Weaver ants *(Oecophylla longinoda)* carry a leaf to repair their nest in Papua New Guinea.

Mark Moffett/Minden Pictures

29 Animal Phylogeny, Acoelomates, and Protostomes

STUDY PLAN

WHY IT MATTERS

In 1909, a lucky fossil hunter named Charles Wolcott tripped over a rock on a mountain path in British Columbia, Canada. Under the force of his hammer, the rock split apart, revealing the discovery of a lifetime. Wolcott and other workers soon found fossils of more than 120 species of previously undescribed animals from the Cambrian period. These creatures had lived on the muddy sediments of a shallow ocean basin. About 530 million years ago, an underwater avalanche buried them in a rain of silt that was eventually compacted into finely stratified shale. Over millions of years, the shale was uplifted by tectonic activity and incorporated into the mountains of western Canada. It is now known as the Burgess Shale formation.

Some animals in the Burgess Shale were truly bizarre **(Figure 29.1).** For example, *Opabinia* was about as long as a tube of lipstick; it had five eyes on its head and a grasping organ that it may have used to capture prey. No living animals even remotely resemble *Opabinia*. The smaller *Hallucigenia* sported seven pairs of large spines on one side and seven pairs of soft organs on the other. Recent research suggests that *Hallucigenia* may belong in the phylum Onychophora, described in Section 29.7. Nevertheless, most species of the Burgess

Opabinia

Hallucigenia

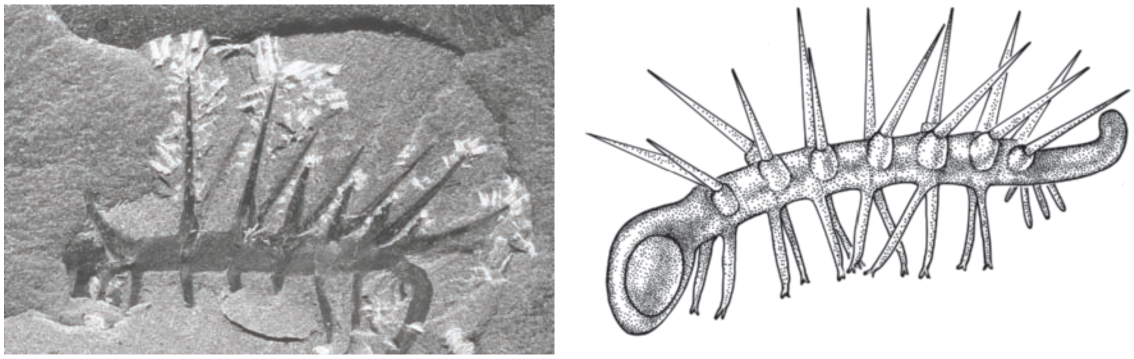


Figure 29.1 Animals of the Burgess Shale. *Opabinia* had five eyes and a grasping organ on its head. *Hallucigenia* had seven pairs of spines and soft protuberances. (Images: Dr. Chip Clark, National Museum of Natural History, Smithsonian Institution.)

Shale left no descendants that are still alive today. Thus, this remarkable assemblage of fossils provides a glimpse of some evolutionary novelties that—whether through the action of natural selection or just plain bad luck—were ultimately unsuccessful.

Other animal lineages have shown much greater longevity. Zoologists have described nearly 2 million living species in the kingdom **Animalia**, about five times as many as in all the other kingdoms combined. The familiar **vertebrates**, animals with a backbone, encompass only a small fraction (about 47,000 species) of the total. The overwhelming majority of animals fall within the descriptive grouping of **invertebrates**, animals without a backbone.

The remarkable evolutionary diversification of animals resulted from their ability to consume other organisms as food and, for most groups, their ability to move from one place to another. Today animals are important consumers in nearly every environment on Earth. Their diversification has been accompanied by the evolution of specialized tissues and organ systems as well as complex behaviors.

In this chapter, we introduce the general characteristics of animals and a phylogenetic hypothesis about their evolutionary history and classification. We also survey some of the major invertebrate phyla; a *phylum* is an ancient monophyletic lineage with a distinctive body plan. In Chapter 30 we examine the deuterostome lineage, which includes the vertebrates and their nearest invertebrate relatives.

29.1 What Is an Animal?

Biologists recognize the Kingdom Animalia as a monophyletic group that is easily distinguished from the other kingdoms.

