete, the inner end of the archenteron proliferates, as do one or two evaginations of mesoderm, into the blastocoel. Thus, coelom formation is by archenteric pouching (enterocoely).

Some types of echinoderm larvae also develop a **larval skeleton**, composed of spicules and ossicles. The functions of the larval skeleton include defense, physical support, sites of muscle attachment, and passive orientation of larvae in the form of "arms" (not homologous to arms of starfish and other echinoderm adults) that aid in swimming and feeding. The larvae



G from R. B. Emlet. 1982. *Biol Bull* 163: 264–275. Courtesy of R. Emlet. H courtesy of and © M. Abley

FIGURE 26.17 Echinoderm larval types. (A) Vitellaria larva of a sea lily (Crinoidea). (B,C) Bipinnaria and later brachiolaria larvae of a starfish (Asteroidea). (D) Ophiopluteus larva of a brittle star (Ophiuroidea). (E) Echinopluteus larva of a sea urchin (Echinoidea). (F) Auricularia larva of a sea cucumber (Holothuroidea). (G) Scanning electron micrograph (SEM) of isolated larval spicule from the sand dollar *Dendraster* (Echinoidea). (H) SEM of late pentacula stage (postlarva) of a sea cucumber (Holothuroidea); notice the rudimentary tube feet already formed.

of some echinoderms have distinctive reddish pigment spots that contain carotenoproteins, red pigments that can react to light and change the characteristics of cell membranes. The specific functions of these pigments in echinoderm larvae remain unknown. Planktotrophic echinoderm larvae use bands of cilia along the "arms" or on the body itself to swim and generate feeding currents. However, lecithotrophism is common and apparently evolved numerous times within some echinoderm classes.

In order to understand the development of echinoderm larvae and their eventual metamorphosis to radially symmetrical adults, it is necessary to examine the embryogeny and fates of the coeloms. There are some differences in details among groups, but there is enough similarity to allow a generalized summary. The initial archenteric pouching occurs from the blind end of the developing gut, either as a pair of coeloms or as one cavity that divides into two. These coeloms pinch off another pair of cavities posteriorly, and then a third pair between the anterior and posterior ones (Figure 26.18A). From front to back, these pairs of coelomic spaces are the left and right **axocoels** (known in other deuterostomes as the protocoels), the hydrocoel and "dorsal sac" (left and right mesocoels), and left and right somatocoels (metacoels in the nonechinoderm literature), as seen in other trimeric deuterostomes. The left axocoel and hydrocoel remain connected to one another. From the left axocoel-hydrocoel complex, a "hydrotube" extends to the "dorsal" surface of the larva, opening to the outside via a hydropore. The dorsal sac becomes associated with the hydrotube leading to the hydropore. Usually, the right axocoel disappears.

The fates of coelomic derivatives are outlined in Table 26.1. As the time for metamorphosis approaches, the larva swims to the bottom, selecting and attaching to an appropriate substratum. In general, the larval left and right sides become the adult oral and aboral surfaces, respectively, although this pattern does not always reflect a precise 90° reorientation. The change from bilateral to radial symmetry involves shifts in the positions of mouth and anus, which both close during

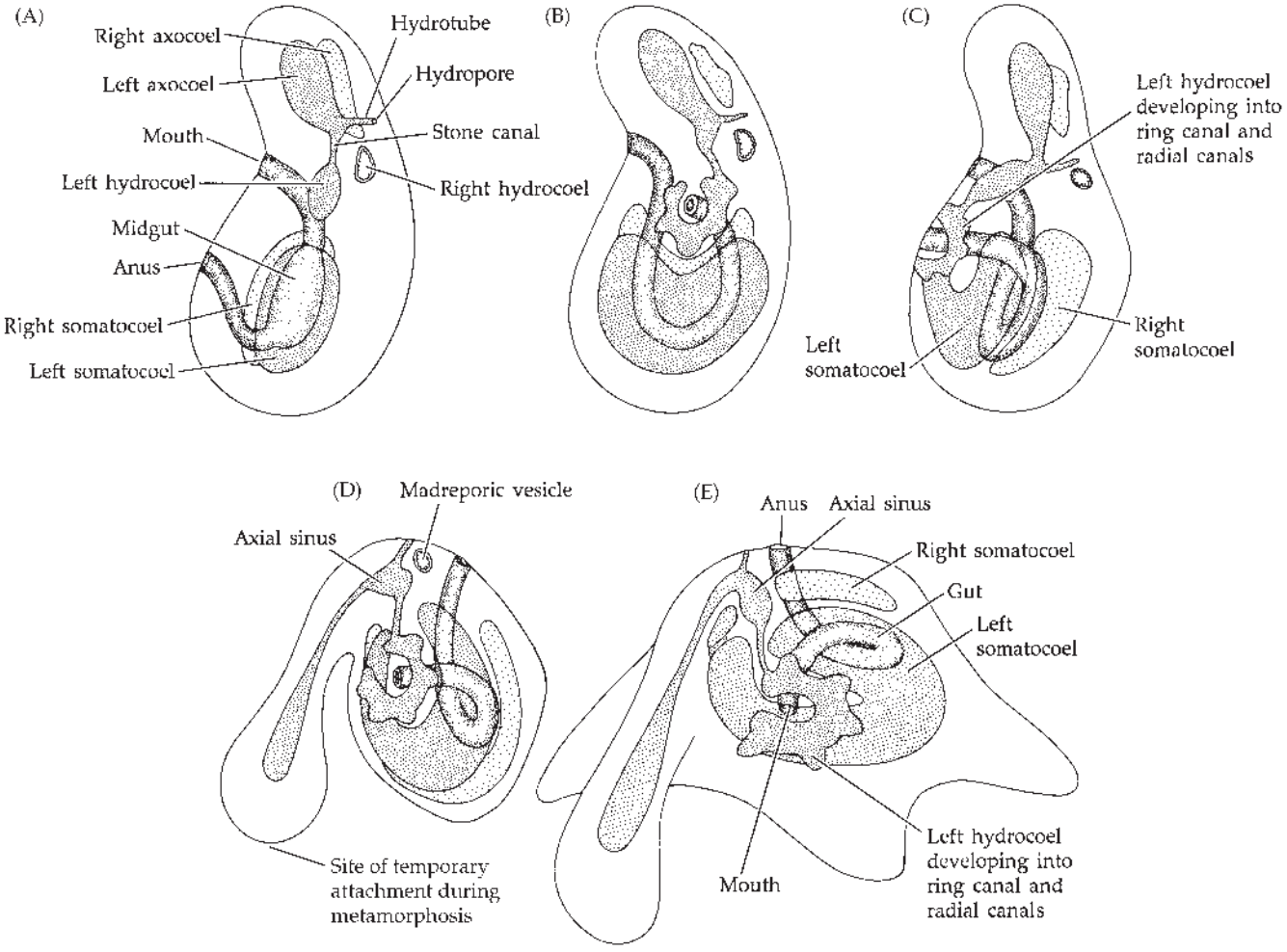


FIGURE 26.18 Development of the coelom and its derivatives in a starfish (Asteroidea). (From P. A. Meglitsch. 1972. *Invertebrate Zoology*. Oxford University Press, London.)

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TABLE 26.1 Adult Fates of the Major Coelomic Derivatives in Generalized Echinoderm Development

Embryonic Coelomic Structure	Adult Fate
Right somatocoel	Aboral perivisceral coelom; imperforate extraxial body wall
Left somatocoel	Oral perivisceral coelom; genital sinuses; most of the hyponeural sinus; perforate extraxial body wall
Right axocoel	Largely lost
Hydropore	Incorporated into madreporite
Hydrotube and dorsal sac	Parts of madreporite vesicle and ampulla
Stone canal	Stone canal
Left hydrocoel	Axial region; ring canal; radial canals; lining of tube feet lumina, plus other components of the water vascular system, including Tiedemann's bodies and Polian vesicles

metamorphosis. Typically, embryonic openings disappear, and the stump of the foregut swings from its larval anteroventral location to the left side within the developing rudiment. The hindgut moves anteriorly and to the right (Figure 26.18B,C). Once in the adult positions, the mouth and anus reopen. Aborally, the madreporite complex arises from various parts of the left axocoel and its derivatives plus the dorsal sac. The axial sinus arises from an outpocketing of the left axocoel. The hydrocoel forms a crescent around the foregut as precursor to the ring canal, which grows radial extensions (Figure 26.18D,E), the primary lobes, destined to become the radial canals and all their derivatives. The ring canal closes to form a torus. Outgrowths of the left somatocoel produce the hyponeural sinus, interacting with the primary lobes to elaborate the structure of the rudiment. The left somatocoel comes to lie just internal to the hydrocoel, interacting with it to pattern the body cavities of the adult. The right somatocoel "stacks" just internal to the left somatocoel, forming a quasi-linear anterior-posterior axis during a process called "coelomic stacking." As these transformations take place, much of the original larval body is lost or resorbed, and the juvenile assumes benthic life. Although echinoderms are noted for this remarkable metamorphosis, it is expressed to varying degrees in the different classes because of differential expression of the axial and extraxial components that are related to the rudiment and larval body, respectively.

Echinoderm Phylogeny

Living echinoderms are so highly derived compared with other deuterostomes that meaningful comparisons of adult body plans seem almost futile. In spite of a rich fossil record and many decades of work, the origin and subsequent evolution of echinoderms remain controversial, stemming from differing interpretations of echinoderm homologies originating from various sources in paleontology, morphology, and embryology. Importantly, however, all data support the idea that each extant class is monophyletic. But there is much more contention concerning the relationships among fossil taxa.

First Echinoderms

Echinoderms have an abundant fossil record with 13,000 to 15,000 recognized species. They likely originated with a Precambrian/Cambrian infaunal bilaterian deuterostome with similarities to the sister group of the echinoderms, the hemichordates. Echinoderms diversified rapidly, and fundamental body plans of almost all groups have roots in the early Cambrian, possibly back to the Fortunian Age. By the end of the Ordovician, all the extant classes had been established. Diversity and disparity among what seem now to be bizarre forms reached their zenith during the early to mid-Paleozoic (Figure 26.19). By the beginning of the Mesozoic, this disparity among major taxa had declined greatly, leaving the five extant classes persisting to the present.

Echinoderm origins involved modifications to the ancestral, bilaterian trimeric larval trajectory such that the hydrocoel could initiate the appearance of the pentaradial adult with its unique water vascular system. Coupled with evolution of the stereom endoskeleton, these traits make it easy to distinguish echinoderms from all other early phyla (Figure 26.20). However, all echinoderm larvae retain their ancestral bilateral, trimeric condition. The expression of genes that dictate radiality thus occur relatively late in development, and the evolution of radiality must have involved major modifications of the roles of certain homeobox genes.

There are differing opinions about the significance of extinct groups such as the carpoids, helicoplacoids, and ctenocystoid homalozoans. Some members of these groups did not have the full complement of five rays (Figure 26.19A,B), and they are thus considered by some to be fossilized representatives of the transition to

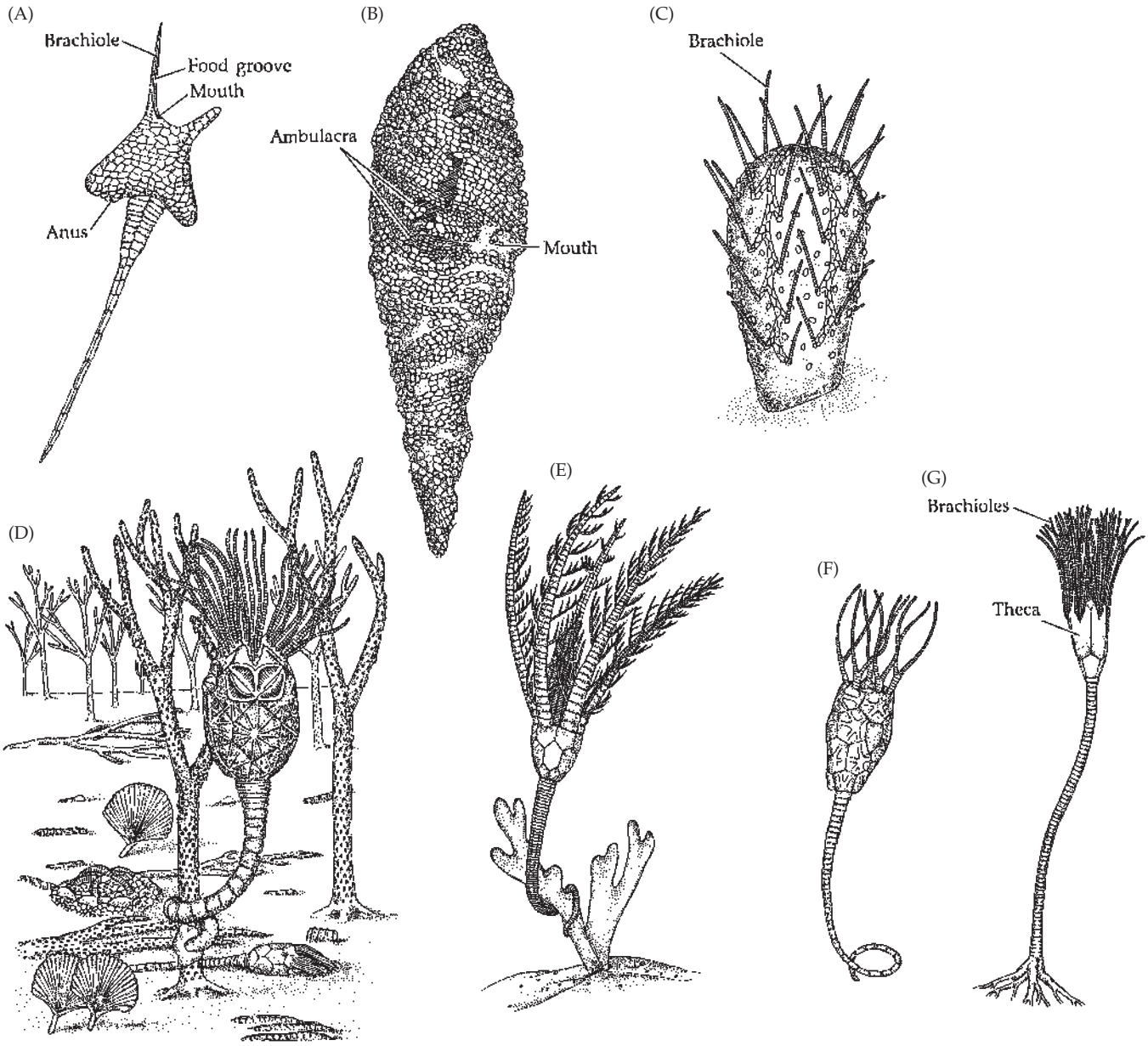

FIGURE 26.19 Fossil echinoderms. (A) *Dendrocystites*, an early Cambrian carpoid with a single brachiole. (B) *Helicoplacus*, a triradiate echinoderm from the lower Cambrian. (C) A generalized cystoid. (D) *Lepadocystis*, a stalked Ordovician cystoid. Note the edrioasteroid in the background, attached to the substratum. (E) *Eifelocrinus*, an extinct crinoid. (F) The eocrinoid *Macrocystella*. (G) A generalized blastoid from the Carboniferous.

pentaradiality. This hypothesis makes certain assumptions about the homologies of various feeding appendages, structures supposed to be gill slits, and a superficial bilateral morphology in the skeleton.

Other workers have applied models of echinoderm homology and embryology to argue that the first echinoderms were likely already pentaradial. If this is true, forms such as *Stromatocystites* are representative of the earliest echinoderms, with the pentaradial axial region expressed as narrow ambulacra. These thin rays remain embedded in the oral, perforate extraxial region marked by the hydropore, anus, and other small body openings (Figure 26.4A). The imperforate extraxial region is a large component devoid of orifices that aborally sealed the body wall. Under this view, nonpentaradial forms (Figure 26.19A), or the bizarre helicoplacoids (Figure 26.19B), are not representatives of earliest echinoderms, but offshoots from the main lineages leading to other major echinoderm clades—lineages that were ancestrally pentaradial (Figure 26.20). Thus, this view sees the first echinoderms as already being pentaradial, and the hydrocoel having already established pentaradiality at the cost of larval bilaterality (which is completely obliterated in the adult). Also in this view, there can be

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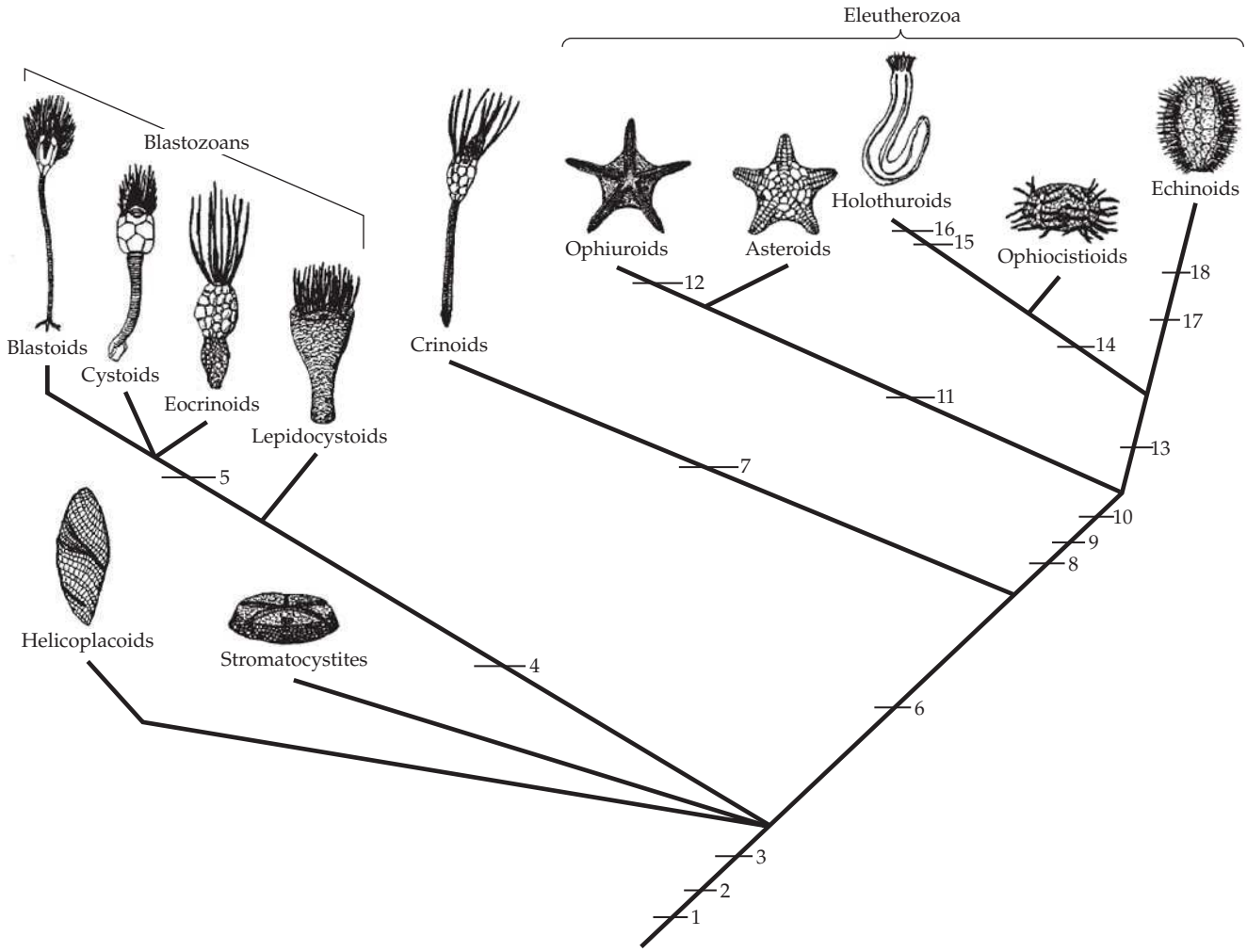

FIGURE 26.20 A phylogenetic hypothesis for the main groups of echinoderms, with suggested major synapomorphies. Echinoderms probably evolved from an infaunal ancestor similar to the sister group Hemichordata by inducing pentaradiality through a rudiment produced from the hydrocoel (1) and the evolution of a stereom endoskeleton (2). *Stromatocystites* is an edrioasteroid-like taxon likely representing the morphology of the first echinoderms—sessile animals with narrow rays (axial region), anus, and hydropore set in an upward-facing perforate extraxial region. Enigmatic derivations from this morphology had already appeared in triradial helicoplacoids. The imperforate extraxial region became an elongated sac enclosing aboral portions of the viscera (3). A diverse, entirely extinct clade, the blastozoans, are distinguished by possession of brachioles (4), feeding structures distinct from arms and made entirely of axial body wall, representing "naked" ambulacra unaccompanied by left or right coelom elements. Elaborations from the earliest blastozoans (*Lepidocystis*), included development of a stalk fashioned from imperforate extraxial region (5). Eocrinoids show the earliest morphology, with development into a demarcated stalk in cystoids and blastoids. Early, derived echinoderms such as carpoids fall into this clade by possession of a brachiole and highly defined stalk. The clade with the first extant forms is characterized by true arms containing extensions of left and right somatocoels (6). Crinoids independently evolved a stem inserted as a module within the imperforate extraxial region (7). Starfish, brittle stars, sea urchins, and sea cucumbers possess a madreporic sieve plate (8), robust tube feet for locomotion and food gathering in ambulacra lacking cover plates (9), a downward-directed mouth with the anus on the opposite (aboral) surface in which the imperforate extraxial region is virtually lost (10). Ophiuroids and asteroids are characterized by specialized plate systems such as lateral arm plates (11). Ophiuroids evolved fused ambulacral plates (vertebrae) that demarcate arms from the central disk (12). The ancestor of echinoids and holothuroids possessed an outpocketing of the left somatocoel (peripharyngeal coelom) in which the jaw apparatus develops (13). Aristotle's lantern is expressed in echinoids and early holothuroid-like forms (ophiocistioids), which begin shortening the rays and enlarging tube feet that become restricted to the oral region (14). Holothuroids take this to the extreme, suppressing the lantern as paedomorphic "giant larvae" (15). Earliest holothuroids were like modern apodids, lacking tube feet along the body. Only in more recent taxa do secondary, interradial canals (not homologous to the radial canals of other echinoderms) induce formation of tube-foot-like structures along the body (16). Echinoids lost nearly all of the extraxial region, restricting it to a few plates in the unique apical system (17). Echinoids also uniquely internalized the radial water vessel (18). The earliest echinoids did not actually have a rigid test (the plates did not tightly suture together to make the test until later).

no "head," no "tail," and clearly no "gill slits" in any member of the phylum, fossil or extant, despite attempts to identify these structures in the fossil record.