All Animals Share Certain Structural and Behavioral Characteristics

Animals are eukaryotic, multicellular organisms. Their cells lack cell walls, a trait that differentiates them from plants and fungi. The individual cells of most animals are similar in size, so that very large animals like elephants have many more cells than small ones like fleas. In large animals, most cells are far from the body surface, but specialized tissues and organ systems deliver nutrients and oxygen to them and carry wastes away.

All animals are **heterotrophs:** they acquire energy and nutrients by eating other organisms. Food is ingested (eaten) and then digested (broken down) and absorbed by specialized tissues. Animals use oxygen to metabolize the food they eat through the biochemical pathways of aerobic respiration, and most store excess energy as glycogen, oil, or fat.

All animals are **motile**—able to move from place to place—at some time in their lives. They travel through the environment to find food or shelter and to interact with other animals. Most familiar animals are motile as adults. However, in some species, such as mussels and barnacles, only the young are motile; they eventually settle down as **sessile**—unable to move from one place to another—adults. The advantages of motility have fostered the evolution of locomotor structures, including fins, legs, and wings. And in many animals, locomotion results from the action of muscles, specialized contractile tissues that move individual body parts. Most animals also have sensory and nervous systems that allow them to receive, process, and respond to information about the environment.

Animals reproduce either asexually or sexually; in many groups they switch from one mode to the other. Sexually reproducing species produce short-lived, haploid **gametes** (eggs and sperm), which fuse to form diploid **zygotes** (fertilized eggs). Animal life cycles generally include a period of development during which mitosis transforms the zygote into a multicelled **embryo**, which develops into a sexually immature juvenile or a free-living **larva**, which becomes a sexually mature adult. Larvae often differ markedly from adults, and they may occupy different habitats and consume different foods.

The Animal Lineage Probably Arose from a Colonial Choanoflagellate Ancestor

An overwhelming body of morphological and molecular evidence indicates that all animal phyla had a common ancestor. For example, all animals share similarities in their cell-to-cell junctions and the molecules in their extracellular matrices (see Section 5.5) as well as similarities in the structure of their ribosomal RNAs.

Most biologists agree that the common ancestor of all animals was probably a colonial, flagellated protist that lived at least 700 million years ago, during the Precambrian era. It may have resembled the minute, sessile choanoflagellates that live in both freshwater and marine habitats today (see Figure 26.21). In 1874 the German embryologist Ernst Haeckel proposed a colonial, flagellated ancestor, suggesting that it was a hollow, ball-shaped organism with unspecialized cells. According to his hypothesis, its cells became specialized for particular functions, and a developmental reorganization produced a double-layered, sac-within-a-sac body plan **(Figure 29.2).** As you will see in Chapter 48, the embryonic development of many living animals roughly parallels this hypothetical evolutionary transformation.

STUDY BREAK

1. What characteristics distinguish animals from plants?
2. How does the ability of animals to move through the environment relate to their acquisition of nutrients and energy?

29.2 Key Innovations in Animal Evolution

Once established, the animal lineage diversified quickly into an amazing array of body plans. Before the development of molecular sequencing techniques, biologists used several key morphological innovations to unravel the evolutionary relationships of the major animal groups.

Tissues and Tissue Layers Appeared Early in Animal Evolution

The presence or absence of **tissues,** groups of cells that share a common structure and function, divides the animal kingdom into two distinct branches. One branch, the sponges, or Parazoa (*para* = alongside; *zoon* = animal), lacks tissues. All other animals, collectively grouped in the Eumetazoa (*eu* = true; *meta* = later), have tissues.

During the development of eumetazoans, embryonic tissues form as either two or three concentric **primary cell layers.** The innermost layer, the **endoderm,** eventually develops into the lining of the gut (digestive system) and, in some animals, respiratory organs. The outermost layer, the **ectoderm,** forms the external cover-