Helicoplacoids that appeared in the early Cambrian and died out soon thereafter were cigar shaped, with only three ambulacra arising from a lateral mouth and spiraling around the body among interradial plating (Figure 26.19B). How these echinoderms made their living remains conjecture. It is tempting to consider the three-ray pattern of helicoplacoids to be a precursor to the 2-1-2 pattern seen in the ambulacral branches of other fossil genera, such as *Stromatocystites*, in which there seem to be two bifurcating branches (the "2" in the pattern) and one nonbifurcating branch (the "1") to make a total of five rays. However, there are no parsimonious arguments against the idea that helicoplacoids (or any of the echinoderms with fewer than five rays) represent a reduction in ray number. The 2-1-2 pattern is also expressed in modern crinoids, but the five radial canals come off the ring canal in perfect pentaradiality, suggesting that the 2-1-2 pattern does not reflect embryological patterning of the water vascular system itself.

The one-armed carpoids seem to be derived members of the Blastozoa, a large, extinct group that includes cystoids, blastoids, and rhombiferans (Figures 26.19A,C,D,F,G and 26.20). All these taxa possess unique "free ambulacra" composed only of axial elements called **brachioles**. The earliest blastozoans were primitively pentaradial and derived from fossils such as *Lepidocystis* that illustrate origins of brachioles, as well as origins of the multiplated stalk derived independently from the stem seen in crinoids. Brachioles are not homologous to arms, as they do not include any coelomic elements other than the hydrocoel. "True" arms such as those seen in crinoids comprise both axial and extraxial elements, incorporating major coelomic outpocketings of both the left and right somatocoels.

Modern Echinoderms

The oldest fossil record of an extant echinoderm group is for Crinoidea, and among living taxa the crinoids constitute the sister group to the four classes that comprise a clade called Eleutherozoa. Crinoids include extinct forms, the protocrinoids, as well as sea lilies that proliferated during the Paleozoic. Crinoids bear attachment stems (distinct from the stalks of blastozoans in the nature of their ontogeny, as well as overall anatomy) arising from the aboral surface (Figure 26.2A). Protocrinoids possessed calcified ambulacral plates in the arms, but these were lost in more highly derived forms.

Eleutherozoa (composed of asteroids, ophiuroids, echinoids, and holothuroids) are the more mobile echinoderms in which the mouth was directed toward the substratum (except in the unusual holothuroids). The tube feet became more robust and deeply involved in all aspects of life, including locomotion and active hunting of prey. Asteroids, ophiuroids, and echinoids do not appear in the fossil record until the Ordovician; the holothuroids first appear in the Upper Ordovician, perhaps having evolved by way of paedomorphic reduction from strange extinct forms, the ophiocistioids. Recent evidence, including molecular phylogenetics, strongly supports placing asteroids and ophiuroids in one clade, and echinoids and holothuroids in another, sister clade. Asteroids and ophiuroids are constructed along very much the same body plan—so close in fact that there remain arguments over which fossils should be placed in which of the two groups.

With molecular evidence, a close relationship between echinoids and holothuroids is well supported. However, holothuroids are not simply decalcified echinoids, as once supposed. With the realization that holothuroids are likely paedomorphic, morphological synapomorphies linking them with echinoids are difficult to identify and will require examination of ontogenetic patterns, such as those involved in formation of the peripharyngeal coelom and Aristotle's lantern.

In summary, the ancient origin of the stereom and pentaradial hydrocoel patterning to induce adult pentaradiality are keys to understanding echinoderm evolution. These features allowed a transformation, from infaunal creatures like hemichordates to epibenthic surface-dwelling animals. The water vascular system probably originally served for suspension (and perhaps detritus) feeding, facilitated by small tube feet in narrow ambulacra oriented around an upward-facing mouth. The small ambulacra (i.e., axial region) in the body plan of early echinoderms indicate that they retained large amounts of extraxial region during development, even as the bilaterality of the larva was lost. As tube feet and the attendant water vascular system became increasingly significant in echinoderm lifestyles, pentaradial expression in the body plan also increased, leading to more pronounced larval metamorphosis to suppress the extraxial larval body in the adult. Concomitant with the more errant, active feeding lifestyle of modern taxa, specialized feeding structures such as enlarged suckered tube feet, buccal feeding tentacles, and even jaws and teeth were elaborated.

The proliferation of the echinoderm body plan since the Cambrian might seem surprising given the unique adoption of radial morphology. But it is clear that the combined qualities of supportive endoskeleton, coelomic water vascular system, and pentaradial symmetry have provided the basis for diversification and extremely disparate variations on this basic theme among the echinoderm lineages.

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Chapter Summary

This chapter introduced you to some of the animal kingdom's strangest creatures, the phylum Echinodermata. No other phylum has pentaradial body symmetry or such strange expressions of body form. The 7,300 described echinoderm species include the familiar starfish (Asteroidea), brittle stars (Ophiuroidea), sea urchins and sand dollars (Echinoidea), and sea cucumbers (Holothuroidea), as well as the less familiar sea lilies and feather stars (Crinoidea). Ranging in size from 10 mm to over 3 m in length (some sea cucumbers), echinoderms occur exclusively in the sea, where they are found at all depths, and can be extremely abundant in some deep-sea environments. Adults of almost all species are benthic, but a few pelagic holothurians are known. Larvae in all classes are almost always pelagic, but many species adapted to cold environments have become brooders. All living echinoderms possess a well-developed coelom and a mesodermally derived endoskeleton composed of unique calcareous elements—ossicles and plates formed by microscopic, secreted crystals of calcium carbonate with small amounts of organic tissue forming a skeletal material called stereom. Echinoderm adult pentaradiality is coupled with another unique body feature known as the water vascular system, a complex of tubes and canals derived from the coelom. The water vascular system serves a variety of functions, notably in giving rise to tube feet, which are crucial to nearly every interaction between echinoderms and their environment. Echinoderms comprise one of the three deuterostome phyla (the other two being Hemichordata and Chordata) and thus have radial cleavage, enterocoely, and a mouth not derived from the blastopore. Important areas of future research for echinoderms include understanding their unusual regenerative capabilities, including their nervous system, and their ecological roles in maintaining or disrupting ecosystem function, given their regulation of algal growth and coral health, among other effects.

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CHAPTER 27

Phylum Chordata

Cephalochordata and Urochordata

We are chordates (Latin, *chorda*, "cord"). So are cats and dogs, lemurs and anteaters, birds and fishes, frogs and snakes, whales and elephants—all conspicuous by their size and familiarity. All of these animals have a vertebral column (backbone) housing the dorsal nerve cord, and this is the key feature defining the subphylum Vertebrata. But, besides the vertebrates there are two other subphyla in the Chordata, and they both lack backbones. These are the invertebrate chordates—the subphyla Cephalochordata and Urochordata. The Cephalochordata comprise about 35 species of small, fishlike animals called lancelets, or amphioxus. The Urochordata (= Tunicata) are composed of about 3,000 species of marine, filter-feeding chordates usually organized into three classes: the planktonic larvalike tunicates called appendicularians, or larvaceans (class Appendicularia); the sessile sea squirts, or ascidians (class Ascidiacea); and the pelagic tunicates, or salps (class Thaliacea). However, because recent phylogenetic studies show thaliaceans to be a clade of derived ascidians, we demote them from class status and incorporate them within the Ascidiacea. An additional group of abyssal, carnivorous ascidians, the sorberaceans, were also once designated a separate class, but these too have been shown to be embedded within Ascidiacea. It was the body-covering tunic of urochordates that led Lamarck to combine these animals in one group.

Vertebrates, chordates with a backbone, account for only about 4% (about 58,000 species) of all described animal species. Those chordates that do not possess a backbone (plus the other 31 animal phyla previously described in this book) constitute the invertebrates. So we see that the division of animals into invertebrates and vertebrates is based more on tradition and convenience, reflecting a dichotomy of interests among

Classification of The Animal Kingdom (Metazoa)

PHYLUM PORIFERA
PHYLUM CTENOPHORA
PHYLUM PLACOZOA
PHYLUM CNIDARIA
Bilateria (a.k.a. triploblasts)
PHYLUM XENACOELOMORPHA
Nephrozoa
PROTOSTOMIA
Spiralia
PHYLUM DICYEMIDA (=RHOMBOZOA)
GNATHIFERA
PHYLUM CHAETOGNATHA
PHYLUM GNATHOSTOMULIDA
PHYLUM ROTIFERA
PHYLUM MICROGNATHOZOA
PLATYTROCHOZOA
PHYLUM ENTOPROCTA
PHYLUM CYCLIOPHORA
Lophotrochozoa
PHYLUM MOLLUSCA
PHYLUM NEMERTEA
PHYLUM ANNELIDA*
LOPHOPHORATA
PHYLUM PHORONIDA
PHYLUM BRYOZOA (=ECTOPROCTA)
PHYLUM BRACHIOPODA
Rouphozoa
PHYLUM GASTROTRICHA
PHYLUM PLATYHELMINTHES
Ecdysozoa
SCALIDOPHORA**
PHYLUM KINORHYNCHA
PHYLUM PRIAPULA
PHYLUM LORICIFERA
NEMATOIDA
PHYLUM NEMATODA
PHYLUM NEMATOMORPHA
PANARTHROPODA
PHYLUM TARDIGRADA
PHYLUM ONYCHOPHORA
PHYLUM ARTHROPODA
SUBPHYLUM CHELICERATA
MANDIBULATA
SUBPHYLUM MYRIAPODA
PANCRUSTACEA
SUBPHYLUM CRUSTACEA***
SUBPHYLUM HEXAPODA
DEUTEROSTOMIA
PHYLUM CHORDATA
AMBULACRARIA
PHYLUM HEMICHORDATA
PHYLUM ECHINODERMATA

* Annelida includes Sipuncula, Echiura, and Orthonectida
** Molecular phylogenetic support for a monophyletic Scalidophora is ambivalent
*** Paraphyletic (excludes Hexapoda)

zoologists, than it is on the recognition of natural biological groupings. "Invertebrates" is a paraphyletic group because it excludes the clade Vertebrata, a subgroup of the phylum Chordata. The vertebrates, on the other hand, are a monophyletic group.

The monophyly of the phylum Chordata has (in modern times) never been seriously questioned. One of the key synapomorphies defining the phylum is the **notochord**, a dorsal, elastic rod derived from a mid-dorsal strip of embryonic (archenteric) mesoderm, that provides structural and locomotory support in the body of larval or adult chordates. In addition, chordates have (at some point in their life history) a hollow **dorsal neural tube**, **pharyngeal gill slits**, and a **postanal tail** (a tail that extends beyond the anus) (Box 27A; Figure 27.9). They are an ancient group, with a fossil record dating to the early Cambrian, at least 530 million years ago, and with dated molecular phylogenies suggesting even an earlier age. Recent molecular phylogenomic studies have overturned the older view that Cephalochordata is the sister group to vertebrates, and instead the evidence today suggests that Urochordata is the sister group to Vertebrata (a clade known as Olfactores) and Cephalochordata is the sister group to those (Figure 27.9 and the Chordate Phylogeny section).

BOX 27A Characteristics of the Phylum Chordata

1. Bilaterally symmetrical, coelomate deuterostomes (coelom greatly reduced in some groups)
2. Pharyngeal gill slits present at some stage in development; used for feeding in Cephalochordata and Urochordata
3. Mesodermally derived, dorsal notochord present at some stage in development; notochord lying dorsal to the digestive tube and ventral to the neural tube
4. Dorsal, hollow nerve cord, at least in some stage of life history; compartmentalized anteriorly and, in Vertebrata, giving rise to the brain
5. Muscular, locomotor, postanal tail at some stage in development
6. With an endodermal, pharyngeal endostyle (Urochordata, Cephalochordata) or thyroid gland (Vertebrata)
7. Gut complete, usually regionally specialized
8. Circulatory system with a contractile blood vessel or heart; gas exchange across the body wall or across epithelial tissues
9. Gonochoristic or hermaphroditic; development variable; cleavage radial, holoblastic, subequal, or slightly unequal; tadpole larva stage expressed at some point in the life history of all taxa

CLASSIFICATION OF CHORDATA

SUBPHYLUM CEPHALOCHORDATA The lancelets or amphioxus. Marine, fishlike chordates (to 7 cm) with notochord extending anteriorly to the brain; gill slits, dorsal nerve cord, unique wheel organ, and postanal tail present in adults, but without vertebral column or cranial skeleton structure; gonads numerous (25–38) and serially arranged. Found in marine and brackish water environments, usually associated with clean sand or gravel sediments in which they burrow. (e.g., *Asymmetron, Branchiostoma, Epigonichthys*)

SUBPHYLUM UROCHORDATA (= TUNICATA)
The tunicates. Adult body form varies, but typically covered by thick or thin tunic (test) of a cellulose-like polysaccharide; without bony tissues; notochord restricted to tail and usually found only in larval stage (and in adult appendicularians); gut U-shaped or straight, pharynx (branchial chamber) typically with numerous gill slits (stigmata); coelom not substantively developed; dorsal nerve cord present in larval stages. Strictly marine; 2 recognized classes.

CLASS APPENDICULARIA (= LARVACEA)
Appendicularians, or larvaceans. Solitary planktonic tunicates; body enclosed in a complex, temporary, secreted gelatinous "house" used for feeding. (e.g., *Fritillaria, Oikopleura, Stegosoma*)

CLASS ASCIDIACEA Ascidians, or sea squirts and salps. Benthic or planktonic, solitary or colonial, sessile or free-living tunicates; the sessile sea squirts with incurrent and excurrent siphons generally directed upwards, away from the substratum; without dorsal nerve cord in adult stages; occurring at all depths. About 13 families of sea squirts and many genera. (e.g., *Ascidia, Botryllus, Chelyosoma, Ciona, Clavelina, Corella, Diazona, Didemnum, Diplosoma, Lissoclinum, Megalodicopia, Molgula, Octacnemus* [formerly in the class Sorberacea], *Psammascidia, Pyura, Styela, Trididemnum*). The relationships of three traditional ascidian orders (Aplousobranchia, with simple branchial sacs; Phlebobranchia, with vascular branchial sacs; Stolidobranchia, with folded branchial sacs) are in flux. Also, we include the former class Thaliacea (pelagic tunicates, or salps) within Ascidiacea. Salps are solitary or colonial; have incurrent and excurrent siphons at opposite ends, providing locomotory current; lack a tail as adults; and have gill clefts not subdivided by gill bars. There are 3 groups: Pyrosomida, Salpida, and Doliolida (e.g., *Dolioletta, Doliolum, Pyrosoma, Salpa, Thetys*).

SUBPHYLUM VERTEBRATA (= CRANIATA)
The vertebrates. Chordates with a skeletal brain case and, except for members of the Agnatha, jaws and a vertebral column (backbone) that forms the axis of the body skeleton; most with paired appendages. Several classes are generally recognized, although not all are strictly monophyletic: classes Myxini and

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Cephalaspidomorphi are the hagfishes and lampreys, respectively (united as the jawless or agnathan fishes); Chondrichthyes are the sharks, skates, and rays; Osteichthyes are the bony fishes (e.g., trout, tuna, perch); Amphibia includes the salamanders, frogs, toads, caecilians; Reptilia (a paraphyletic group) traditionally included the turtles, snakes, lizards, and crocodilians, but modern classifications place birds and reptiles together as Sauropsida (or Reptilomorpha). Mammalia comprises the vertebrates with mammary glands.

Phylum Chordata, Subphylum Cephalochordata: The Lancelets

Like all chordates, cephalochordates—the lancelets—possess a notochord, dorsal hollow nerve cord, pharyngeal gill slits, postanal tail (that persists into adulthood), and true coelom (Figures 27.1 and 27.2). The name (Greek *cephala*, "head"; *chordata,* "chord") derives from the unique extension of the notochord beyond the brain into the animal's head. Lancelets are small (to 7 cm), resembling a colorless anchovy but without obvious eyes or lateral fins. The vernacular name "amphioxus" is frequently used for the common species *Branchiostoma lanceolatum* (and sometimes for others as well). Cephalochordates are cosmopolitan in shallow marine and brackish waters at tropical and warm-temperate latitudes, where they lie burrowed in clean sands with only the head protruding above the sediment. Generally, they reside semivertically in burrows, or they rest on their sides on surfaces. They can and do swim, and locomotion is important to their dispersal and mating habits. However, they tend to swim erratically and without clear dorsoventral orientation. A few fossil lancelets have been described, as old as the early Cambrian.

Surprisingly, most biologists have never seen a living lancelet in the field. They can be somewhat common, but only in the right environment, and seeing them requires a bit of time on one's knees on tidal flats. Most species seem to prefer clean, fine-grained sediments, which in some places are referred to as "amphioxus sands," but even when they are present, it takes a keen eye to spot them. They can be seen swimming about in very shallow tidal pools on sand flats, darting in and out of the sediment. During spawning season, the sex of an individual is quickly revealed by the white testes of the males and yellowish ovaries of the females, both visible through the translucent body wall. In some areas of Asia they are common enough to be harvested for human and animal food. Written records of lancelets date back to Tang dynasty of China in the seventh to tenth centuries. Ernst Haeckel was convinced lancelets were the ancestors of the vertebrates, and he devoted so much thought and writing to this subject that he was served lancelets (with black caviar) at his sixtieth birthday party.