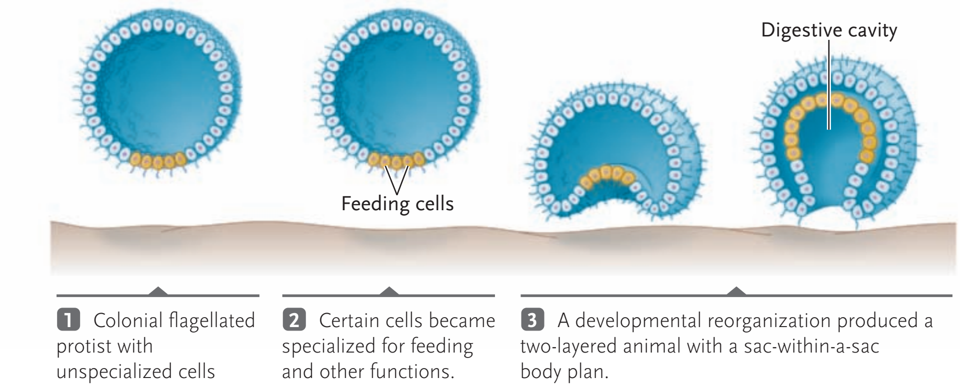


Figure 29.2
Animal origins. Many biologists believe that animals arose from a colonial, flagellated protist in which cells became specialized for specific functions and a developmental reorganization produced two cell layers. The cell movements illustrated here are similar to those that occur during the development of many animals, as described in Chapter 48.

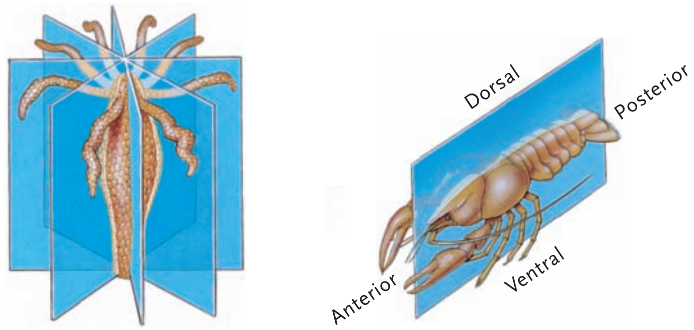
ing and nervous system. Between the two, the **mesoderm** forms the muscles of the body wall and most other structures between the gut and the external covering. Some simple animals have a **diploblastic** body plan that includes only two layers, endoderm and ectoderm. However, most animals are **triploblastic**, having all three primary cell layers.

Most Animals Exhibit either Radial or Bilateral Symmetry

The most obvious feature of an animal's body plan is its shape **(Figure 29.3).** Most animals are **symmetrical;** in other words, their bodies can be divided by a plane into mirror-image halves. By contrast, most sponges have irregular shapes and are therefore **asymmetrical.**

Most eumetazoans exhibit one of two body symmetry patterns. The Radiata includes two phyla, Cnidaria (hydras, jellyfishes, and sea anemones) and Ctenophora (comb jellies), which have **radial symmetry.** Their body parts are arranged regularly around a central axis, like the spokes on a wheel. Thus, any cut down the long axis of a hydra divides it into matching halves. Radially symmetrical animals are usually sessile or slow moving and receive sensory input from all directions.

All other eumetazoan phyla fall within the Bilateria, animals that have **bilateral symmetry.** In other words, only a cut along the midline from head to tail divides them into left and right sides that are essentially mirror images of each other. Bilaterally symmetrical animals also have **anterior** (front) and **posterior** (back) ends as well as **dorsal** (upper) and **ventral** (lower) surfaces. As these animals move through the environment, the anterior end encounters food, shelter, or enemies first. Thus, in bilaterally symmetrical animals, natural selection also favored **cephalization,** the development of an anterior head where sensory organs and nervous system tissue are concentrated.



Radial symmetry

Bilateral symmetry

Figure 29.3
Patterns of body symmetry. Most animals have either radial or bilateral symmetry.

Many Animals Have Body Cavities That Surround Their Internal Organs

The body plans of many bilaterally symmetrical animals include a body cavity that separates the gut from the muscles of the body wall **(Figure 29.4). Acoelomate** animals (*a* = not; *koilos* = hollow), such as flatworms (phylum Platyhelminthes), do not have such a cavity; a continuous mass of tissue, derived largely from mesoderm, packs the region between the gut and the body wall (see Figure 29.4a). **Pseudocoelomate** animals (*pseudo* = false), including the roundworms (phylum Nematoda) and wheel animals (phylum Rotifera), have a **pseudocoelom,** a fluid- or organ-filled space between the gut and the muscles of the body wall (see Figure 29.4b). Internal organs lie within the pseudocoelom and are bathed by its fluid. **Coelomate** animals have a true **coelom,** a fluid-filled body cavity completely lined by the **peritoneum,** a thin tissue derived from mesoderm (see Figure 29.4c). Membranous extensions of the inner and outer layers of the peritoneum, the **mesenteries,** surround the internal organs and suspend them within the coelom.

Biologists describe the body plan of pseudocoelomate and coelomate animals as a "tube within a tube"; the digestive system forms the inner tube, the body wall forms the outer tube, and the body cavity lies between them. The body cavity separates internal organs from the body wall, allowing them to function independently of whole-body movements. The fluid within the cavity also protects delicate organs from mechanical damage. And, because the volume of the body cavity is fixed, the incompressible fluid within it serves as a **hydrostatic skeleton,** which provides support; in some animals muscle contractions can shift the fluid, changing the animals' shape and allowing them to move from place to place (see Section 41.2).

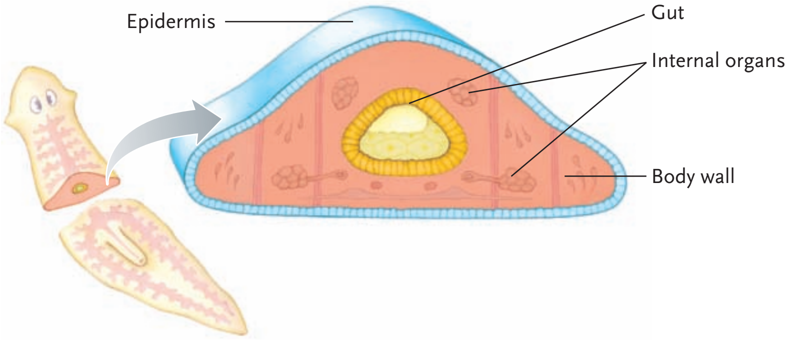
Developmental Patterns Mark a Major Divergence in Animal Ancestry

Embryological and molecular evidence suggests that bilaterally symmetrical animals are divided into two lineages: the protostomes, which includes most phyla of invertebrates, and the deuterostomes, which includes the vertebrates and their nearest invertebrate relatives. Protostomes and deuterostomes differ in several developmental characteristics **(Figure 29.5).**

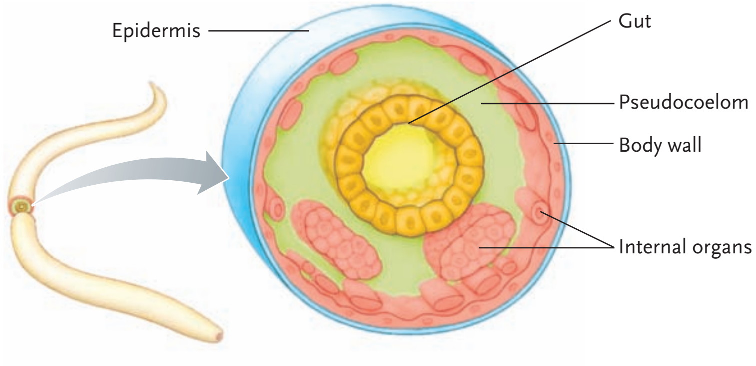
Shortly after fertilization, an egg undergoes a series of mitotic divisions called **cleavage** (see Section 48.1). The first two cell divisions divide a zygote as you might slice an apple, cutting it into four wedges from top to bottom. In many protostomes, subsequent cell divisions produce daughter cells that lie *between* the pairs of cells below them; this pattern is called **spiral cleavage** (left side of Figure 29.5a). In deuterostomes, by contrast, subsequent cell divisions produce a mass

Figure 29.4
Body plans of triploblastic animals.

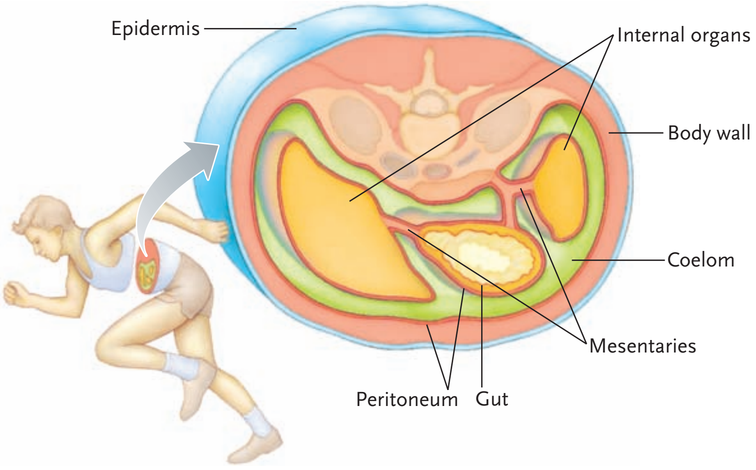
a. In acoelomate animals, no body cavity separates the gut and body wall.