The Cephalochordate Body Plan

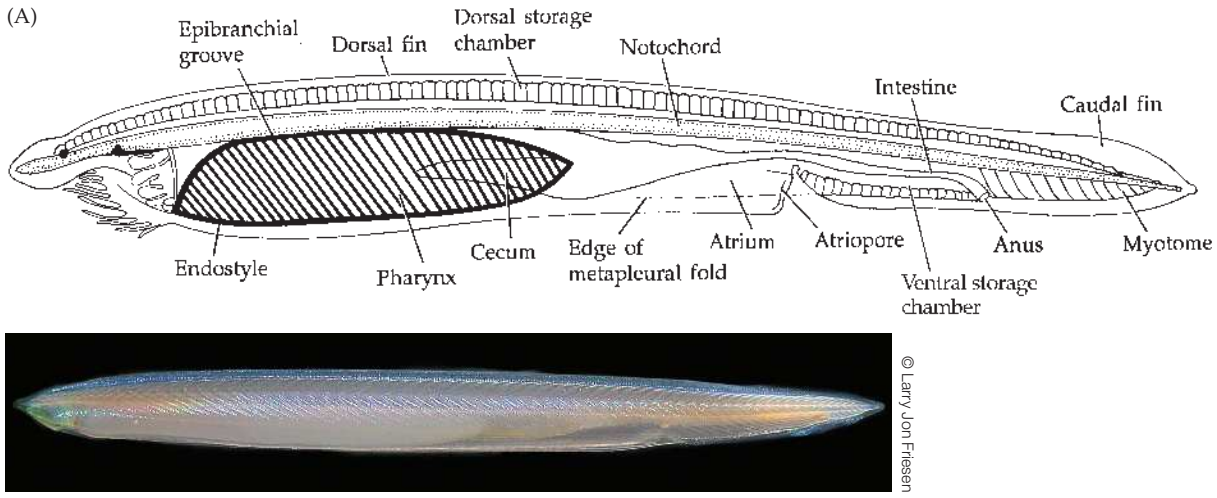
Body Wall, Support, and Locomotion

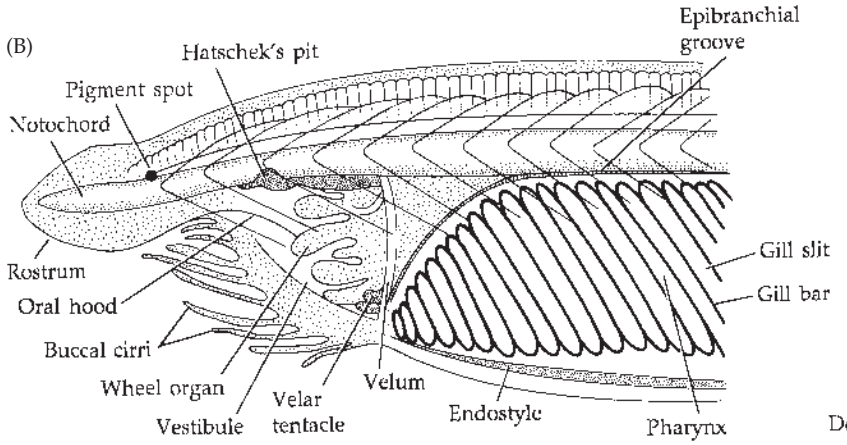
The body of cephalochordates is completely covered by an epidermis of simple columnar epithelium, underlain by a thin connective tissue dermis. The body wall muscles are vertebrate-like and occur as chevron-shaped blocks called **myotomes** arranged longitudinally along the body. These muscle blocks are large and occupy much of the interior of the body, thereby reducing the coelom to relatively small spaces. The notochord persists in adults and provides the major structural support for the body (Figure 27.1A–C).

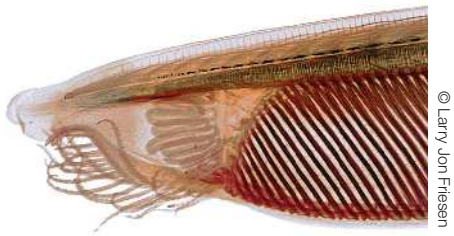
The notochord also plays a major role in locomotion in lancelets. As a result of the action of segmental myotomes, swimming in cephalochordates is much like that of fishes, consisting largely of lateral body undulations that drive water posteriorly to provide a forward thrust. The propulsive action of these body movements is enhanced by a vertically aligned caudal fin. Unlike the vertebral column and its articulating bones, however, the notochord is a flexible elastic rod. It prevents the body from shortening when the muscles contract, causing lateral bending instead. Its elasticity tends to straighten the body, and it thus assists the antagonistic action of paired myotomes. The notochord extends beyond the myotomes both anteriorly and posteriorly, providing support beyond those muscles, and apparently aids in holding the body stiff during burrowing.

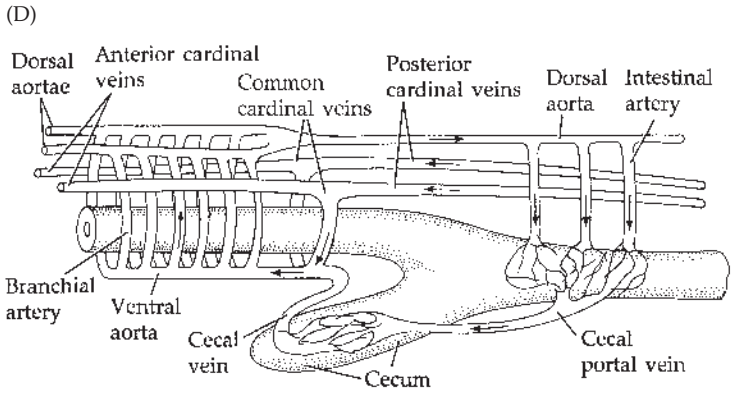
Although the notochord of cephalochordates is homologous with the same structure in other chordates, it displays some unique and rather remarkable structural and functional characteristics associated with its persistence into the adult stage. The notochord of lancelets is built of discoidal lamellae that are stacked like poker chips along its length and surrounded by a sheath of collagenous connective tissue. The lamellae are composed of muscle cells whose fibers are oriented transversely. A significant amount of extracellular fluid exists in spaces and channels around and between the lamellae within the collagenous sheath. These muscle cells are innervated by motor neurons from the dorsal nerve cord. Upon contraction, the hydrostatic pressure in the extracellular spaces increases, thereby resulting in increased stiffness of the whole notochord complex. It is suspected that this action may facilitate certain kinds of movement patterns, especially burrowing.

Although commonly called "fins," the unique dorsal and ventral finlike structures are perhaps more appropriately called **dorsal and ventral storage organs** (Figure 27.1A,C). They are not homologous with the fins of fishes, and their function appears to be housing a buildup of nutritional reserves for gamete formation.









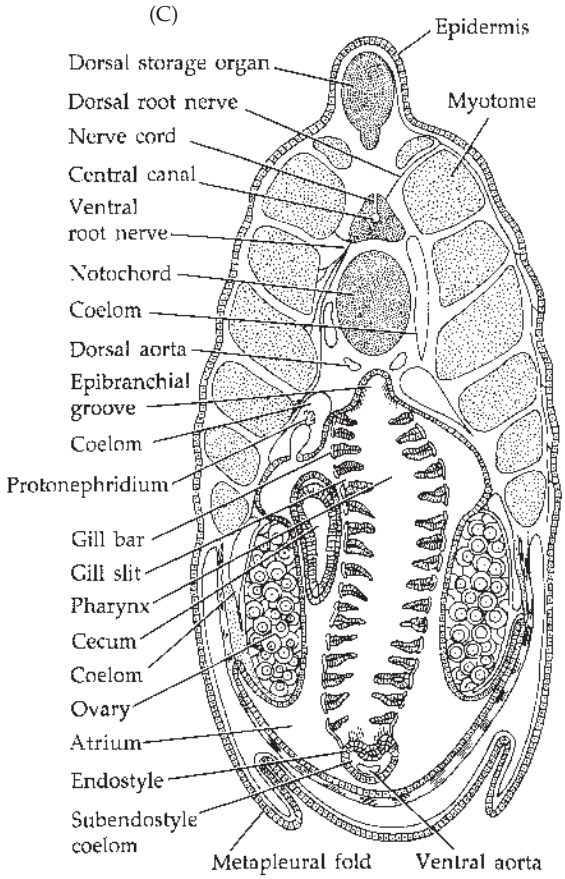


FIGURE 27.1 General anatomy of a cephalochordate (*Branchiostoma*). (A) General external and internal anatomy. (B) The anterior end. (C) The region of the pharynx (cross section). (D) The major blood vessels in the area of the gut cecum.

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Feeding and Digestion

Cephalochordates are ciliary-mucous suspension feeders, and they employ a food-gathering mechanism very similar to that of tunicates (see below). Water is driven into the mouth and pharynx via cilia in the **branchial chamber**, which creates the so-called **branchial pump**, and out through the pharyngeal gill slits into a surrounding **atrium**; it exits the body through a ventral **atriopore** (Figure 27.1A). Unlike the gill ventilation currents of aquatic vertebrates that are generated by muscular action, the feeding currents (the branchial pump) of lancelets are driven largely by pharyngeal cilia, as in tunicates. The pump is driven by metachronal waves of lateral cilia on the branchial bars. The gill slits in lancelets function largely for feeding and have little to do with gas exchange. There are up to 200 gill slits, separated from one another by gill bars, which are supported by cartilaginous rods.

Filter feeding in lancelets involves the trapping of food, primarily phytoplankton, from the inflowing water, combined with complex handling and sorting activities that occur before the water enters the mouth. The mouth is housed within a depression called the **vestibule**, which is formed by an anterior extension of the body called the **oral hood** (Figure 27.1B). The oral hood is supported by the notochord and bears fingerlike projections called **oral cirri** (= **buccal cirri**). As water enters the vestibule, the cirri act as a coarse filter to prevent sediments and other large particles from reaching the mouth. The mouth itself is a perforation in a membranous velum, which bears a set of **velar tentacles**; the tentacles provide a second screen, preventing large material from entering the mouth. The lateral walls of the vestibule bear complex ciliary bands that collectively constitute the wheel organ. The **wheel organ** appears as brown, thickened, folded epithelium in the roof and sides of the vestibule and is visible through the translucent skin of living animals. Cilia of the wheel organ drive food particles to the mouth and give the impression of a rotation, hence the name. Lying on the roof of the vestibule is a mucus-secreting structure called **Hatschek's pit** (Figure 27.1B). Mucus from this pit flows over the wheel organ, and food particles trapped by the mucus are carried to the mouth along the ciliary tracts. This material is then incorporated into the general water current moving through the mouth and into the pharynx. Threadlike feces are ejected from the anus, which is several millimeters posterior to the atriopore, just to the left of the ventral midline.

When feeding, most lancelets lie completely or partially buried in the bottom sand with the ventral side turned upward and the mouth opening free from interference of sand or sediment. Experiments have shown that, in *Branchiostoma lanceolatum*, particles greater than or equal to 4 μm are retained by the mucus filter with 100% efficiency. Both the oral cirri and velar tentacles bear numerous sensory cells that respond to mechanical and chemical stimulation. If the velar tentacles are stimulated, contraction of the velar muscles flicks them forward and a "cough" reaction is evoked. Clogging of the oral tentacles by detritus also results in a rapid body contraction, forcing water out of the mouth such that the buccal region is flushed and cleaned.

The ventral surface of the pharynx bears the **endostyle**, or hypobranchial groove (Figure 27.1A–C). An endostyle is found in Cephalochordata and Urochordata (the so-called **protochordates**) that filter feed using the pharynx and gill slits, as well as in primitive vertebrates (e.g., lampreys), and it is generally viewed as a synapomorphy of the Chordata. It functions by secreting mucus on which suspended particles are trapped and conveyed into the midgut. As in tunicates, the endostyle of lancelets binds iodine, although the specific cells involved differ between the two lineages. Many workers view the endostyle of urochordates and cephalochordates as homologous and a possible precursor to the vertebrate thyroid gland. As in tunicates, the endostyle produces strings of mucus that trap food from the water as it passes through the gill slits and into the atrium. The food-laden mucus is then passed dorsally along the walls of the pharynx by ciliary tracts and into the epibranchial groove, which carries the material by cilia along the dorsal midline of the pharynx and into a short esophagus. The gut extends posteriorly as an elongate intestine and opens through the anus just in front of the caudal fin. Near the junction of the pharynx and esophagus, there arises an anteriorly projecting pouch called the **digestive cecum** (sometimes called the hepatic cecum, or hepatic diverticulum). Studies indicate that this organ functions in lipid and glycogen storage and protein synthesis, and it is regarded by most workers as the evolutionary precursor of the vertebrate liver and perhaps the pancreas. Just as the liver does in vertebrates, the digestive cecum synthesizes vitellogenin, a yolk protein precursor that is carried in the blood to the ovary, where it is used in the production of yolk proteins in eggs. Digestion initially is extracellular in the gut lumen and is completed intracellularly in the walls of the intestine and especially in the cecum. In addition to storage in the cecum, food reserves accumulate in longitudinally arranged dorsal and ventral storage chambers (the "fins") along the dorsal midline and along the ventral body margin posterior to the atriopore (Figure 27.1A).

Circulation, Gas Exchange, and Excretion

The circulatory system of lancelets comprises a set of closed vessels through which blood flows in a pattern similar to that in primitive vertebrates (e.g., fishes). It is generally said that lancelets are heartless, but the main contractile vessel running ventral to the pharynx (often referred to as an aorta) is probably homologous with a structure in tunicates that has been called the heart, and the vessel's muscular contractions are powered

by cells thought to be homologous with the vertebrate myocardial cells. Blood flows posteriorly along the pharyngeal region in a pair of dorsal aortae. Just posterior to the pharynx, these vessels merge into a single median dorsal aorta that extends into the region of the caudal fin (Figure 27.1D). Blood is supplied to the myotomes and notochord via a series of short segmental arteries and to the intestine through intestinal arteries. A capillary network in the intestinal wall collects the nutrient-laden blood and leads to a series of intestinal veins that join a large subintestinal vein called the cecal portal vein, which carries blood forward beneath the gut to another capillary bed in the digestive cecum. As in vertebrates, the vein that connects two capillary beds is called a portal vein (e.g., the hepatic portal vein and renal portal veins in fishes). Indeed, the cecal portal vein of cephalochordates is probably the homologue of the hepatic portal vein of vertebrates. In the digestive cecum, the nutrient and chemical composition of the blood is regulated somewhat before being distributed to the body tissues. (The vertebrate liver serves the same function via the hepatic portal system.)

Leaving the cecal capillaries is a cecal vein, which is joined by a pair of common cardinal veins formed by the union of paired anterior and posterior cardinal veins returning from the body tissues. These vessels merge to form the ventral aorta beneath the pharynx. From here blood is carried through the gill bars via afferent and efferent branchial arteries to the paired dorsal aortae, thus completing the circulatory cycle. Blood is moved through this system by peristaltic contractions of the major longitudinal vessels and by pulsating areas at the bases of the afferent branchial arteries.

The blood contains no oxygen-carrying pigments or cells and is thought to function largely in nutrient distribution rather than in gas exchange and transport. Although some diffusion of oxygen and carbon dioxide may occur across the gills, most of the gas exchange probably takes place across the walls of the **metapleural folds**, thin flaps off the body wall that lie just anterior to the atriopore (Figure 27.1C).

The excretory units in cephalochordates are protonephridia similar to the solenocytes of some other invertebrates. Numerous clusters of protonephridia accumulate nitrogenous wastes, which are carried by a nephridioduct to a pore in the atrium. However, despite the structural similarities, the homology of lancelet protonephridia with those of other invertebrates is uncertain, and some specialists regard this as a case of convergent evolution.

Nervous System and Sense Organs

The central nervous system of cephalochordates is very simple. A dorsal, hollow nerve cord extends most of the length of the body and is generally expanded slightly as a **cerebral vesicle** in the base of the oral hood. Segmentally arranged nerves arise from the cord along the body in the typical vertebrate pattern of dorsal and ventral roots. The epidermis is rich in sensory nerve endings, most of which are probably tactile and important in burrowing. Some lancelets have a single simple eyespot (sometimes called a "frontal eye") near the anterior end of the dorsal nerve cord.

Reproduction and Development

Cephalochordates are gonochoristic, but the sexes are structurally very similar. Rows of 25 to 38 pairs of gonads are arranged serially along the body on each side of the atrium (Figure 27.1C). The volume of gonadal tissue varies seasonally, and during the reproductive period it may occupy so much of the body as to interfere with feeding. Spawning typically occurs at dusk. The atrium wall ruptures, and eggs or sperm are released into the excurrent flow of water from the atrium; external fertilization follows.

The ova are isolecithal, with very little yolk. Cleavage is radial, holoblastic, and subequal; the first cleavage starts at the animal pole, the second is at right angles, and the third cleavage divides the embryo into an animal and vegetal half, forming a coeloblastula. The coeloblastula then gastrulates by invagination (Figure 27.2). The roof of the archenteron eventually produces first a solid middorsal strip of mesoderm destined to become the notochord and then, sequentially, an anterior-to-posterior series of paired archenteric pouches along each side of the notochord. These enterocoelic pouches form the coelom and the other mesodermally derived structures such as the muscle bundles. The roof of the archenteron closes following mesoderm proliferation.

Dorsally the ectoderm differentiates into a neural plate. The neural plate eventually rolls inward, separating from the bordering cells, and then sinks inward as a neural tube, which forms the dorsal hollow nerve cord. As this process occurs at the posterior end of the embryo, the developing nervous tissue contacts the blastopore, which remains open temporarily and connects the archenteron to the lumen of the nerve cord as a **neuropore**. Later the two structures separate, and the blastopore opens to the exterior as the anus. The mouth breaks through as a secondarily produced opening at the front end of the developing gut, an event that is arbitrarily taken to divide the embryonic and larval stages.

In the absence of abundant yolk reserves, development of the ciliated embryo into a free-swimming larva takes place rapidly. As soon as they are able, the planktotrophic larvae swim upward in the water column, where they remain planktonic for 75 to 200 days.

Lancelet larvae resemble the adult form but are notable for their body asymmetry (in the right–left axis), including having the mouth opening on the left side of the head, the initial lack of gill slits and atrium, possession of only a few myotomes, and a

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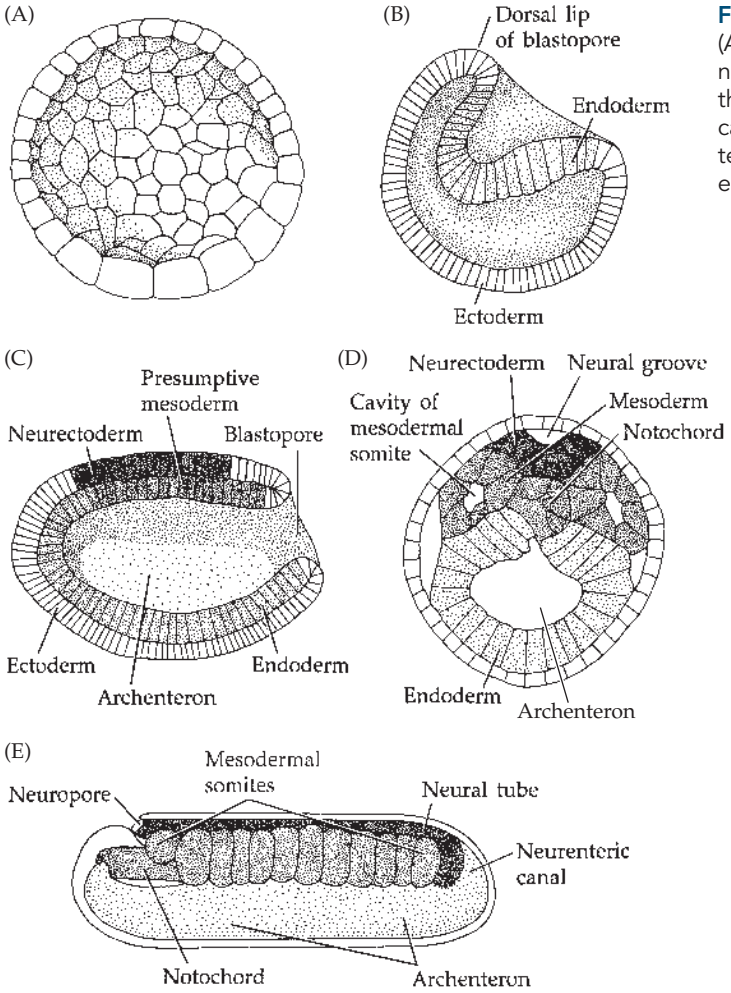

FIGURE 27.2 Development in a cephalochordate. (A) Coeloblastula. (B,C) Early and late gastrulae. (D) The neural groove stage (section). Note the proliferation of the mesoderm as central notochord and later coelomic cavities. (E) Lateral view showing major structures and a temporary confluence of the gut and neural tube (neurenteric canal).

heavily ciliated epidermis that is used for locomotion. The asymmetry of the body causes the larva to move in a helical or spiral fashion, ciliate-like, as it moves through the water driven by metachronal waves of beating epidermal cilia. However, most of its time is spent alternating between hovering in the sea, with the metachronal beat of the body cilia holding it more or less head up in the water column, and passively sinking, with its body held horizontally and the mouth directed downward, feeding on plankton and other suspended matter. Larvae gradually increase in size, following a nearly linear growth curve. As metamorphosis approaches, the atrium and gill slits form, the number of myotomes (muscle blocks) increases, and movement by cilia is gradually replaced by muscular propulsion. As more gill slits are enclosed by the growing atrium, the amount of water exiting the atriopore increases, and the motile cilia gradually disappear from the external epidermis. As the larval-juvenile transition ensues, body flexions increase in complexity until a complete undulatory wave propagates down the body in an adult manner. Metamorphosis is completed as ciliary locomotion ceases and the larva settles to the bottom.

Phylum Chordata, Subphylum Urochordata: The Tunicates

Once relegated to near obscurity, tunicates are getting more attention lately; some ascidians have become model organisms whose genomes have been studied to better understand chordate development and gene regulatory networks. The genomes of tunicates have not undergone whole genome duplications, which has provided a simplified system closely related to the more complex genomes of vertebrates. Ascidians are also getting substantial ecological attention as some of the most dangerous marine invasive species, covering and smothering thousands of square meters of benthic substrate and causing economic losses in aquaculture worldwide. The developmental and ecological attention focused on tunicates has in turn highlighted the surprising gaps in knowledge about their systematics, distribution, reproductive and larval biology, ecology, evolutionary relationships, and regeneration abilities.

Members of the three urochordate classes are almost all marine suspension feeders, but they conduct their lives in very different ways (Figures 27.3 and 27.4). The sessile ascidians (class Ascidiacea) include both solitary and colonial forms, with individuals ranging in size from less than 1 mm to 60 cm, and some colonies measuring several meters across or more. Ascidians are found worldwide and at all ocean depths, attached to nearly any substratum. They are most abundant and diverse in rocky littoral habitats and on deep-sea muds. The unusual *Octacnemus* (formerly in the class Sorberacea, but now regarded as ascidians) are carnivorous, abyssal, benthic species possessing a dorsal nerve cord in adult stages and lacking the typical perforated branchial chamber of other tunicates. The free-living salps (thaliaceans; also now in the class Ascidiacea) are pelagic tunicates that float about singly or in cylindrical or chainlike colonies sometimes several meters

(A)

Minette Layne/Wikipedia/CC BY-SA 2.0

(B)

Courtesy of R. Brusca

(C)

agefotostock/Alamy Stock Photo

(D)

Water-Frame/Alamy Stock Photo

(E)

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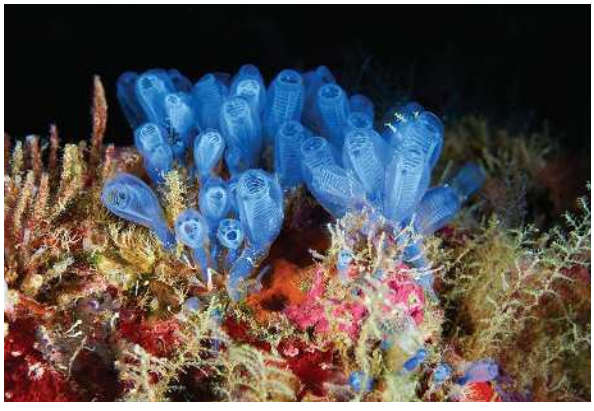

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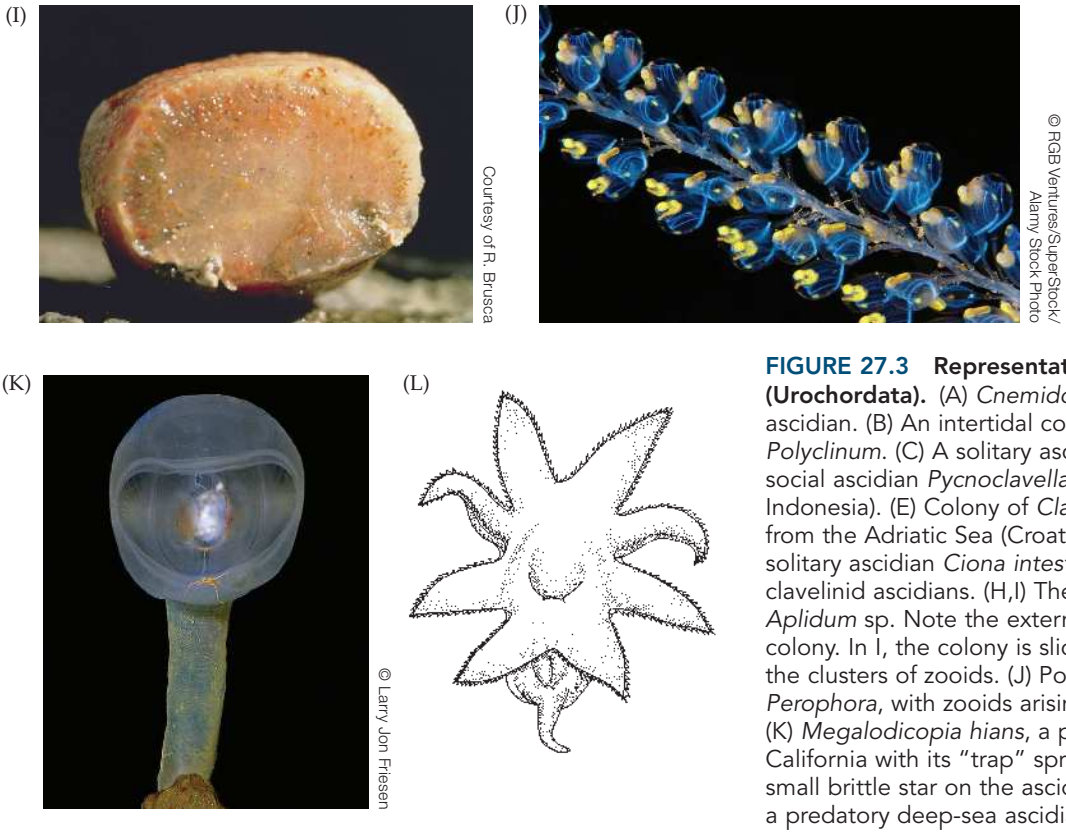

FIGURE 27.3 Representative ascidians (Urochordata). (A) *Cnemidocarpa*, a solitary ascidian. (B) An intertidal compound ascidian, *Polyclinum*. (C) A solitary ascidian, *Styela*. (D) The social ascidian *Pycnoclavella diminuta* (Sulawesi, Indonesia). (E) Colony of *Clavelina lepadiformis* from the Adriatic Sea (Croatia). (F) The common solitary ascidian *Ciona intestinalis*. (G) Colorful clavelinid ascidians. (H,I) The compound ascidian *Aplidium* sp. Note the external appearance of the colony. In I, the colony is sliced open to expose the clusters of zooids. (J) Portion of a colony of *Perophora*, with zooids arising from stolons. (K) *Megalodicopia hians*, a predatory ascidian from California with its "trap" spread open (note the small brittle star on the ascidian). (L) *Octacnemus*, a predatory deep-sea ascidian.

long. They are known from all oceans but are especially abundant in tropical and subtropical waters. Salps occur from the surface to depths of about 1,500 m. The larvaceans (class Appendicularia), or appendicularians, are solitary bioluminescent planktonic creatures generally not more than about 5 mm long. They resemble in certain ways the larval stages of some other tunicates, hence the name "larvaceans." Their retention of a notochord and a nerve cord in the adult stage indicates that these are plesiomorphic characters for chordates. The feces of salps and larvaceans, and the abandoned houses of the latter, constitute important sources of food and particulate organic carbon in the open sea and the seabed. In fact, the filtering of submicron particles by pelagic tunicates, and subsequent repackaging as denser fecal pellets that sink more quickly, is considered to be an important aspect of biogeochemical cycling towards the deep ocean affecting carbon budgets and nutrient supplies. It has been shown that discarded mucus feeding structures of larvaceans carry a substantial portion of the upper ocean's productivity to the deep seabed.

With the increasing application of DNA barcoding to identify cryptic species, the number of extant species of ascidians appears to be growing substantially. Ascidians, or their ancestors, probably date to the Precambrian. However, morphological change is so slow among living ascidian species that it is often impossible to distinguish sister species without genetic analysis, despite large genetic distances. Rapid genetic change has been documented in both mitochondrial and nuclear genomes of tunicates. Further, recent studies of mitochondrial gene order reveal rearrangements, even among species in the same genus. And nuclear genomes show dramatic changes in gene content (e.g., loss of a Hox gene cluster) and dramatic changes in intron organization. Appendicularians have been shown to have some of the fastest evolving metazoan genomes known.

Biogeographical distributions of tunicates are not well known in many cases, due to several factors: a historic lack of attention in comparison with many other groups, habitats that are challenging to survey in some cases, difficult morphological characters for taxonomic identification, anthropogenic effects on distributions, and challenges in working with preserved specimens. More recently, combined technological advances in morphological and genetic analysis, along with targeted collection efforts in areas of high biodiversity, are beginning to result in rapid advances in our understanding of tunicate distributions and evolutionary relationships.

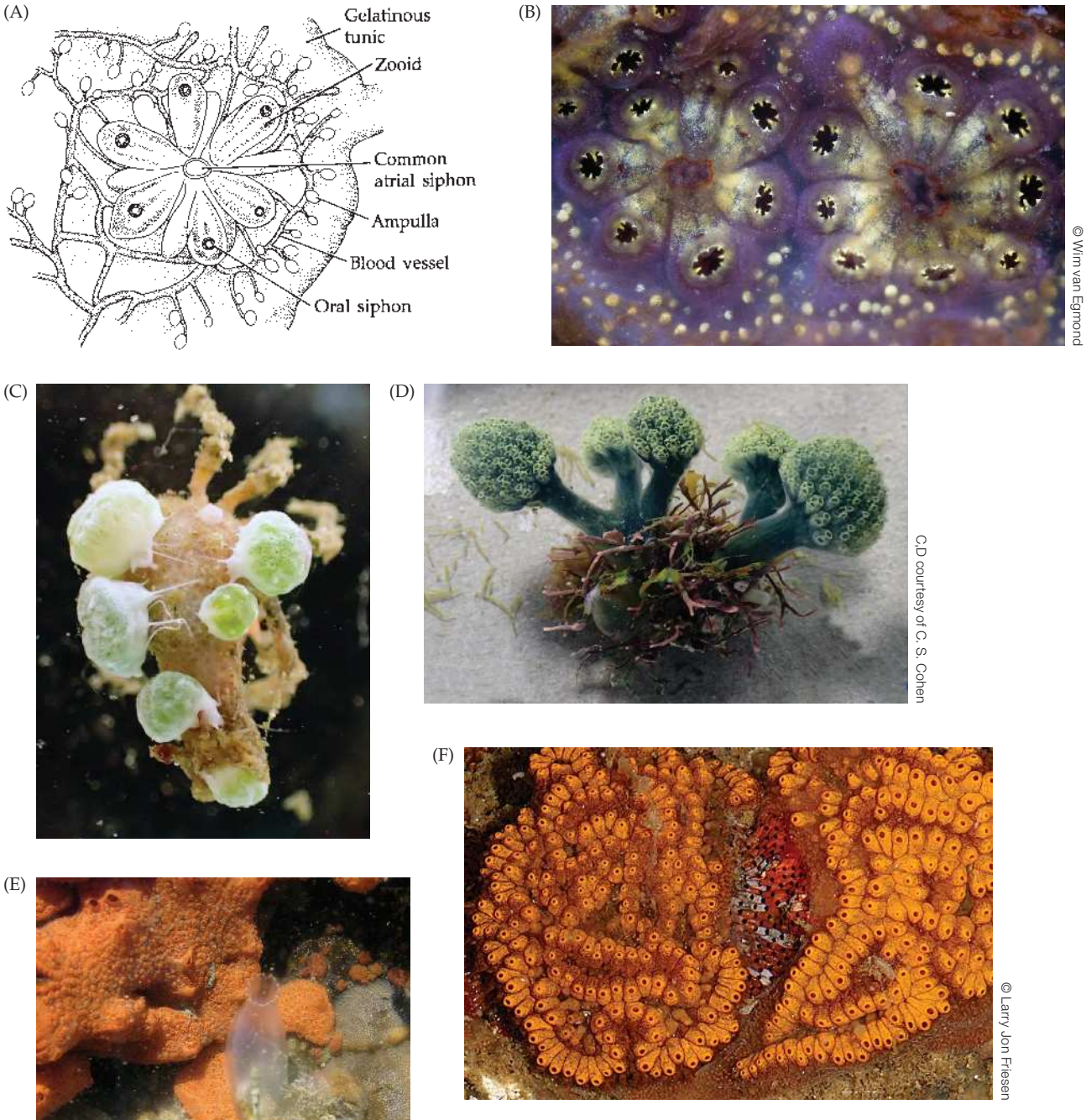

FIGURE 27.4 Some social, colonial, and compound ascidians. (A,B) The compound ascidian *Botryllus*. (A) Anatomical drawing; (B) living specimen. (C) Individual didemnid colonies, containing green symbionts, "walking" over the substratum (which, in this case, is the back of a small decapod crustacean in the Philippines). (D) The social ascidian *Oxycorynia*. Individual zooids are born on shared stalks that attach at their bases. Here the stalks are attached to a marine alga (Philippines). (E) Colony fusion in *Botryllus schlosseri*. Notice the junction of the salmon-colored colony in the lower right with the orange colony above; a beginning fusion event that will continue as the colonies merge. (F) A *Botrylloides diegensis* colony.

The Tunicate Body Plan

Tunicates are bilaterally symmetrical, at least during early developmental stages. Most utilize mucus-covered **pharyngeal gill slits** (= **stigmata**) for suspension feeding (Figure 27.5A,B,H). Although the feeding system is modified in the appendicularians, water still flows into the mouth and pharynx by way of an incurrent **oral** (**branchial**) **siphon**, passes through the pharyngeal gill slits into a spacious water-filled atrium (**cloaca**), and exits through an excurrent **atrial siphon**. The gut is simple, straight or U-shaped, with the anus emptying into the excurrent flow of water as it leaves the body. Because urochordates differ greatly

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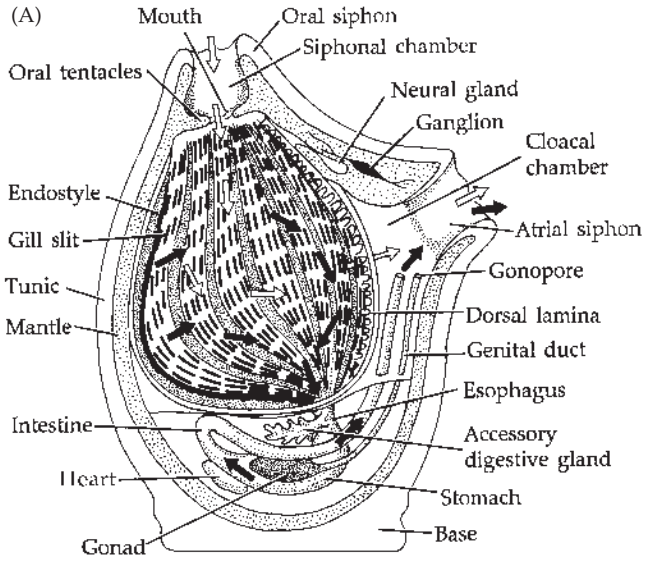
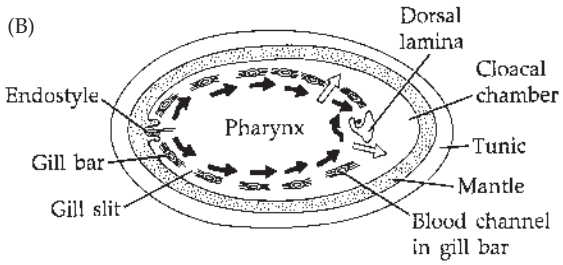
in body form from the more familiar chordates, the general orientation of the bodies of urochordates is not immediately apparent and can only be fully understood by examining the events of metamorphosis. The oral siphon is generally anterior, and the atrial siphon is either anterodorsal (in ascidians) or posterior (in thaliaceans) (Figures 27.5 and 27.6). However, the dorsoventral orientation of the body can be determined internally by the locations of the dorsal ganglion and a thickened ciliated groove, called the endostyle, that runs along the ventral side of the pharynx or branchial chamber (Figures 27.5A–E and 27.6C,D,H). The oral





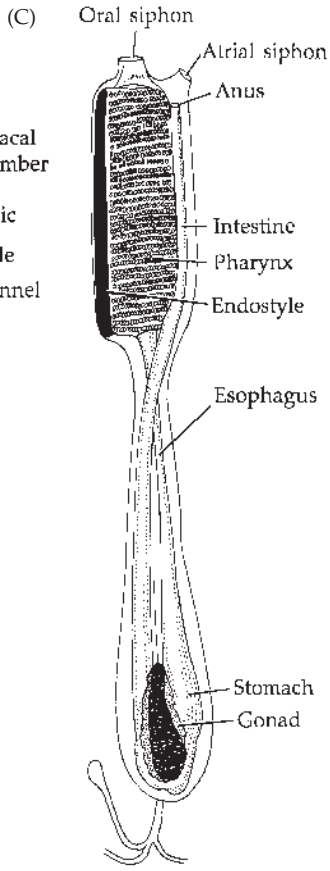
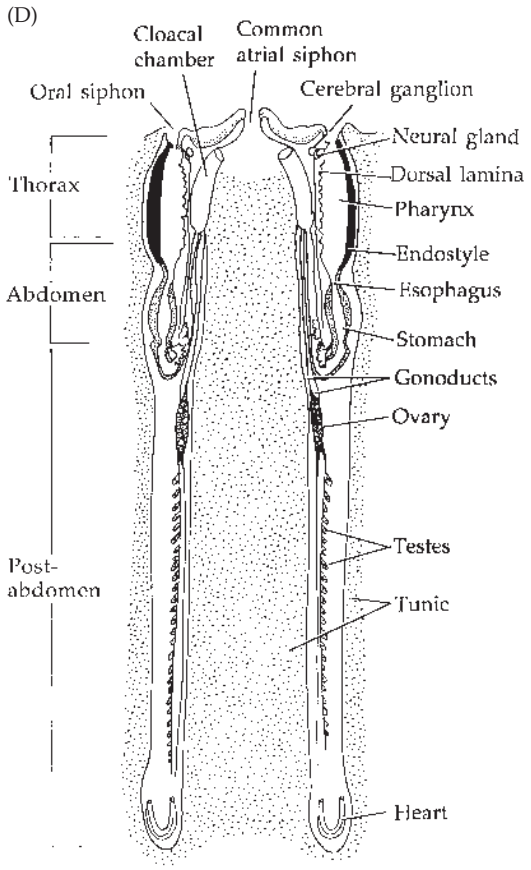
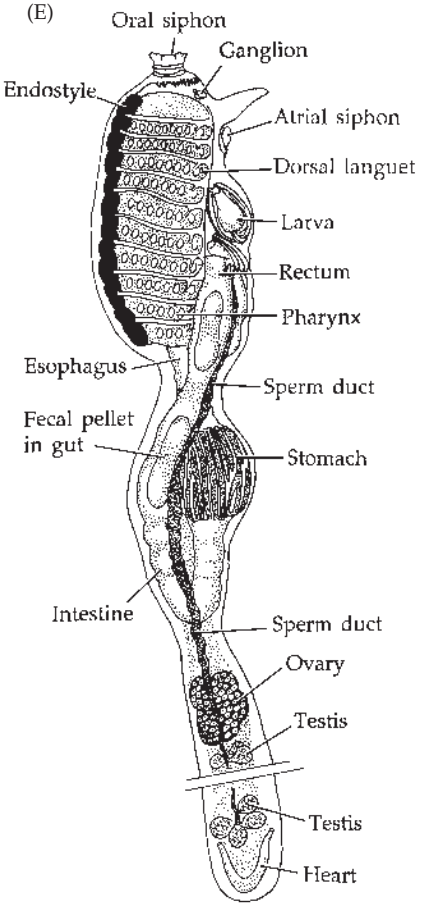
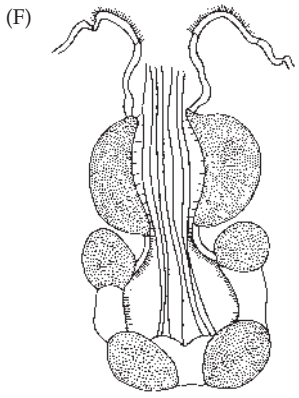


FIGURE 27.5 General anatomy of ascidians. (A) A solitary ascidian (cutaway view). (B) The pharyngeal region of the same animal (cross section). White arrows indicate water flow; black arrows indicate path of food material. (C) A single zooid isolated from a colony of the compound ascidian *Diazona*. (D) A colony of the compound ascidian *Aplidium* (section). Two zooids are sharing a common atrial siphon. (E) A single *Aplidium* zooid brooding a larva in the atrium. (F) The endostyle of *Ciona* (cross section). The shaded cells are largely responsible for secretion of the mucus used in filter feeding.

(*Continued*)







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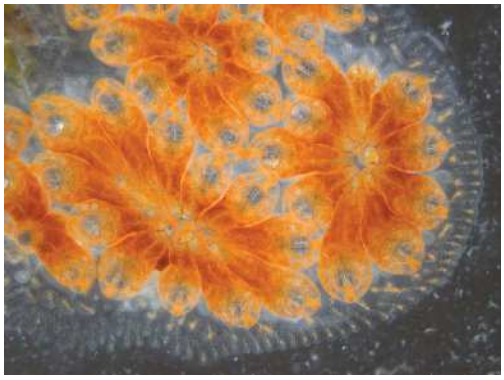

Courtesy of Christopher Rieken

FIGURE 27.5 (*continued*) General anatomy of ascidians. (G) The elaborate oral tentacles of the solitary ascidian *Herdmania momus* (Philippines). (H) Interior view of a bisected solitary ascidian (*Herdmania momus*) showing the elaborate folds of the branchial chamber, oral siphon bisected (whitish fingers near base of siphon are oral tentacles), larger atrial siphon intact, reddish gonads, and thick tunic. (I) A colony of *Botryllus* sp. showing three systems with the arrangements of zooids around a shared atrial siphon (in the center of each system). Fringing the entire colony are the terminal ends of the shared blood-vascular system, embedded in the tunic, that unites all the systems in the colony. (F after A. Thorpe and M. C. Thorndyke. 1975. In E. J. W. Barrington and R. P. S. Jefferies [Eds.], *Protochordates*, pp. 159–178 Academic Press, New York.)

and atrial siphons are generally directed away from the substratum and set at an angle to one another, thereby reducing the potential for recycling wastewater.