b. In pseudocoelomate animals, the pseudocoelom forms between the gut (a derivative of endoderm) and the body wall (a derivative of mesoderm).



c. In coelomate animals, the coelom is completely lined by peritoneum (a derivative of mesoderm).



KEY

- 🟦 Derivatives of ectoderm
- 🟥 Derivatives of mesoderm
- 🟨 Derivatives of endoderm
- 🟩 Body cavity

of cells that are stacked directly above and below one another; this pattern is called **radial cleavage** (right side of Figure 29.5a).

Protostomes and deuterostomes often differ in the timing of important developmental events. During cleavage, certain genes are activated at specific times, determining a cell's developmental path and ultimate fate. Many protostomes undergo **determinate cleavage:** each cell's developmental path is determined as the cell is produced. Thus, one cell isolated from a two- or four-cell protostome embryo cannot develop into a functional embryo or larva. By contrast, many deuterostomes have **indeterminate cleavage:** the developmental fates of cells are determined later. A cell isolated from a four-cell deuterostome embryo will develop into a functional, although smaller than usual, embryo or larva. Like other deuterostomes, humans have indeterminate cleavage; thus, the cells produced by the first few cleavage divisions sometimes separate and develop into identical twins.

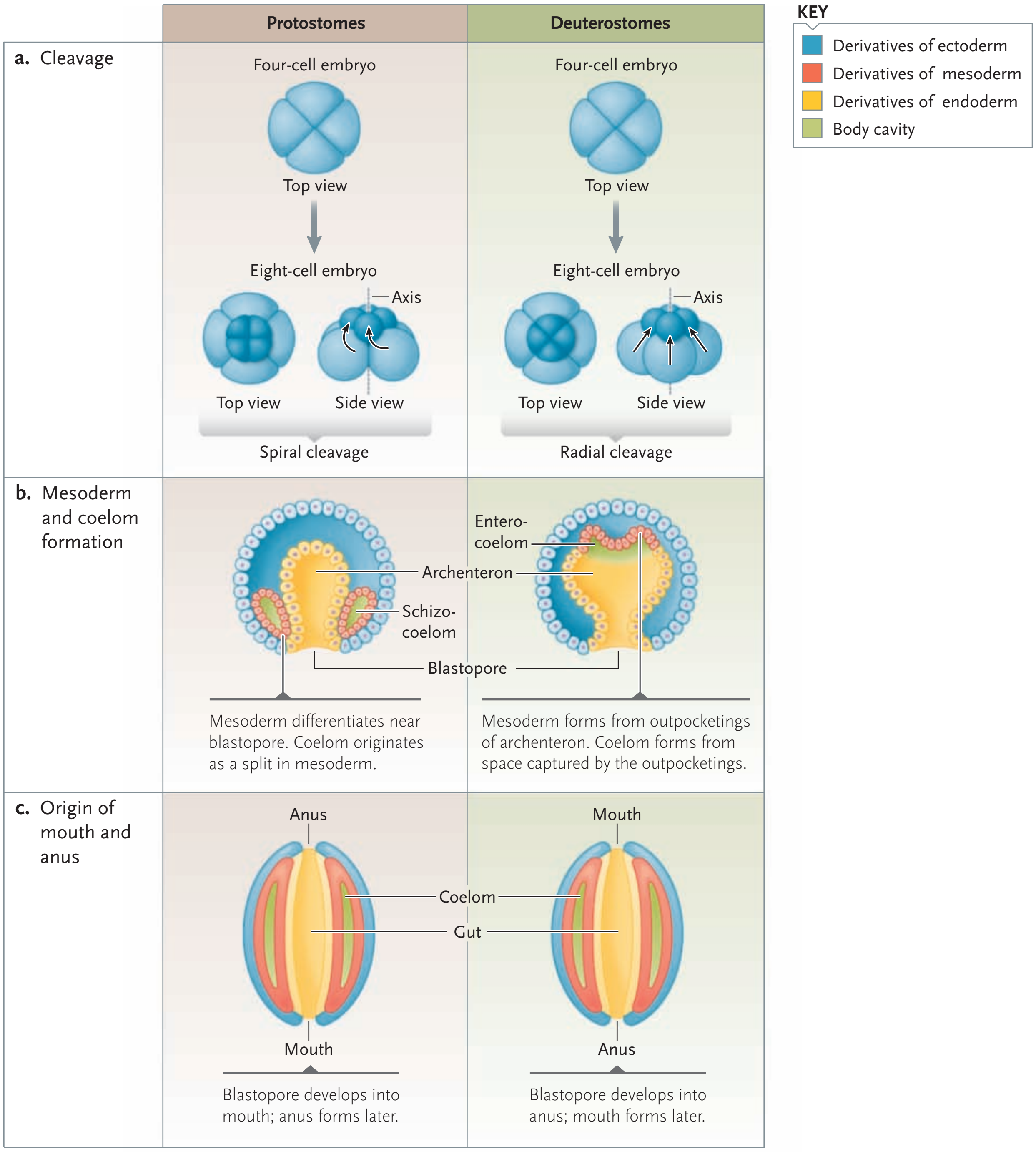


Figure 29.5
Protostomes and deuterostomes. The two lineages of coelomate animals differ in **(a)** cleavage patterns, **(b)** the origin of mesoderm and the coelom, and **(c)** the polarity of the digestive system.

As development proceeds, an opening on the surface of the embryo connects the developing gut, called the **archenteron**, to the outside environment. This initial opening is called the **blastopore** (see Figure 29.5b). Later in development, a second opening at the opposite end of the embryo transforms the pouchlike gut into a digestive tube (see Figure 29.5c). In protostomes (*protos* = first; *stoma* = mouth), the blastopore develops into the mouth, and the second opening forms the anus. In some deuterostomes (*deuteros* = second), the blastopore develops into the anus, and the second opening becomes the mouth.