The Ascidiacea is the largest and most diverse class of tunicates. Some interstitial forms are known, and a few live anchored in soft sediments, but the majority of ascidians are attached to hard substrata (Figure 27.3), whereas the salps are free-living. Three general morphological body plans of ascidians are usually recognized, although these categories do not relate directly to formal taxa, since they have evolved multiple times in separate orders. The bodies of some solitary, social, and colonial forms are set on stalks and elevated off the substratum, although the compound forms typically grow as thin or thick sheets generally conforming to the topography of the surface on which they live. Many larger species (up to 60 cm long) are solitary ascidians, with each individual developing from a single larva and being genetically unique (e.g., *Ciona, Molgula, Styela*; Figure 27.3A,C). Some solitary ascidians are found in dense aggregations, particularly on artificial substrata such as docks, pilings, and submerged ropes, where their tunics may even appear glued together, although they are still physiologically distinct. These aggregations may result from gregarious settlement or simply limited dispersal in brooding species. Social ascidians tend to live in clumps of individuals that are at least initially vascularly attached to one another at their bases (e.g., *Clavelina*; Figure 27.3D,E), although in some taxa these connections may degenerate over time (e.g., *Metandrocarpa*). Finally, a great number of species are colonial and compound ascidians and are characterized by many small feeding and reproductive units (zooids) held together in a common gelatinous matrix (e.g., *Aplidium, Botryllus*; Figures 27.3B,H,I and 27.4 A,B) and proliferating via asexual reproduction following establishment by a single sexually produced colonizing larva. In extreme cases, colonies may measure several meters across or potentially even larger in some taxa (e.g., colonial didemnid ascidians) by way of fusion of distinct genetic individuals to form chimeric colonies. Colonial ascidians may regress or fragment as well, leaving a pattern of physically isolated colonies that are genetic clones distributed across the substratum.

In compound ascidians, zooids are arranged in regular (or irregular) rosettes and share a common atrial chamber that leads to a shared excurrent siphon within the outer body wall, or tunic (Figure 27.4A,B,E,F), while in colonial species, each zooid retains a distinct atrial siphon associated with each single branchial

FIGURE 27.6 Thaliaceans and appendicularians (larvaceans). (A,B) External and sectional views of the colonial thaliacean *Pyrosoma*. (C) A solitary thaliacean (*Salpa*). (D) The solitary thaliacean *Doliolum*. (E) A colonial form of *Salpa*. (F) A pelagic tunicate (Thaliacea). Note the circular bands of muscles in the body wall. (G) The appendicularian *Stegosoma* in its gelatinous house. (H) *Oikopleura*, an appendicularian removed from its gelatinous house. (I) *Oikopleura* in its house. The arrows represent water currents.

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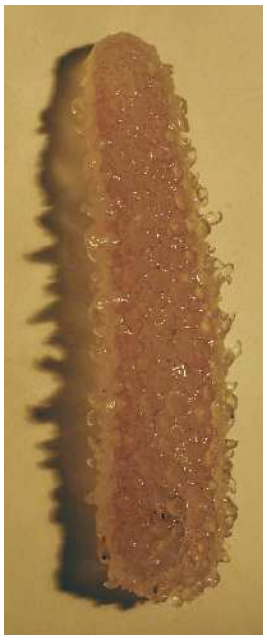

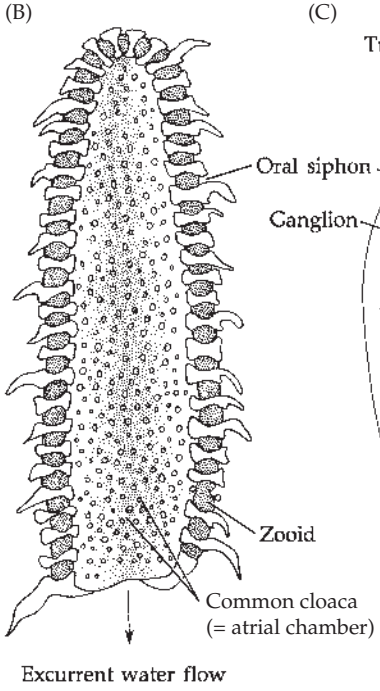

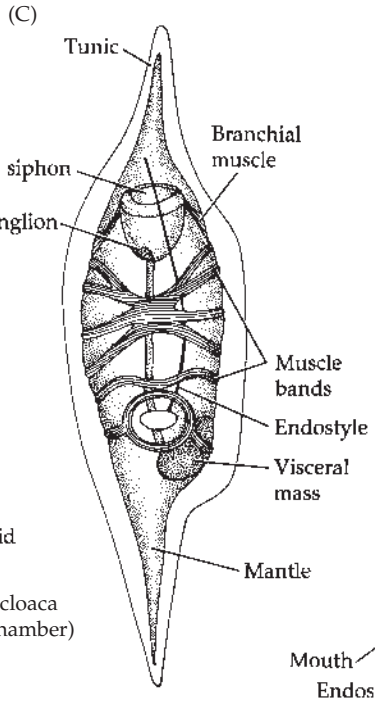

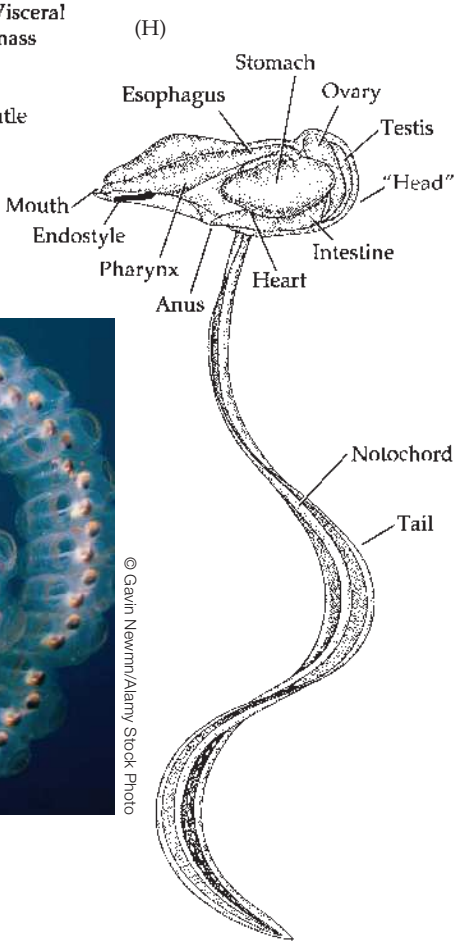

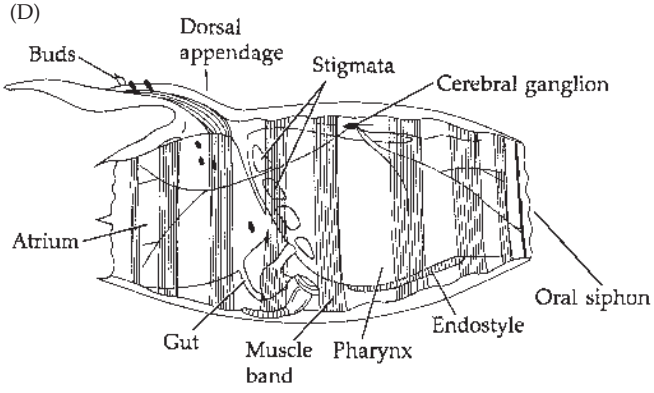

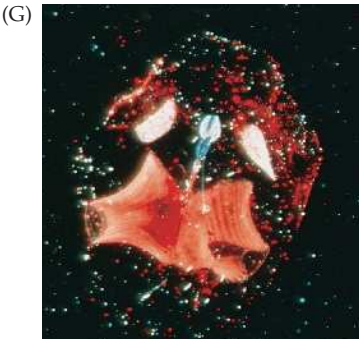

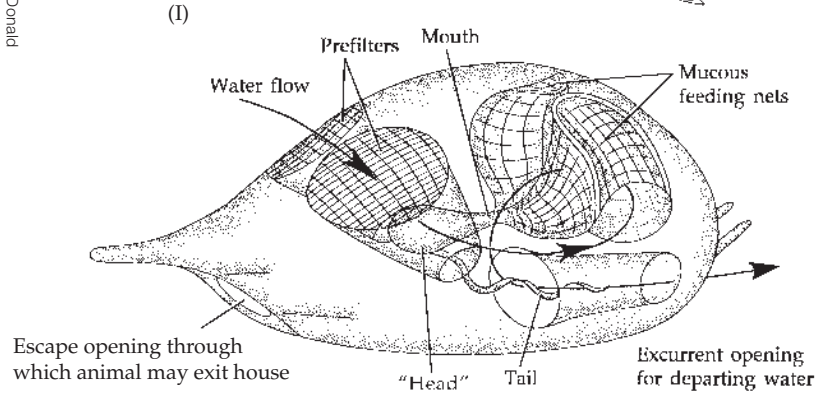

siphon. Zooids in some taxa are arranged seemingly haphazardly in the tunic, while in other taxa the zooids are arranged in regular patterns called "systems." The tunic varies from thick to thin, and from smooth and slick to wrinkled and leathery. In some families, the tunic can be reinforced with calcareous spicules—as in the Didemnidae. Many ascidian species are brightly colored, in some cases due to pigmented cells associated with the blood and in some tropical taxa due to symbionts. Compound ascidians frequently are some of the most colorful animals living on lower intertidal rocks and in the subtidal environment. Some solitary and social tunicates have clear tunics, so most parts of the internal anatomy are visible, sometimes highlighted with dramatic, seemingly fluorescent coloring (e.g., the pink endostyles of "light bulb" tunicates, such as *Clavelina*). Ascidians are eaten by people in both the Mediterranean region and the Far East. Interestingly, in 2015 the Yamauchi Company in Japan began brewing beer using the ascidian *Halocynthia roretzi*, a species that has been eaten raw or cooked for many years in Japan and Korea (with a flavor likened to rubber dipped in ammonia, by Western palates).

Ascidians have become so highly modified during their evolution as sessile suspension feeders that adults are not easily recognizable as chordates. The larval pharyngeal gill slits persist into adulthood. However, the dorsal hollow nerve cord and the notochord, present in the larval stage, are lost in adults, and additional neural differentiation occurs that provides sensory abilities more relevant to a sessile adult lifestyle. This neural differentiation is currently being studied with regard to relationships to vertebrate neural crest differentiation and neural placodes (embryonic ectodermal thickenings on the edge of the neural crest that give rise to neurons and sensory structures). In vertebrates, cells generated from the neural crest migrate throughout the body to give rise to diverse cell lineages producing nervous system elements and many other structures.

Thaliaceans are pelagic ascidians called salps (Figure 27.6A–F). They are constructed much like their sessile counterparts except that the oral and atrial siphons are at opposite ends of the body, and in many forms the pharyngeal filtering basket is modified to accommodate the linear flow of water through the animal. The exiting water provides a means of "jet propulsion." Most are highly gelatinous and transparent. Thaliaceans comprise three lineages: Pyrosomatida, Doliolida, and Salpida. Pyrosomes are remarkable colonies of tiny ascidian-like zooids embedded in a dense gelatinous matrix and arranged around a long central, tubular chamber called a common cloaca (Figure 27.6A,B). The cloaca receives exhalant water from the inwardly directed atrial siphons of all the zooids; the water then exits through a single large aperture, thereby propelling the barrel-shaped colony slowly through the water. As in the ascidians, water movement in pyrosomes is generated entirely by ciliary action of the individual zooids. The remarkable light displays of large pyrosomes have long attracted interest and awe, as the size of the entire colony can be several meters in length. On viewing a smaller captured specimen in a bucket on board a ship, the famed naturalist Thomas Henry Huxley commented in 1851, "The phosphorescence was intermittent, periods of darkness alternating with periods of brilliancy. The light commenced in one spot, apparently on the body of one of the 'zooids,' and gradually spread from this as a centre in all directions; then the whole was lighted up; it remained brilliant for a few seconds, and then gradually faded and died away." Huxley made these observations on his single specimen after noting that the entire sea was lighted intermittently by "miniature pillars of fire" producing "an ever-waning, ever-brightening soft bluish light as far as the eye could reach on every side."

Doliolids and salps include thaliaceans that alternate between solitary sexual forms and colonial asexual stages (Figure 27.6C–E). Doliolid individuals are generally small, less than 1 cm long, whereas a single salp may be 15 to 20 cm long but form a chainlike colony several meters in length. The members of these two groups move water through their bodies but propel themselves partially (salps) or wholly (doliolids) by muscular action, contracting their circular muscles to jet propel themselves through the water.

Thaliaceans are predominately warm-water creatures, although certain species are found in temperate and even polar seas. They are particularly abundant over the continental shelf and are frequently captured in surface waters or seen stranded on wave-swept sandy beaches after storms. Some, however, have been recorded from depths to 1,500 m. It has been suggested that the very fine mesh filters of thaliaceans are easily clogged in nutrient-rich waters, potentially explaining their abundance in offshore and tropical waters.

Appendicularians may be the strangest of all urochordates, and they are characterized by the retention of a notochord and a nerve cord in the adult stage, as in the other chordate lineages. Because they were once thought to be derived ascidians, this condition was interpreted as paedomorphosis. However, given their current phylogenetic position, it seems that the derived condition is that found in Ascidiacea. These solitary animals live in a gelatinous casing, or **house**, that they secrete around their body (Figures 27.6G–I), a synapomorphy of the group. The bulbous trunk of the body contains the major organs, including the gut, and bears a muscular tail in which the notochord is retained. The dorsal nerve cord, though reduced, extends partway along the length of the tail. (The phenomenon of paedomorphosis is discussed in Chapter 4.)

The pharynx of appendicularians is reduced and bears only two clefts. When positioned within its house, the animal produces a complex water current

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by beating its tail. Filtering is accomplished by meshes in the house wall and by mucous nets secreted by the animal (Figure 27.6I). The mesh filters are complex and vary among species, often being constructed of more than one size of interlaced fibers. The exiting water provides the locomotor force. Appendicularians are found near surface waters of all oceans and are sometimes extremely abundant. Large species attain lengths to 60 mm, and their fragile gelatinous houses can exceed a meter in diameter.

Body Wall, Support, and Locomotion

The body wall of tunicates includes a simple epithelium overlain by a secreted tunic of varying thickness and consistency (Figure 27.5A,D,H). The tunic is most well developed in the ascidians and some thaliaceans. It varies from soft and gelatinous to tough and leathery, and it sometimes includes calcareous spicules. The matrix of the tunic contains fibers and is composed largely of a cellulose polymer called tunicin produced by cellulose synthase genes that are thought to have been acquired via horizontal gene transfer from an actinobacterial genome. The tunic is not a simple, secreted, nonliving cuticle, however, since it also contains amebocytes and, in some cases, blood cells and even blood vessels. The tunic is an exoskeleton providing support and protection. Some ascidians harbor symbiotic bacteria in their tunics. These bacteria include a variety of species from several major groups, including taxa unique to tunicates. The ability to construct protective coverings with a cellulose material may have been a key innovation providing protection to these soft-bodied organisms.

Beneath the epidermis are muscle bands. In many species, especially among ascidians, these muscles lie within an ectodermally produced mesenchyme called the mantle (Figures 27.5A,B). Ascidians possess longitudinal muscles extending along the body wall that serve to pull the flared siphons down against the body, while circular sphincter muscles close the siphonal openings. Fine neural control of these muscles is part of the development that occurs during the transition from the motile larval to the sessile adult stage. This control allows the filter feeders to respond quickly to unwanted particles or predators near the siphonal openings. Doliolids and salps have well-developed bands of circular muscles that pump water through the body for feeding and locomotion. When they contract, water within the body is forced out the atrial siphon, thereby propelling the animal forward. When they relax, the body expands because of the resilience of the tunic, and water is drawn in through the oral siphon. In appendicularians, the tail muscles provide action for moving water through the houses.

Tunicates have an extremely reduced coelom, considered absent by some researchers; the body cavity has been lost in concert with the evolution of the large pharynx and cloacal chamber. The cloaca is a saclike, ectodermally derived structure continuous with the epidermis of the atrial siphon (Figure 27.5A,B). The inner wall lies against the pharynx and is perforated over the gill slits, or stigmata. Thus, water enters the pharynx via the oral siphon, flows through the stigmata, into the cloacal chamber, and out the atrial siphon.

Feeding and Digestion

We have hinted at various aspects of the feeding biology of tunicates in our comments. Most of these animals are suspension feeders and use various kinds of mucous nets to filter plankton and organic detritus from the seawater. A few ascidians live partially embedded in soft sediments and feed on organic material in the substratum, and certain bizarre deep-sea species actually prey on small invertebrates by grasping them with the lips of the oral siphon (Figure 27.3K). Next we provide a more detailed description of feeding and digestion in a suspension-feeding ascidian and then compare this with feeding in thaliaceans and appendicularians.

Water is moved through the body of an ascidian largely by the coordinated action of cilia lining the expanded pharynx, called the **pharyngeal chamber** (also known as the branchial chamber, branchial basket, or branchial sac). Water enters the oral siphon and passes through a short siphonal chamber, at the inner end of which is the mouth. A ring of fleshy tentacles encircles the mouth and prevents the entrance of large particles (Figure 27.5A,G). Food-laden water passes into the pharynx, which bears a ventral longitudinal groove, the **endostyle**. The bottom of the groove is lined with mucus-secreting cells and bears a longitudinal row of flagella; the sides of the groove bear cilia (Figure 27.5F). The mucus, a complex mucoprotein containing iodine, is moved to the sides of the endostyle by the basal flagella and then outward by the lateral cilia. Cells near the opening of the endostyle are responsible for binding environmental iodine and incorporating it into the mucus. Sheets of mucus then move dorsally along the inner wall of the pharynx and pass over the **stigmata**. The slitlike stigmata are arranged in rows and bear lateral cilia that drive water from the pharynx into the surrounding atrial water chamber (Figure 27.5A–D,H). Thus, water passing through the stigmata also passes through the mucous sheets, on which food particles are retained. On the dorsal surface of the pharynx is a longitudinal curved ridge called the **dorsal lamina**, or a row of ciliated projections called **languets**, or both (Figure 27.5A–E). These structures serve to roll the mucous sheets into cords, which are then passed posteriorly to a short esophagus and then to the stomach. Attached to the stomach is a small pyloric gland that

extends around the intestine as a network of small tubes. Some species also bear an accessory digestive gland (Figure 27.5A). Digestive enzymes are secreted into the stomach lumen by secretory cells of the gut wall and perhaps by the associated glands, and digestion is largely extracellular. From the stomach, the gut loops forward as an intestine, through which undigested material passes to the anus, which opens into the atrium near the excurrent siphon.

The family Didemnidae comprises some of the compound ascidians in which the cloacal systems are shared and the colonies are usually hardened with aragonitic "spiculospheres." Among certain tropical genera (e.g., *Didemnum, Diplosoma, Lissoclinum, Tridemnum*) are species that maintain symbiotic bacteria in the tunic, the pharyngeal chamber, or the cloacal system. Three broadly different types of bacteria are found in apparent symbiotic association with tropical ascidians: cyanobacteria (including the genus *Prochloron*, a unicellular oxygenic photosynthetic prokaryote), alphaproteobacteria, and gammaproteobacteria. These bacteria produce a variety of secondary metabolites, including some unusual compounds found at startlingly high concentrations in the ascidians. Unusual oxidation states of vanadium are found at high levels in some taxa, and some secondary metabolites are highly toxic biomolecules currently used in cancer treatment and antivirals more potent than remdesivir, which has been tested for COVID-19. The roles of these compounds in ascidians are not well known, but it is assumed there are antipredator benefits to the toxic compounds and nutritive benefits to hosting photosynthetic organisms, such as those found in corals and sponges. Some didemnid ascidians housing such symbiotic bacteria are also remarkable for their powers of locomotion, limited though it is—colonies have been clocked at speeds of 4.7 mm per 12-hour period. Such movement may allow these ascidians to position themselves in light conditions favorable to their bacterial symbionts.