Protostomes and deuterostomes also differ in the origin of mesoderm and the coelom (see Figure 29.5b). In most protostomes, mesoderm originates from a few specific cells near the blastopore. As the mesoderm grows and develops, it splits into inner and outer layers. The space between the layers is called a **schizocoelom** (*schizo* = split). In deuterostomes, mesoderm often forms from outpocketings of the archenteron. The space pinched off by the outpocketings is called an **enterocoelom** (*enteron* = intestine).

Several other characteristics also differ in adult protostomes and deuterostomes. For example, the central nervous system of protostomes is generally positioned on the ventral side of the body, and their brain surrounds the opening of the digestive tract. By contrast, the nervous system and brain of deuterostomes lie on the dorsal side of the body.

Segmentation Divides the Bodies of Some Animals into Repeating Units

Some phyla in both the protostome and deuterostome lineages exhibit varying degrees of **segmentation**, the production of body parts as repeating units. During development, segmentation first arises in the mesoderm, the middle tissue layer that produces most of the body's bulk. In humans and other vertebrates, we see evidence of segmentation in the vertebral column (backbone), ribs, and associated muscles, such as the "six-pack abs" that sit-ups accentuate. In some animals, segmentation is also reflected in structures derived from the endoderm and ectoderm. For example, the ringlike pattern on an earthworm or a caterpillar matches the underlying segments.

Segmentation provides several advantages. In markedly segmented animals, such as earthworms and their relatives, each segment may include a complete set of important organs, including respiratory surfaces and parts of the nervous, circulatory, and excretory systems. Thus, a segmented animal may survive damage to the organs in one segment, because those in other segments perform the same functions. Segmentation also improves control over movement, especially in wormlike animals. Each segment has its own set of muscles, which can act independently of those in other segments. Thus, an earthworm can move its anterior end to the left while it swings its posterior end to the right. The segmented backbone and body wall musculature of vertebrates allow greater flexibility of movement than would unsegmented structures.

STUDY BREAK

1. What is a tissue, and what three primary tissue layers are present in the embryos of most animals?
2. What type of body symmetry do humans have?
3. What is the functional significance of the coelom?
4. What are some advantages of having a segmented body?