Adult filtration rates for solitary species are extremely high, on par with the bivalve filter feeders such as mussels and oysters with which they are commonly found, especially in fouling communities. Intriguingly, a large solitary *Pyura* species, invasive in Chile, has taken on the ecological role of a mussel bed, with masses of these large solitary ascidians packed together in a broad swath of the intertidal. Ecologically, ascidians have long been known to be highly efficient filtration engineers on reefs and in other habitats, including man-made structures such as marinas, pilings, and aquaculture facilities. The high filtration and growth rates of some solitary and colonial ascidians allow them to compete effectively with aquaculture species such as bivalves. The removal of these ascidians is a costly and unwelcome addition to bivalve culture operations. Unfortunately, the rate of human-accelerated ascidian range spread is increasing globally. Recently, ascidians have become particularly infamous and menacing invasive species, in the case of *Didemnum vexillum* even covering acres of benthic habitat in the Gulf of Maine in the northwest Atlantic. In some cases, ascidians have been observed in invasions of natural habitat, outside of harbors and bays where they have long been observed as suspiciously "cosmopolitan" species. These incursions may reflect broad changes in community structure in marine environments, including the elimination of many predators, an increase in available particulate food, and increasing sea surface temperatures.

Thaliaceans feed in much the same way as the sessile ascidians, except that the siphons are at opposite ends of the body. The number of pharyngeal stigmata is usually reduced, especially in doliolids, and restricted to the posterior portion of the pharynx (Figure 27.6D). The intestine extends posteriorly from the pharynx and opens into the enlarged cloacal chamber.

Appendicularians (Figure 27.6F–H) secrete an intricate, hollow, gelatinous (mucopolysaccharide) house in which they reside and upon which they depend for feeding. The animal's tail is directed through a tube in the house structure toward an excurrent opening. Sinusoidal beating of the muscular tail generates a current that pulls water into the house through coarse, meshlike, mucous filters that screen out large particles; eventually the water leaves the house via the excurrent opening. The pharynx of appendicularians bears only two small gill slits, which open directly to the exterior. Mucous feeding nets are secreted through the mouth and lie within the house chamber. The water current is directed through these fine-mesh nets, where food particles are concentrated, and the fragile house collapses when water is no longer pumped through it. The food, net and all, is periodically ingested by way of a short buccal tube. The houses of most appendicularians bear an additional opening that serves as an escape hole through which the animal can leave and reenter. The houses are fragile and easily damaged. Damaged or clogged houses are abandoned, and new ones are manufactured rapidly, in a matter of seconds or minutes. In some species a new or "spare" house may be found beneath the functional house; after the animal escapes the clogged house, the "spare" is rapidly inflated.

The gut of appendicularians is U-shaped, and the anus opens directly to the outside rather than into a cloacal chamber. Fecal material is released into the path of excurrent water leaving the filter nets. Appendicularians are primarily herbivorous, feeding on minute phytoplankton and bacteria even below a size of 0.1 μm. They sometimes constitute the dominant planktonic herbivores in waters over the continental shelf, reaching densities of many thousands per cubic meter.

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Circulation, Gas Exchange, and Excretion

The circulatory system is weakly developed in urochordates, especially in the planktonic thaliaceans and appendicularians. It is best understood in ascidians, which possess a short, valveless, tubular heart that lies posteroventrally in the body near the stomach and behind the pharyngeal chamber (Figure 27.5A,D,E). The heart is surrounded by a pericardial sac, sometimes referred to as a vestige of the coelom. Blood vessels extend anteriorly and posteriorly, opening into spaces around the internal organs and also providing the blood supply to the tunic. The heartbeat is by peristaltic action driven by two myogenic pacemakers, one at either end of the tubular heart, and the direction of this motion is periodically reversed, flushing the blood first one way through the heart and then the other. Blood physiology and function are still largely matters of speculation. Curiously, many ascidians accumulate high concentrations of certain heavy metals in their blood, especially vanadium and iron. Some evidence suggests that the presence of high vanadium levels in at least some species serves to deter would-be predators. In addition, the blood includes a large variety of cell types, including amebocytes that are thought to function in nutrient transport, tunic deposition, and accumulation of metabolic wastes.

Gas exchange occurs across the body wall in tunicates, especially across the linings of the pharynx and the cloacal chamber. Little is known about respiratory physiology in these animals. In most ascidians and some other tunicates, two evaginations arise from the posterior wall of the pharynx and lie along each side of the heart. These structures are called **epicardial sacs**, and they are thought to represent coelomic remnants. In some species the epicardial sacs are involved in bud formation during asexual reproduction, and they may also function in the accumulation of nitrogenous waste products by forming storage capsules called **renal vesicles**. Other than by these vesicles and certain blood cells (nephrocytes), it is likely that much of the metabolic waste is lost from the body by simple diffusion.

Nervous System and Sense Organs

While the nervous system of tunicates is reduced, perhaps reflecting their relatively inactive sessile or floating planktonic lifestyles, it has recently received attention as possibly containing precursors of nervous system elements thought to be vertebrate innovations, such as placodes and the neural crest. In addition, a secondary mechanoreceptor organ, the **circumoral ring**, is found in some ascidians (including thaliaceans). This ring may be a precursor to the vertebrate secondary mechanoreceptor hair cells found in the ear and the lateral line organ. In ascidians the secondary mechanoreceptors are located around the siphons, and they show varying complexity among taxa that may relate to different feeding strategies.

A small cerebral ganglion lies just dorsal to the anterior end of the pharynx and gives rise to a few nerves that go to various parts of the body, especially the muscles and siphonal areas. A well-developed dorsal nerve cord is present in the tails of tunicate larvae, but this structure is lost during metamorphosis, except in the appendicularians. Most tunicates possess a **neural**, or **subneural**, **gland** located between the cerebral ganglion and the anterodorsal portion of the pharynx (Figure 27.5A,D). This gland opens to the pharynx through a small duct, but its function is unknown. Some workers have suggested that it may be the precursor of the pituitary gland of vertebrates. Sensory receptors are poorly known in tunicates, although touch-sensitive neurons are prevalent around the siphons.

Ascidian larvae are well known to be responsive to light and gravity, often with a general pattern of initially swimming upwards, toward the light, but then eventually settling in darker, shaded areas, though the pattern varies among species. Ascidian larvae possess several sensory receptors that function in settling and probably substratum selection, but they are absent from the adults. A small **sensory vesicle** lies near the anterior end of the dorsal nerve cord adjacent to the developing cerebral ganglion (see Figure 27.8C). This vesicle houses a light-sensitive ocellus and a statocyst (called an otolith). Most, though not all, ascidian larvae become negatively phototactic and positively geotactic at the time of settlement. The anterior end of the larva bears two or three **adhesive papillae**, each of which is supplied with two sets of neurons. A primary, more exposed set of papillae may serve in determining an appropriate settlement location via chemosensory abilities, while the secondary set of more protected neurons may be more involved in aspects of metamorphosis related to mechanoreception following attachment.

Reproduction and Development

Asexual reproduction While appendicularians are probably entirely sexual in their reproductive habits, thaliaceans and many other ascidians include asexual processes in their life history strategies. In social and especially colonial and compound ascidians, asexual budding allows rapid exploitation of available substrata and recovery from partial predation, as we have seen in other sessile invertebrates such as sponges and bryozoans. Remarkably, some colonial ascidians can regenerate their entire bodies from small amounts of vascular tissue, an impressive feat for a chordate and a subject of ongoing investigation into the nature of regeneration pathways that differ to some extent from asexual proliferation. In fact, regeneration studies in

the solitary ascidian *Ciona intestinalis* and colonial botryllid ascidians have been going on for over a century.

Budding in tunicates occurs in a great variety of ways and from different organs and germinative tissues (Figure 27.7). In general, initial buds are formed by a sexually produced individual (**oozooid**), then the asexually produced individuals (**blastozooids**) produce additional buds. The simplest and perhaps most primitive budding process occurs in certain social ascidians, including species of *Perophora* and *Clavelina*, where blastozooids arise from the body wall of stolons. In more complicated budding processes, the germinal tissues include various combinations of the epidermis, gonads, epicardial sacs, and gut. Doliolid thaliaceans often produce chains of buds. The chains are sometimes released intact, but eventually each blastozooid breaks loose as a separate individual. Budding in pyrosomes results in the characteristic floating colonies seen in species of this family (Figure 27.6A,B).

Some workers have divided the various types of budding among ascidians into two categories on the basis of their functional significance. Propagative budding generally occurs during favorable environmental conditions and serves to increase colony size and exploit available resources. On the other hand, survival budding tends to take place during the onset of adverse conditions and may be viewed as an overwintering or other survival device. With the return of more favorable growing conditions, these "prebuds" quickly develop as new blastozooids. More recently, particular attention to aspects of asexual reproduction has focused on the model colonial species *Botryllus schlosseri*, where a regular weekly cycle of zooid degeneration and replacement by developing buds (**pallial budding**) has served as a platform to investigate the relationship between developmental processes and regeneration. Recent discoveries have uncovered the presence of stem cell niches associated with the ascidian endostyle, as well as stem cells circulating in the vascular system that allow whole-body regeneration from isolated fragments of vascular tissue (**vascular budding**).

In botryllid ascidians, including *Botryllus schlosseri*, studies have shown that variation in blood pigments is genetically determined. The blood also contains several vertebrate-like hormones, including thyroxine, oxytocins, and vasoconstrictors. Compound species, such as those in the genera *Botryllus* and *Botrylloides*, have special blood components that play a vital role in rejecting adjacent conspecific colonies unless they are closely related (e.g., close relatives and clonemates), in which case the interaction may lead to colony fusion. This system is of great interest to comparative immunologists. Through breeding studies and genetic analyses, the "fusibility system" continues to be elucidated in these species. Populations of botryllids are highly genetically polymorphic at fusibility loci, with hundreds of alleles present even in invasive populations worldwide. Colonies that share at least one fusibility allele can fuse to form chimeras, while non-allele-sharing colonies undergo cytotoxic rejection processes and form permanent borders. The fate of the chimeras after fusion is less well known and also a subject of ongoing inquiry. Ascidian species vary in the intensity of the physiological engagement and subsequent rejection cytotoxicity when it occurs, and additional genes (and environmental variation) are thought to also play a role in determining the outcome of these immune-like interactions. This system is also being studied as a model for the evolution of kin recognition interactions in a medical context using natural transplantation phenomena related to host-graft acceptance or rejection.

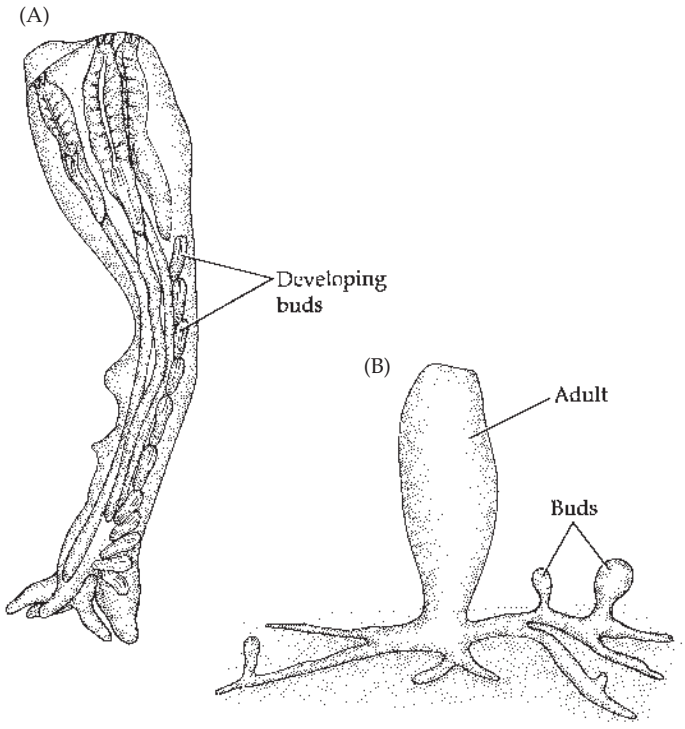

FIGURE 27.7 Asexual reproduction in ascidians.
(A) Formation of buds in the colonial ascidian *Aplidium*.
(B) General pattern of stoloniferous budding in an ascidian.

Sexual reproduction Tunicates are hermaphroditic, with relatively simple reproductive systems. Generally a single ovary and a single testis lie near the loop of the digestive tract in the posterior part of the body and, in most cases, connect through a separate sperm duct and oviduct to the cloacal chamber near the anus (Figure 27.5). However, some species have a single gonad (ovotestis), with one gonoduct, and members of a few families (e.g., Pyuridae, Styelidae) have multiple gonads. In some species, the ovaries contain high amounts of silica, but the significance of this is unknown.

There is considerable variation in overall reproductive strategies among tunicates. Most large solitary

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ascidians produce high numbers of ova with little yolk, which are shed into the sea coincident with the release of sperm from other individuals. External fertilization is followed by the development of a free-swimming **tadpole larva**, which eventually settles and metamorphoses to an oozooid (Figure 27.8). In contrast to this fully indirect life history pattern, many compound ascidians composed of tiny zooids produce relatively few eggs, but each egg has a high yolk content. These eggs are fertilized and subsequently brooded while attached to a parent zooid, or they are detached but located in various places within the tunic or within the cloacal chamber; they are not released until the swimming tadpole larvae develop. Some compound ascidian larvae are smaller with less yolk, but they retain a nutritive connection to the parent zooid in what is called a placental developmental mode. And various degrees of larval suppression also occur among some ascidians with this mixed life history strategy, with some species undergoing fully direct development. For example, *Protostyela longicauda* produces nonswimming larvae that are brooded. In this species, the larval "tail" is simply an extension of the tunic and contains no cellular material. The larva is sticky and when it is released, it quickly adheres to any object it contacts, later making a permanent attachment. At least some of these tailless species have been shown to be derived from tailed species, and genes controlling tail development are present but suppressed in expression.

Although all thaliaceans lack a free-swimming larva, they differ markedly in their approaches to direct development. In pyrosomes, each zygote develops directly to an oozooid, with no evidence of a larval stage. The oozooid then buds to produce a colony. Doliolids produce tailed larvae, but each is encased in a cuticular capsule and does not swim. The larva metamorphoses to an oozooid. Salps undergo internal fertilization in the oviduct. The zygotes implant and form a placenta-like association with the parent in a uterine chamber in the oviduct. Here the embryos develop directly to the adult form.

Appendicularians free-spawn, and fertilization occurs externally. They develop to a tadpolelike stage and then mature into the characteristic adults that resemble the larvae of ascidians.

In most tunicate species studied, cleavage is radial, holoblastic, and slightly unequal; it leads to the formation of a coeloblastula, which undergoes gastrulation by invagination. The blastopore lies at the presumptive posterior end of the body but closes as development proceeds. There is a long history of experimental work on developmental stages of ascidians, which has led to insights in areas such as cytoplasmic regulation within the egg and the relationship of egg and larval body axes. More recently, developmental studies in basal chordates including urochordates have focused intensely on understanding the derivation of vertebrate neural development. The solitary ascidian *Ciona intestinalis* has been the subject of a complete cell fate mapping project, including neural mapping of the larva, which has allowed extensive comparison of the transition from the larval sensory architecture to the very different adult architecture, with particular attention being paid to the search for homologies to vertebrates.

The development of chordate features is most easily seen and understood in those species that form free tadpole larvae, such as most Ascidiacea. In fact, the larvae of most ascidians consist of countable numbers of cells, making these animals excellent models for studying cellular events early in chordate development; gastrulation in ascidians starts as early as the 110-cell stage. As the embryo elongates, the gut proliferates three longitudinal strips of mesoderm—a middorsal strip that becomes the notochord, and lateral strips that form the mesenchyme and body musculature. Thus, even though the mesoderm arises from the archenteron (endoderm), it does not pouch substantively from the gut wall. A middorsal strip of ectoderm differentiates as a neural plate, which sinks inward and curls to produce the dorsal hollow nerve cord. The epidermis secretes a larval tunic, which often develops dorsal and ventral **tail fins**. The anterior part of the gut differentiates as the pharyngeal chamber (or basket) during larval life, and the rudiment of a cloacal water cavity forms by an ectodermal invagination producing the atrial siphon. However, these ascidian larvae are all lecithotrophic, and the gut and filtering devices do not become functional until metamorphosis. Social and colonial tunicate larvae are usually much larger than solitary larvae. The greater size includes a more highly developed adult rudiment in the trunk of the tadpole along with additional yolk, generally rendering the larval features more difficult to visualize. However, some colonial larvae are smaller and less yolky but maintain a nutritive connection to an adult zooid with a longer development time, in comparison to solitary larvae. Some species with symbiotic photosynthetic partners show a variety of structures associated with the larval and adult forms for housing the symbionts. Similarity in such structures does not necessarily correlate to phylogenetic affinities; instead, it suggests that the partnerships have evolved multiple times.

Ascidian larvae outside of the parent are short-lived. When development is fully indirect, the larvae are planktonic for only about two days or less. In some forms with a mixed life history pattern (e.g., *Botryllus*), the free larval life lasts only a few minutes and larvae may even settle and metamorphose upon the releasing parent colony, which then resorbs them. While the larval body is no longer visible, the germline of the resorbed larva may actually take over the germline of the resorbing adult in a phenomenon known as **germ cell parasitism**. This phenomenon is thought to be driven by kin selection and potentially

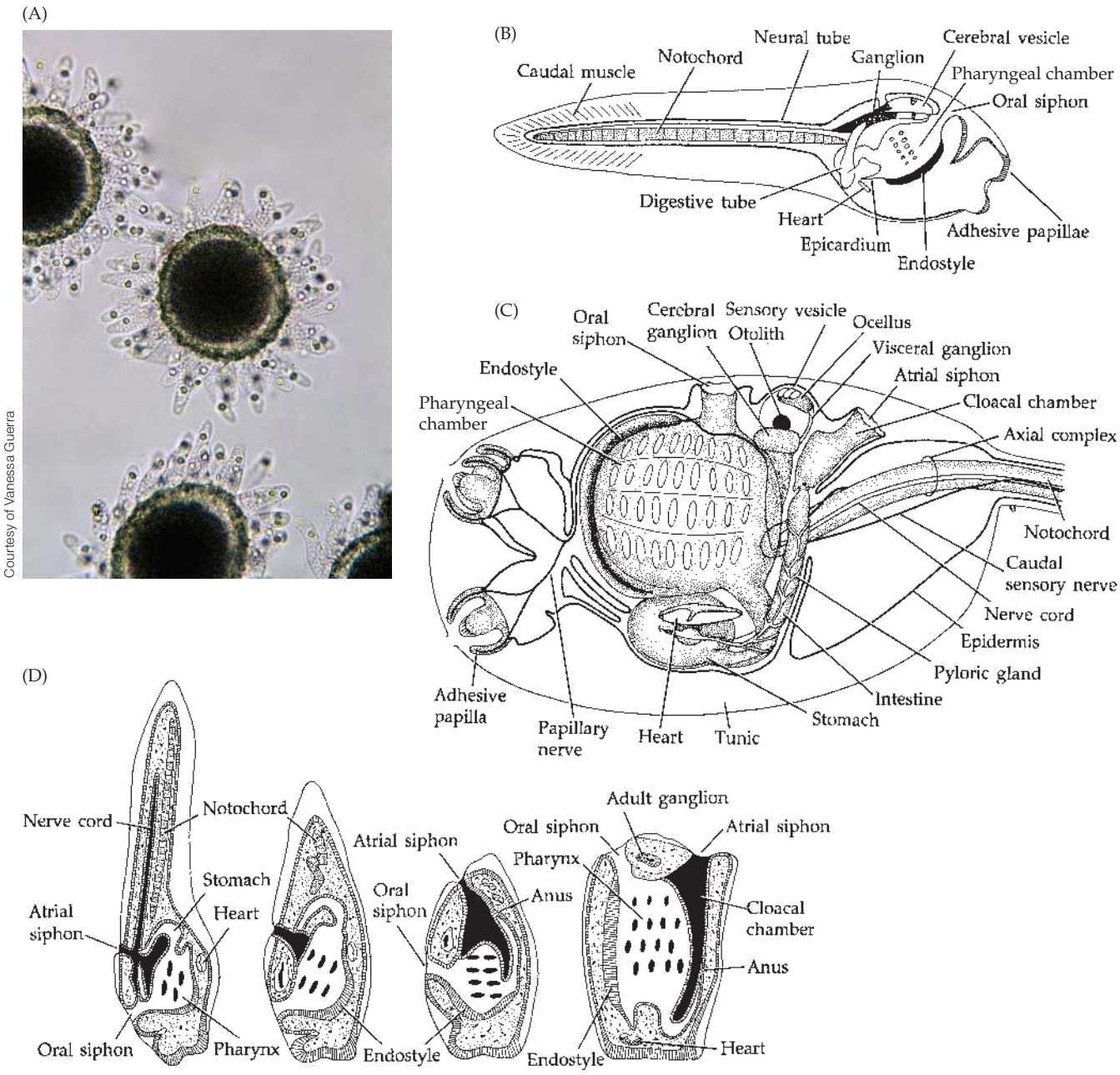

FIGURE 27.8 Sexual reproduction, larvae, and metamorphosis. (A) *Ciona intestinalis* eggs surrounded by follicle cells. (B) An ascidian tadpole larva has many chordate features. (C) The anterior end of the larva of *Distaplia occidentalis*. (D) Metamorphosis of a settled tadpole larva. Tail resorption is followed by a reorientation of the body to bring the siphons to the adult position. (E) Internal and external fertilization in the solitary ascidian *Corella*. Arrows show direction of water flow, in the branchial siphon and out the atrial siphon. In *C. willmeriana* eggs are being released from the atrial siphon, to be fertilized in the water (self-fertilization in this species is rare). In *C. inflata*, embryos and larvae are found within the atrial brood chamber, resulting from internal fertilization (which may be self-fertilization under certain conditions). (F) Tadpole larva of *Botryllus schlosseri* (with ampulla).

by advantages accrued to both partners. Larvae may escape the high mortality common for young juvenile stages and find a ready place to settle in space-limited environments. Adults may gain benefits in avoiding senescence through an infusion of juvenile stem cells. Even though a short larval life allows dispersal over only small distances, the larvae probably play a key role in the selection of suitable substrata. The events of settling and metamorphosis of ascidian larvae are complex and varied.