29.3 An Overview of Animal Phylogeny and Classification

For many years, biologists used the morphological innovations and embryological patterns described earlier to trace the phylogenetic history of animals. These efforts were sometimes hampered by the difficulty of identifying homologous structures in different phyla and by morphological data that led to contradictory interpretations. Recently, biologists have used molecular sequence data to reanalyze animal relationships. Although biologists now recognize nearly 40 animal phyla, we focus primarily on the phyla that include substantial numbers of species.

Molecular Analyses Have Refined Our Understanding of Animal Phylogeny

Molecular analyses of animal relationships are often based on nucleotide sequences in small subunit ribosomal RNA and mitochondrial DNA (see Chapter 15). Recent analyses of *Hox* gene sequences provide similar results. (*Hox* genes are described in Sections 22.6 and 48.6.) These molecular analyses are still reasonably new, and they include studies of relatively few genes. Thus, the phylogenetic tree based on molecular sequences **(Figure 29.6)** represents a working hypothesis; its details will likely change as researchers accumulate more data.

The phylogenetic tree based upon molecular characters includes the major lineages that biologists had defined using the morphological innovations and embryological characters just described. For example, molecular data confirm the distinctions between the Parazoa and the Eumetazoa and between the Radiata and the Bilateria. They also confirm the separation of the deuterostome phyla from all others within the Bilateria.

However, the molecular phylogeny groups many other phyla—including the acoelomate animals, pseudocoelomate animals, protostomes, and a few others—into one taxon, the Protostomia. This group is, in turn, subdivided into two major lineages, the Lophotrochozoa and the Ecdysozoa, groups that were not previously recognized. The name Lophotrochozoa (*lophos* = crest; *trochos* = wheel) refers to both the lophophore, a feeding structure found in three phyla (illustrated in Figure 29.15), and the trochophore, a type of larva found in annelids and mollusks (illustrated in Figure 29.23). The name Ecdysozoa (*ekdysis* = escape) refers to the cuticle or external skeleton that these species secrete and periodically molt (or "escape from") when they experience a growth spurt or begin a different stage of the life cycle (illustrated in Figure 29.34); the molting process is called **ecdysis.**

The Molecular Phylogeny Reveals Surprising Patterns in the Evolution of Key Morphological Innovations

Phylogenetic trees contain explicit hypotheses about evolutionary change, and the molecular phylogeny has forced biologists to reevaluate the evolution of several important morphological innovations. For example, traditional phylogenies based upon morphology and embryology usually inferred that the absence of a body cavity, the acoelomate condition, was ancestral and that the