The settling larva of an ascidian contacts a substratum with its anterior end and may secrete mucus and undergo searching motions before releasing an adhesive from the papillae. In the larvae of many compound ascidians, the papillae evert during this process. The secretion of the adhesive apparently triggers an

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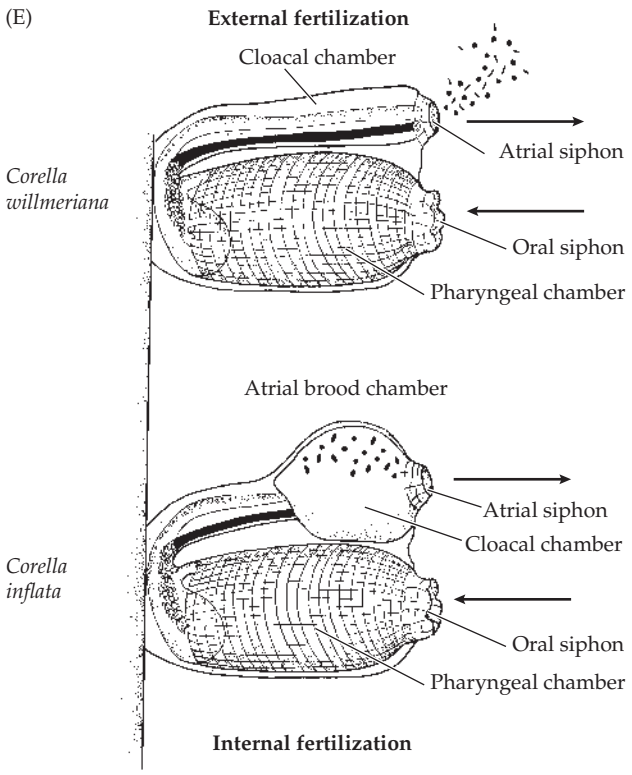

(F)

Courtesy of C. S. Cohen

irreversible sequence of metamorphic events. Within minutes after attachment, resorption of the larval tail commences by one of several methods involving various contractile elements in the tail region. The animal's viscera and siphons then undergo a remarkable 90° rotation that brings these organs to their adult position. The outer layer of the cuticle is shed, removing the larval fins from the settled juvenile (Figure 27.8D). The pharynx enlarges and the filtering mechanism becomes functional as the siphons open to the environment. During all of these processes secondary attachment organs, called **ampullae**, extend from the body and permanently affix the animal to the substratum. Finally, various transient larval organs are lost, such as most of the larval nervous system and sense organs.

Larvae of some species have been reported to practice aggregated settlement. Experimental studies suggest early juvenile mortality rates may be very high. Colonial species may have several advantages at this stage, as they start life at a larger size and are thus able to filter water more efficiently. Tiny early settlers may suffer from a low profile in the hydrodynamic boundary layer where flow rates are near zero, making food capture challenging. Some newly settled juvenile ascidians appear to have adaptations to increase their ability to filter feed near the boundary layer, including temporary growth of a stalk, enlarged siphon diameters relative to body size, and specific orientation relative to flow. As ascidians increase in size and escape the boundary layer, their growth rates sometimes increase dramatically.

Chordate Phylogeny

Recent phylogenomic analyses have largely, though not entirely, resolved the broad structure of chordate relationships (Figure 27.9). Both molecular and morphological analyses agree that the phylum Chordata is monophyletic. Its anatomical synapomorphies include the notochord, the endostyle (thought to be represented by the thyroid gland in vertebrates), and the muscular postanal tail. All chordates also have pharyngeal gill slits, epithelial tissue that binds iodine and secretes iodotyrosine, and a dorsal nerve cord, but these three features also occur in hemichordates, and some consider them synapomorphies of deuterostomes lost in crown-group echinoderms. However, homology of the solid dorsal nerve cord of hemichordates and the hollow cord of chordates has been challenged by recent work and needs further investigation. The notochord plays an important embryological role in inducing the chordate central nervous system, so absence of a notochord in hemichordates might be evidence in support of the idea that the hemichordate dorsal nerve cord may not be homologous with the chordate dorsal nerve cord, although this remains an open question. Gill slit endoderm in both hemichordates and chordates expresses *pax1/9* and *six1* genes, supporting their homology in these two phyla, and some authors consider gill slits to be present in stem-group echinoderms. Some juvenile enteropneusts have a postanal tail that has been homologized with the stalk of pterobranchs (Hemichordata). However, recent work has shown that the enteropneust tail expresses the *Hox11/13* gene, whereas the vertebrate postanal tail expresses the orthologous *Hox10–13* gene, suggesting possible homology in the postanal body regions, though not necessarily in the tail itself (the functions of these structures are altogether different in the two phyla).

Several recent phylogenomic analyses have agreed on some structure for chordate phylogeny (Figure 27.9). Urochordata (tunicates) and Vertebrata are sister groups (a clade named Olfactores by Richard P. S. Jefferies in 1991), and this forms a sister group to Cephalochordata (lancelets). Within the Urochordata,

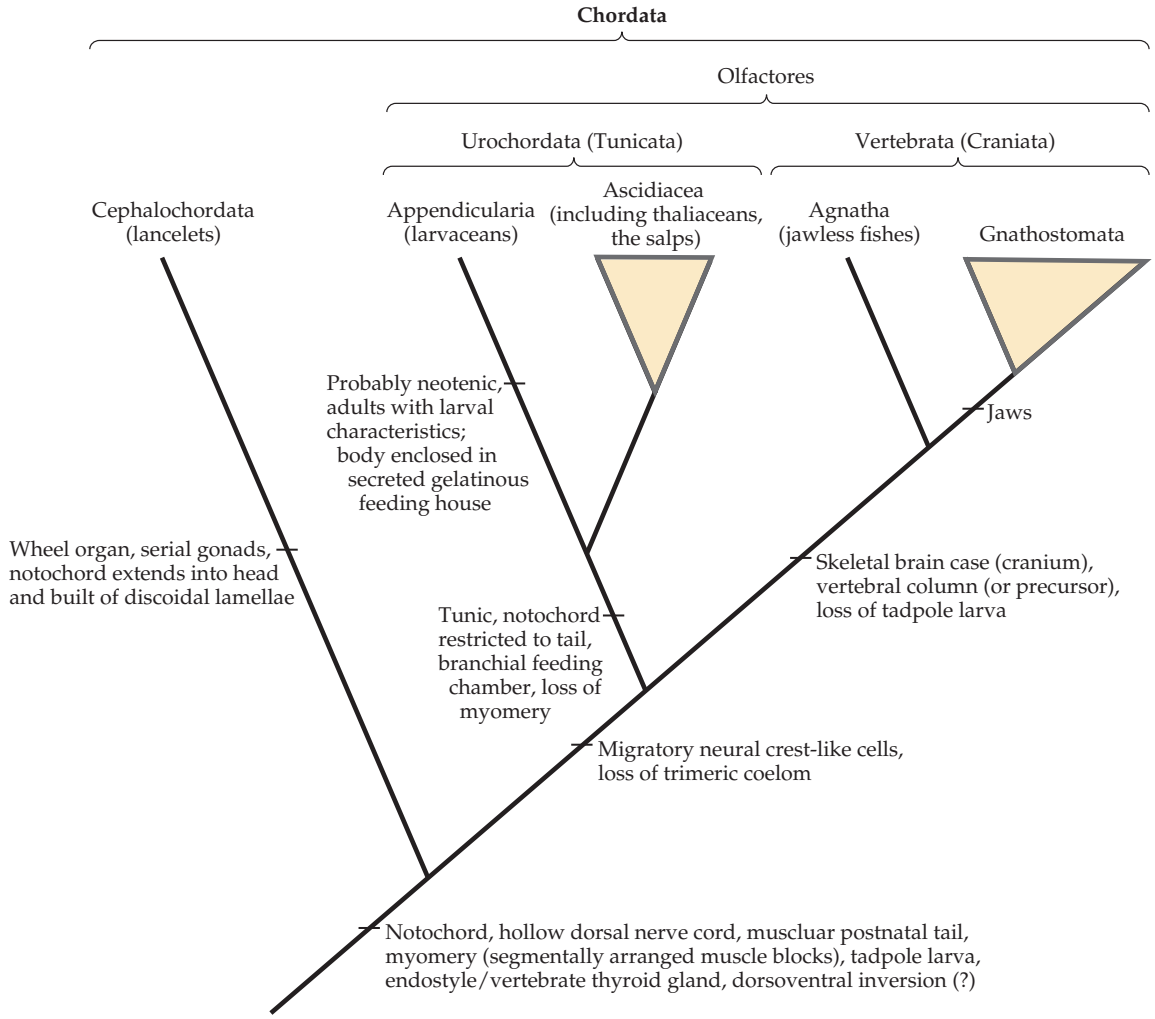

FIGURE 27.9 Phylogeny of the Chordata. See text for details.

Appendicularia (larvaceans) is the sister group of all other urochordates, and thaliaceans are derived ascidians. Ascidiacea is probably not monophyletic as traditionally defined, as it should be redefined to include thaliaceans, as we do here. The implication of this is that thaliaceans reacquired a pelagic lifestyle from their benthic ancestry.

The central nervous system of chordates shows a wide variety of forms, from a few small ganglia with a tail nerve cord in urochordates, to a swimming spinal cord with a hardly recognizable cerebral vesicle in cephalochordates, to a fully developed brain and spinal cord in vertebrates. The nerve cord of chordates develops dorsally as a hollow neural tube above the notochord. In the vertebrates, the nerve cord differentiates during embryogeny into a large brain and usually a well-developed spinal cord protected by the backbone. The notochord is a rodlike, skeletal structure dorsal to the gut and ventral to the nerve cord. It should not be confused with the backbone, or vertebral column, of adult vertebrates. The notochord appears early in embryogeny and plays an important role in promoting or organizing the chordate embryonic development of nearby structures. In most adult chordates, the notochord disappears or becomes highly modified. In some protochordates, and some fishes, it persists as a flexible but incompressible skeletal rod that supports the body during swimming. The embryonic development of the notochord in ascidians has been well studied. In *Ciona intestinalis* (Figure 27.3F) it is composed of only 40 cells, which align to form a single row by an event called convergent extension. The cells undergo vacuolation to transform the notochord into a single hollowed tube. The restricted number of notochord cells is achieved by the regulated number of cell divisions under the control of a key transcription factor, brachyury. The stomochord (buccal diverticulum) of hemichordates, once thought to be homologous with the chordate notochord, is now viewed as evidence of convergence or parallelism.

The vertebrate thyroid gland sequesters iodine and secretes T3 and T4 hormones, which regulate metabolism, postembryonic development, and

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metamorphosis. The lancelet and urochordate thyroid homolog, the endostyle, is primarily involved in mucus production for feeding, but it also incorporates iodine and synthesizes thyroid hormone. However, the exact role of TH in these groups is not well understood. In lampreys, the larva concentrates iodine and synthesizes TH in an endostyle, a thyroid homolog that reorganizes into a follicular thyroid at metamorphosis to the adult. Specialized secretory cells in hemichordates also bind iodine, but these are found throughout the pharynx, so a direct homology with the endostyle may not be appropriate, although these cells could have been the precursors to the chordate endostyle. Although no other animals possess an endostyle, TH does occur in other invertebrates.

Deuterostomes may be a small branch on the tree of life, but there are no stranger animals than echinoderms and chordates (especially vertebrates!). And this brings up one of the most profound synapomorphies of Chordata—the dorsoventral axis, which is thought to be inverted in comparison to the dorsoventral axis of the hemichordates (and probably all other bilaterians). Early in their evolution, chordates apparently turned themselves upside down! Hemichordate gill bars and gill slits are located dorsally (opposite the ventral mouth), while in cephalochordates and craniates the gill bars and slits are located ventrally. Gill openings are also dorsal in stem-group echinoderms. And, the dorsal epibranchial ridge of enteropneusts appears to be the anatomical and histological homolog of the ventral endostyle of chordates. Furthermore, the dorsal side of a juvenile hemichordate is determined by an expression stripe of the bone morphogenetic protein gene (*BMP*), which is expressed dorsally, and its ventral side is shown by an expression stripe of *BMP* antagonists, including chordin, just as has been shown for arthropods. In contrast, in vertebrates *BMP* is expressed ventrally and chordin is expressed dorsally. However, as the mouth is ventral in both chordates and nonchordates, the evolution of chordates must have also entailed moving the mouth from the opposite side of the gill slits to the same side as the gill slits, while presumably also evolving a notochord and dorsal central nervous system from a ventral enteropneust-like nerve net. The hypothesis of chordate dorsoventral axis inversion has been around since the early nineteenth century, and it has not been without its detractors (e.g., van den Biggelaar et al. 2002). However, current evo-devo research tends to support the idea.

But deuterostome (and chordate) oddness doesn't stop there. One of the other trends in deuterostome evolution is gene duplication, which appears to be widespread. The cephalochordates had long been thought to have the basic deuterostome Hox cluster of 14 genes, but in 2008 a fifteenth Hox gene was identified from the lancelet *Branchiostoma floridae*. In addition, in cephalochordates and vertebrates, *Hox9–14* show an independent duplication compared with protostomes. And a duplication of the posterior Hox genes into three genes (named *Hox11/13a*, *Hox11/13b*, and *Hox11/13c*) characterizes both echinoderms and hemichordates. In contrast, *Hox14* has been lost from all tetrapods and teleost fishes so far examined. Many other genes have been identified in amphioxus that show two to four paralogs in vertebrates, derived from two whole-genome duplication events. However, urochordate genomes seem to have lost many genes. Hox gene duplication, of course, is especially important for opening up new evolutionary-developmental avenues, since these are the "master genes" that are involved in anterior–posterior patterning in bilaterians.

The realization that urochordates, and not cephalochordates, are the most closely related group to Vertebrata is a recent discovery resulting from multigene analyses. It appears that earlier phylogenetic studies using a few genes that had hypothesized the cephalochordates to be the sister group of the vertebrates suffered from long-branch-attraction problems. Interestingly, R. P. S. Jefferies had predicted the tunicate-craniate relationship in 1991 on anatomical grounds. It was Jefferies who coined the name Olfactores, on the basis of a putatively homologous olfactory apparatus in fossils that was proposed as the precursor of the tunicate-craniate clade. We now know that the presence of migratory neural crest–like cells in urochordates probably also represents an anatomical-developmental synapomorphy of the Olfactores. The discovery that tunicates and craniates may be sister groups implies that characters common to cephalochordates and craniates (e.g., segmentally arranged muscle blocks) might be ancestral to all Chordata.

Cephalochordate synapomorphies include the unique wheel organ (an anterior vestibule formed by the oral hood bearing buccal cirri and ciliary bands). They share with Vertebrata the segmentally arranged blocks of muscles, developed from rows of mesodermal pockets from the archenteron, and this feature might be a synapomorphy of the Chordata that has been secondarily lost in the Urochordata. Fossil cephalochordates have been described from the middle Cambrian Burgess Shale and from the early Cambrian of China.

Urochordates possess several synapomorphies, including a unique cuticle of tunicin, a greatly enlarged pharynx forming a branchial feeding chamber, and oral and atrial siphons opening to an ectodermally derived atrium (cloacal chamber). Very few fossil tunicates have been described, but those also date to the early Cambrian.

The Vertebrata, or Craniata (as the name implies), are defined by an endoskeletal cranium and, in all but the Agnatha, a vertebral column (backbone). The evolution of the vertebrates from their protochordate ancestor involved a critical developmental innovation that led to the vertebrate head. This was the amplified **neural crest** and a distinctive cell population called the **neural crest cells**. These cells form at the neural plate border

and migrate extensively in the embryo to differentiate into numerous cell and tissue types, including connective tissues of the craniofacial skeleton, much of the peripheral nervous system, and pigment cells. They are responsible for many of the complex structures in the vertebrate head that are absent in cephalochordates and tunicates. Neural crest cells also give rise to various cranial ganglia and craniofacial cartilages and bones, and they even enter the pharyngeal pouches and arches where they contribute to the thymus, bones of the middle ear and jaw, and the odontoblasts of primordial teeth. So unique are these cells, and their derivatives, that some biologists consider them a "fourth germ layer." The migration of neural crest cells represents an epithelial-to-mesenchymal embryonic transition. Long thought to be an innovation of the Vertebrata, a migratory cell population resembling neural crest cells has recently been documented from urochordates. In *Ecteinascidia turbinata*, dye-labeled cells have been shown to emerge from the neural tube, migrate into the body wall and siphon primordium, and subsequently differentiate as pigment cells. These cells even express HNK-1 antigen and *Zic* gene markers as seen in vertebrate neural crest cells. Thus, it seems that the origin of neural crest cells lies in the common ancestor of vertebrates and urochordates. It is highly likely these cells gained additional functions, and were joined by other cell types, to generate the broad variety of derivative tissues typical of vertebrate neural crest cells.

Molecular clock analyses have suggested that the Deuterostomia (indeed, the Bilateria) might have arisen in the Precambrian.

Chapter Summary

The monophyletic phylum Chordata contains three major clades, ranked as subphyla: Cephalochordata (a small group of fishlike invertebrates known as the lancelets or amphioxus), Urochordata or Tunicata (a large group of filter-feeding invertebrates called tunicates that are benthic or planktonic), and Vertebrata (the vertebrates). The first two groups are strictly marine. Modern phylogenomic research shows that Urochordata is the sister group to Vertebrata, a clade known as Olfactores. Future research will continue to investigate the putative vertebrate precursor molecules in urochordates (e.g., thyroxin, oxytocins, and vasoconstrictors) and their evolutionary-developmental pathways, as well as the immunelike system in ascidians that is at play when colonies meet and "fight or fuse." Studies will also continue to use tunicates to better understand the derivation of vertebrate neural development. The question of dorsoventral inversion in Chordata needs further investigation.

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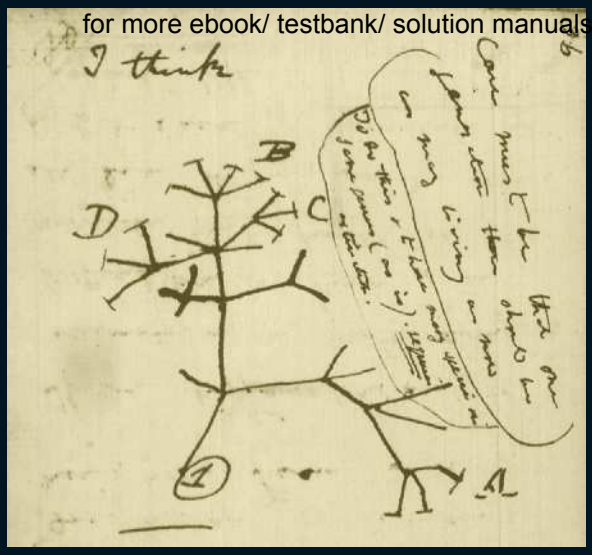

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CHAPTER 28

Perspectives on Invertebrate Phylogeny

By the time you have gotten to this chapter, you will have "toured" almost *all* of the Animal Kingdom, given that invertebrates comprise roughly 96% of all described, living animal species. What an incredible diversity of form and function you have seen! Isn't it curious how unevenly these animals are distributed across the 31 metazoan phyla? Vastly unevenly distributed—82% of all described animals are arthropods, 5% are molluscs, and only 4% are chordates. The other 28 phyla make up the remaining 9%! Six phyla have fewer than 100 described species in them, and half of those have fewer than a dozen known species. What are we to make of this? In fact, only 6 phyla comprise more than 1% each of the described animal species on Earth (Arthropoda, Mollusca, Annelida, Platyhelminthes, Nematoda, and Chordata). It would seem that the world belongs to insects, crustaceans, spiders, molluscs, worms, and vertebrates. Indeed, these are the only animals most humans ever see in their lifetimes (unless they happen to go diving on a tropical coral reef, in which case they are confronted by myriad sponges, cnidarians, and echinoderms). How fortunate that you have now been introduced to all 31 animal phyla, even the smallest and least understood groups.

In reading the "animal chapters" of this text, you have learned a good deal about the evolution of these 31 phyla, how they are related to one another, and what their internal relationships are. You have learned that phylogenies can be constructed from a variety of different kinds of data and that most recently the field of molecular phylogenomics (phylogenetics based on large amounts of genomic data) has proliferated, giving us new ideas about how Earth's creatures are related to one another. The idea of phylogenetic trees should now be quite familiar to you. But let's take one last look, a "higher view" of animal phylogeny, before we close the cover on this fourth edition of *Invertebrates*.

Molecular phylogenetics had only just begun to bear fruit in 2002, when the second edition of this book went to press. While some tantalizing suggestions of new and very different kinds of relationships among the animal phyla had been suggested, these new hypotheses had not yet been broadly tested. Since then, molecular phylogenetics has exploded onto the scene at a pace never imagined, and it now plays the primary role in reconstructing animal phylogeny. In just the past 20 years we have come from analyzing a few ribosomal genes to the point where new genome-level analyses are being published almost daily. Molecular phylogenetics is now being incorporated into studies of ecology, oceanography, biogeography, conservation biology, medicine, archeology, and anthropology. And it is building a new framework for the tree of life.

Unraveling the phylogenetic history of the animal kingdom has been one of biology's great challenges. The "new phylogeny," built with molecular data, has many similarities to older trees built on morphological and developmental data, but some big surprises have emerged and many uncertainties remain. The biggest challenge lies in the fact that life's deep lineages arose and began to diverge from one another so long ago, over half a billion years ago for most phyla. So the traits of animals, whether anatomical or genetic, that might be useful in revealing relationships among these ancient lineages are often obscured by hundreds of millions of years of evolutionary change. But, despite this, many relationships are now well resolved.

Early molecular phylogenetic studies relied heavily on the 18S ribosomal RNA gene (also known as the nuclear small-subunit ribosomal RNA gene, or SSU rRNA). However, it quickly became apparent that understanding deep-level metazoan phylogeny required analysis of additional genes, particularly nuclear protein-coding genes, and this led to an era of multigene trees that continues today as phylogeneticists add more and more loci (and taxa) to their data sets for analysis (reviewed in Chapter 2). Most recently phylogenomic studies using large parts of the genome (sometimes using the transcriptome[1] as a proxy for the whole genome but leaning more towards whole genomes in the past few years) and analyzing hundreds or even thousands of genes have begun to expand the scope of data available for phylogenetic analysis, and this has added increased stability to the structure of our phylogenetic framework. The advent of evo-devo, or evolutionary developmental biology, has also begun to significantly impact our understanding of how genes relate to specific morphologies, how they work, and what roles they might have played in the unfolding of animal radiations. These new techniques have provided answers to fundamental questions, such as the identity of arthropod appendages and the nature of segmentation in animals.

A large body of evidence, anatomical and molecular, has accumulated since the 1960s that supports the view that animals share a common ancestor with the protist group Choanoflagellata. The flagellated collar cells of sponges and choanoflagellates are nearly identical, and similar cells have also been described in a few other animal phyla, including some cnidarians, echinoderms, hemichordates, and ascidians. A few interesting differences between them have been noted, but some divergence over a half billion years is to be expected. The Metazoa are defined by a number of apomorphies, the most obvious being multicellularity arising through the embryonic layering process called gastrulation. Also, unlike coloniality, as seen in many protist groups (including choanoflagellates), in metazoans the epithelial cells are in contact with each other through unique junction structures and molecules, some of which make transport of nutrients between cells possible (e.g., septate or tight junctions, desmosomes, zonula adherens). Additional metazoan apomorphies include striate myofibrils, actin-myosin contractile elements, the possession of animal (type IV) collagen (although collagen, or a collagen homologue, also occurs in some fungi), and a basal lamina beneath the epidermis. In addition, sexual reproduction in animals involves a distinct pattern of egg development from one of the four cells of meiosis, whereas the other three cells degenerate.

Figure 28.1 is a working hypothesis of metazoan phylogeny, based primarily upon the most recent molecular phylogenetic research. Some of these studies have been in agreement that the phylum Porifera, the sponges, is the sister group to all remaining animals and thus could be considered the "oldest" animal phylum. However, other molecular phylogenies have suggested Ctenophora might occupy this position as the sister group to all other metazoans. The draft genome of *Pleurobrachia bachei*, together with other ctenophore transcriptomes, suggests that ctenophores may be rather distinct from other animal genomes in their content of neurogenic, immune, and developmental genes. However, a number of putative apomorphies link Cnidaria and Ctenophora with the Bilateria in a clade that has been called Neuralia. The "basal Ctenophora" hypothesis has been challenged by some authors as an artifact of methodological issues, yet others disagree and have found that the artifacts affect the more traditional placement of sponges. In fact, the placement of Ctenophora is only one area of uncertainty near the base of the animal tree. Strong resolution of the positions of Placozoa and Cnidaria has also yet to be achieved (and placozoans seem to be much more derived than their simple body plan would first suggest, contradicting the Neuralia hypothesis). This is why we represent the first node of our tree as a trichotomy between Porifera, Ctenophora, and the remaining animals, and the second node as a trichotomy between Cnidaria, Placozoa, and Bilateria.

The origin of the Bilateria, likely in the Precambrian, was a transformative event in the evolution of animals. The origination of fundamental bilateral symmetry led to cephalization and the innovation of mesoderm (a third germ layer), the latter allowing for the evolution of a variety of new organs and a new kind of underlying body cavity (the secondary coelom, or eucoelom). The appearance of mesoderm and a true adult coelom in animal evolution led to the ability to penetrate the substrate, which in turn led to three-dimensional ichnofossils such as the ones left by *Treptichnus pedum*, the first

[1] Whereas a genome is the complete set of genes present in a cell (or organism) and is sequenced from DNA, a transcriptome is a subset of those genes that are transcribed (or expressed) in a cell at any given time and is sequenced from RNA.

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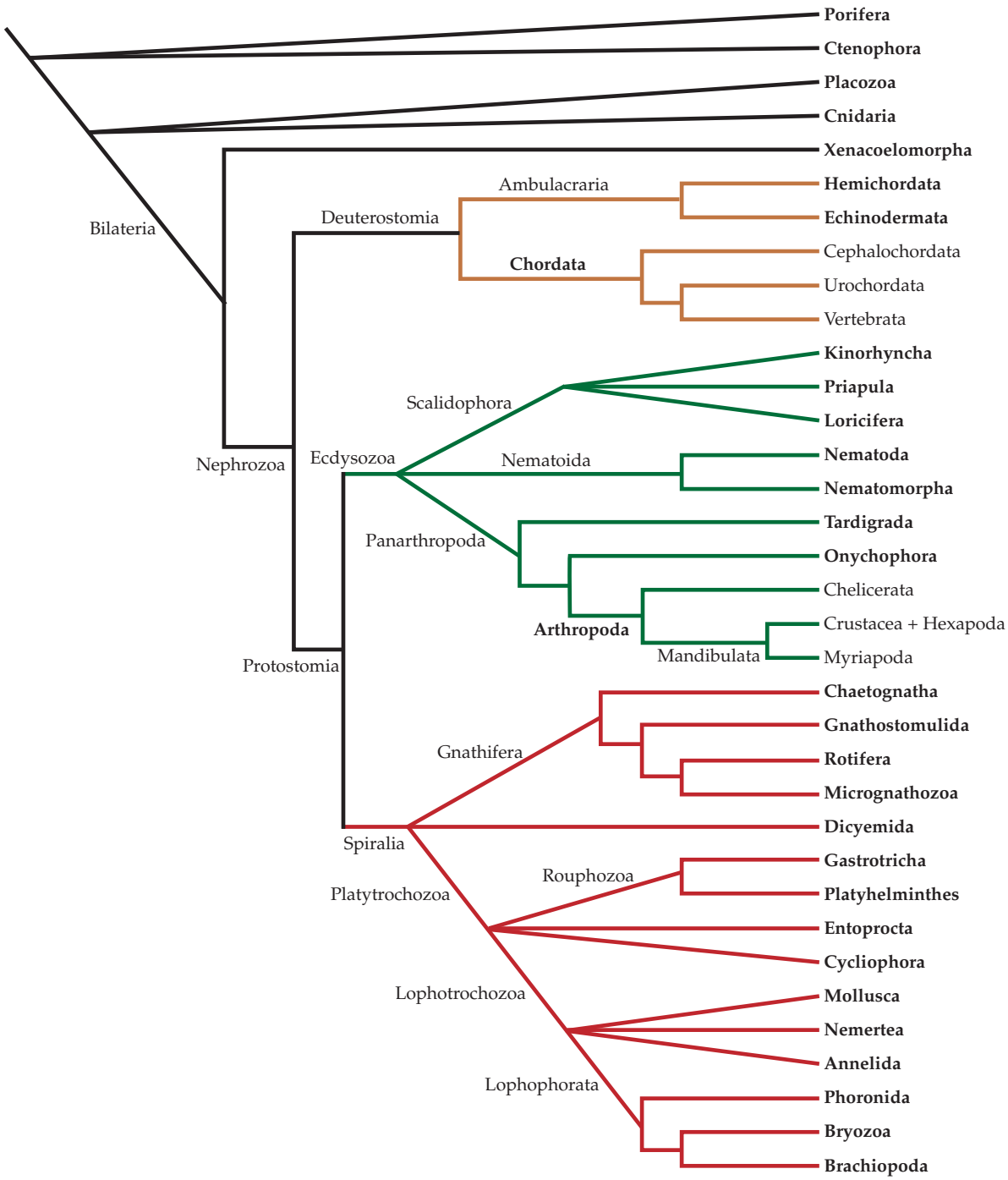

FIGURE 28.1 A phylogeny of Metazoa. This tree reflects a consensus view based primarily on recent molecular phylogenetic analyses. The 31 animal phyla are in boldface, whereas subphyla and other clades are in lightface. Spiralian lineages are in red, ecdysozoan lineages are in green, deuterostome lineages are in tan. Uncertainty still exists in several regions, and these are depicted as polytomies ("starbursts"). Thus, for example, the branching sequence for Placozoa, Cnidaria, and Bilateria is not yet resolved, so it is shown as an unresolved trichotomy. Similarly, two large polytomies exist among the Platytrochozoa, and the relationships of the three ecdysozoan clades are still unresolved, as are those of the three scalidophoran phyla. Due to uncertainty, Dicyemida is depicted in an unresolved trichotomy with Gnathifera and Platytrochozoa.

animal to burrow and consequently form the ichnofossil that defines the base of the Cambrian. It is likely that such anatomical innovation caused a dramatic increase in the depth and intensity of bioturbation in seafloor sediment, known as the "agronomic revolution." One of the earliest living phyla to appear once bilaterality was achieved may have been Xenacoelomorpha (but acoelomorphs are acoelomate and probably not

responsible for the *T. pedum* burrows). Early in the evolution of Bilateria the clade split into two great lineages, Deuterostomia and Protostomia.

The position of the phylum Xenacoelomorpha is still debated, although a general consensus is emerging that it comprises basal bilaterians and does not fall unambiguously within either Deuterostomia or Protostomia. Some molecular research had suggested that Xenoturbellida (and even Xenoturbellida + Acoelomorpha) were deuterostomes, but that hypothesis is not well supported. The weight of molecular and morphological evidence places Xenacoelomorpha as a clade and sister group to all other bilaterians, as shown in our tree. Apomorphies of Xenacoelomorpha may be their unique pulsatile bodies, their unique epidermal cilia, and their frontal organ/pore. Because xenacoelomorphs lack excretory organs and a through gut, and these (in their many forms) are present in most other bilaterians, the sister group to Xenacoelomorpha has been called Nephrozoa. Nephrozoa are distinguished by the presence of a through (complete) gut, discrete excretory organs, and the presence of a *Hox3* gene. Nephrozoa divides clearly into the two clades that have been accepted for many decades, Deuterostomia and Protostomia (although their composition has been in flux).

These two lineages were introduced to you in Chapter 8. Because of their great age, untangling the characteristics of the first deuterostomes and protostomes has been challenging. Deuterostome apomorphies are likely the presence of pharyngeal gill slits, a trimeric coelom, and enterocoelic development, although all three of these features have been lost in some modern forms. Protostomia is even trickier to define by any morphological synapomorphies, since so much animal diversity is encompassed by this clade, although the ventral nerve cord and circumesophageal brain are probably good apomorphies (but they are not distinct in a few soft-bodied worms). The relationships of the Deuterostomia are largely settled with the Ambulacraria (Hemichordata + Echinodermata) being the sister group to the Chordata (Cephalochordata, Urochordata, and Vertebrata/Craniata). Ambulacrarian apomorphies include a unique heart-kidney system and a specific larval form. But the relationships among the protostomian phyla still remain to be fully resolved.

Deuterostomia is a small radiation composed of just three phyla, two of which have been very successful—Echinodermata and Chordata (with 7,300 and 63,000 named living species, respectively). The protostomes, on the other hand, comprise 23 phyla and over 1.3 million living species. The Protostomia are divided into two large clades—Spiralia and Ecdysozoa. Ecdysozoans are distinguished by their molting process, whereas spiralians have spiral cleavage, although this distinctive feature has been lost many times in the course of spiralian evolution.

Relationships among the Ecdysozoa (the molting Protostomia) are partly resolved, although those among the three major clades (Scalidophora, Nematoida, Panarthropoda) remain unclear; thus these three lineages are depicted as a trichotomy in our tree. Similarly, the clade Scalidophora needs further study to verify its monophyly and the relationships of its three included phyla. The Nematoida and Panarthropoda trees are strongly supported, but admittedly, genomic resources are unevenly distributed among lineages, with lots of genomes for arthropods and nematodes and few to none for tardigrades, onychophorans, and nematomorphs, which makes phylogenomic results tentative.

Relationships within Spiralia also need further refinement, but recent phylogenomic data suggest there may be two clades—Gnathifera and Platytrochozoa. The position of Dicyemida (kidney parasites in cephalopods) remains unclear, and our tree shows this phylum unresolved with respect to the other two main spiralian clades. Most chaetognath morphological traits have no clear homologies in other lineages, but molecularly they group with the Gnathifera, and their cerebral ganglia resemble those of the spiralian phyla.

One of the major things we might notice in this view of phylogenetic relationships is that developmental systems are flexible. For example, a trait long thought to define the Deuterostomia is deuterostomous development itself. However, we now know that this mode of embryogeny also occurs in some phyla belonging to the clade Protostomia (e.g., in Nematomorpha, Priapula, Brachiopoda, many Crustacea, perhaps Chaetognatha). Thus, as noted early on in this book, the clade Deuterostomia cannot be defined by deuterostomy, nor can the clade Protostomia be defined by protostomy (which also occurs in Cnidaria and Ctenophora). Similarly, radial cleavage is likely plesiomorphic among Bilateria, while spiral cleavage, which is apomorphic for Spiralia, appears to have reverted back to radial or other idiosyncratic modes multiple times. Thus, the clade Spiralia in our tree has members whose cleavage patterns are radial (e.g., the three lophophorate phyla), whereas the Gastrotricha seems to have a unique form of cleavage. Several phyla of Spiralia have trochophore or trochophore-like larvae (e.g., some members in the phyla Mollusca, Annelida, Nemertea, and possibly Entoprocta), but these have not consistently been grouped together in the molecular phylogenies.

This brings us back to the question of why animal species diversity is so strongly dominated by arthropods, molluscs, annelids, and vertebrates. Unfortunately, there is no easy explanation for why these four groups have enjoyed such expansive radiations. Could it be that this is an artifact of time—perhaps during earlier eras, the Mesozoic or Paleozoic, other phyla dominated Earth's biosphere but simply left us little fossil evidence of their prior dominance, due to their

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fragile bodies? If this were the case, many of those small phyla could be viewed today as "living relicts" (like horseshoe crabs). Did ctenophores, placozoans, acoels, gastrotrichs, nemerteans, chaetognaths, entoprocts, gnathostomulids, and other phyla that today seem almost inconsequential once dominate the world? Or perhaps the "big four" taxa have always been dominant due to something intrinsic in their biology that remains to be elucidated. Another possibility is that we simply haven't looked hard enough, spent enough effort combing through interstitial habitats, deep-sea sediments, and the parasitic world—there might well be an enormous biological diversity still waiting to be discovered in such poorly sampled environments (certainly we know this is true for the roundworms, Nematoda).

We finish this chapter with a note of caution and one of hope. Molecular phylogenies are resolving the puzzle of the animal tree of life one piece at a time, but morphology still has its role in phylogenetics. Gnathifera, for example, was first recognized by analyzing morphological traits, and it has subsequently been consistently recovered by both morphological and molecular analyses. The monophyly of other groups, such as Scalidophora, is supported more strongly by morphological data than by molecular data, but this clade is broadly accepted by invertebrate biologists. Many groups have been shuffled around the tree, mostly because they were once positioned based on single character systems (e.g., radial versus spiral cleavage; acoelomate versus blastocoelomate versus coelomate), and many of these character systems conflict with one other. Molecular phylogenetics has given us a new way to look at the animal tree, and robust and stable results have made us rethink certain long-held paradigms (e.g., Articulata versus Ecdysozoa; Atelocerata versus Pancrustacea). Morphology can be misleading in some cases, as molecular analyses can also be affected by many kinds of biases or be unable to reconstruct the interrelationships of some animal groups. Thus, only by combining the information derived from the careful study of both disciplines will we be able to generate a sound animal phylogeny and be in a position to comprehend what that phylogeny means in terms of the evolution of animal body plans.

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Chapter 4 A sea urchin (*Lytechinus pictus*) embryo at the 16-cell stage. The four large macromeres are behind the four small micromeres, and the eight mesomeres are behind the macromeres. Remnants of the fertilization envelope can be seen attached to some of the cells. Scott Camazine/Science Source.

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Chapter 8 *Xenoturbella bocki*. Live specimen, from 80 m depth, off the west coast of Sweden. Courtesy of G. Rouse.

Chapter 9 It turns on a dime; a live *Xenoturbella bocki* (or possibly an undescribed species) collected by MBARI (Monterey Bay Aquarium Research Institute) from ~600 m depth near a whalefall in Monterey Submarine Canyon, California. Courtesy of Greg Rouse.

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Chapter 23 Rusty millipede (*Trigoniulus corallinus*), Hawaii. The large, shield-like plate behind the head of this millipede is the first trunk ring, the collum, a segment without appendages. The close contact between male (above) and female might suggest mating, but during sperm transfer the partners actually take a different position. This photograph likely shows a preliminary act (i.e., mechanical stimulation by the male) and mating will follow if the female accepts the male. © Larry Jon Friesen

Chapter 24 The armored harvestman *Phareicranaus manauara* (order Opiliones). Courtesy of G. Giribet.

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Chapter 27 *Megalodicopia hians*. © Larry Jon Friesen.

Chapter 28 A page from Darwin's notebook from around July 1837 shows an early sketch of a phylogenetic tree. © Cambridge University Library/CC BY-NC 3.0.

CHAPTER 1

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CHAPTER 21

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CHAPTER 22

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CHAPTER 5

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CHAPTER 6

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CHAPTER 7

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CHAPTER 13

The field of malacology is so large, has had such a long history, and has so embraced the mixed blessings of contributions from amateur shell collectors that dealing with the literature is a daunting task. Many molluscs are of commercial importance (e.g., *Haliotis*, *Mytilus*, oysters, squid), and for these groups hundreds of studies appear annually; others are important laboratory/experimental organisms (e.g., *Doryteuthis*, *Octopus*, *Aplysia*), and many papers are also published on these groups. New taxonomic monographs on various groups or geographical regions also appear each year, as do countless shell guides and coffee-table books. Distilling all of this into a small set of key references useful for entry into the professional literature is difficult; the list below is our attempt to do so.

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CHAPTER 16

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CHAPTER 17

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CHAPTER 21

The amount of published literature on crustaceans is vast. Much of the key work on classification and phylogenetics was reviewed by Martin and Davis (2001), and on larval development by Martin et al. (2014). We refer readers to those works for an entrée into those fields.

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CHAPTER 22

The amount of published information on Hexapoda is overwhelming. We have thus had to be very selective in our reference list, emphasizing texts, conference volumes, and journal articles that present emerging new fundamental knowledge, are solid overviews in their respective fields, or are older classics worthy of mention. These will provide readers with an entry into the primary literature.

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CHAPTER 25

Deuterostomia

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CHAPTER 27

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