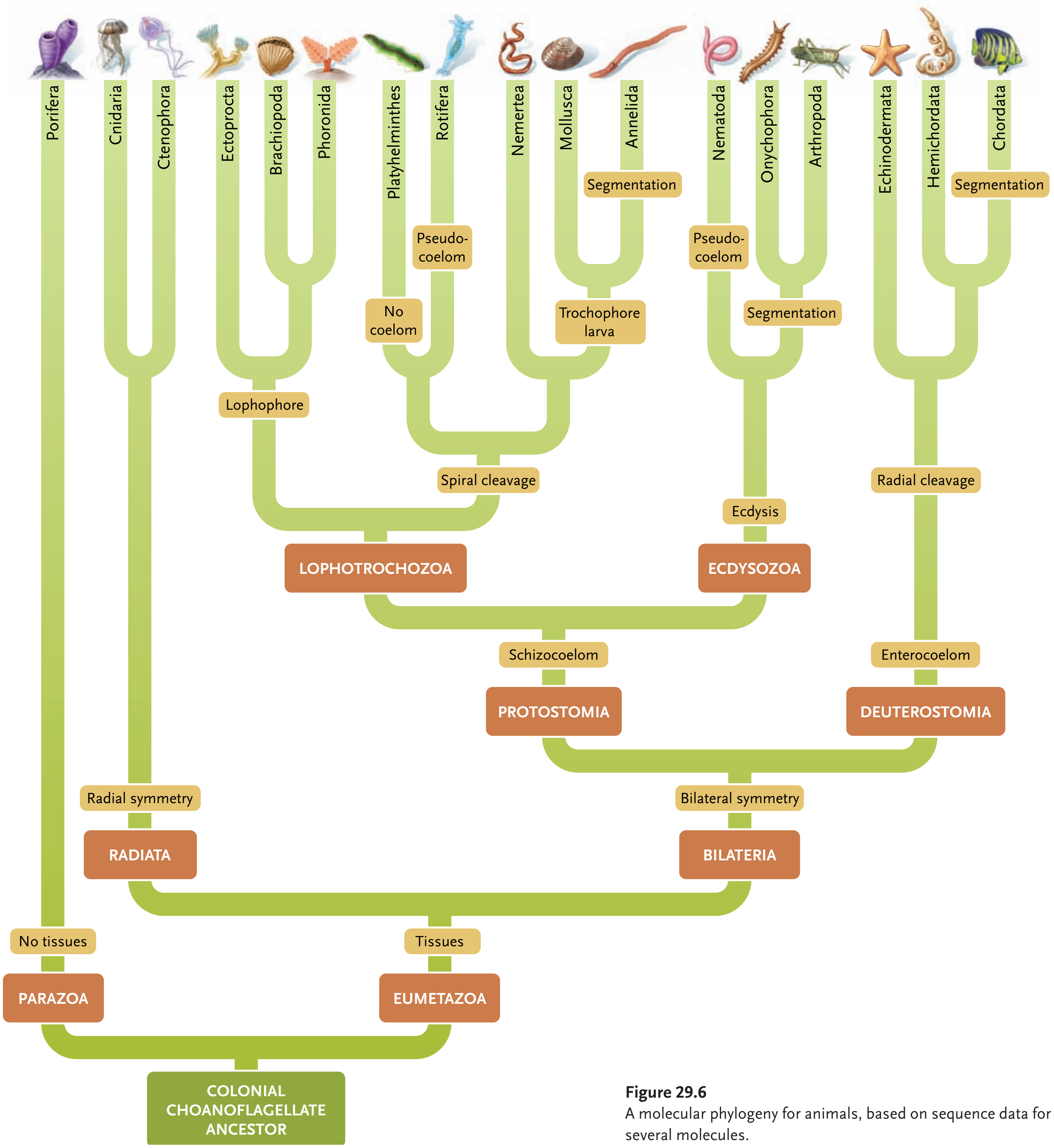


Figure 29.6
A molecular phylogeny for animals, based on sequence data for several molecules.

presence of a body cavity, the pseudocoelomate or coelomate condition, was derived. But the molecular tree provides a very different view. Because most protostome phyla have a schizocoelom, the molecular tree suggests that this trait is ancestral within the lineage, having evolved in the common ancestor of the lineage. If that hypothesis is correct, then the acoelomate condition of flatworms (phylum Platyhelminthes) represents the evolutionary *loss* of the schizocoelom, *not* an ancestral condition. Similarly, the molecular tree hypothesizes that the pseudocoelom evolved independently in rotifers (Lophotrochozoa, phylum Rotifera) and in roundworms (Ecdysozoa, phylum Nematoda) as modifications of the ancestral schizocoelom. Thus, according to the molecular tree, the pseudocoelomate condition of these organisms is the product of convergent evolution.

Traditional phylogenies also suggested that the segmented body plan of several protostome phyla was inherited from a segmented common ancestor and that segmentation arose independently in the chordates by convergent evolution. The molecular tree, by contrast, suggests that segmentation evolved independently in *three* lineages—segmented worms (Lophotrochozoa, phylum Annelida), arthropods and velvet worms (Ecdysozoa, phyla Arthropoda and Onychophora), and chordates (Deuterostomia, phylum Chordata)—rather than in just two lineages.

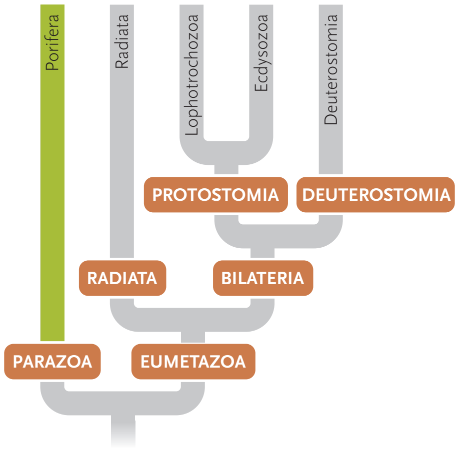
Despite these surprising findings about morphological evolution, most biologists now embrace the hypothesis provided by molecular sequence studies. In the future, new data will undoubtedly foster active discussions, heated disputes, and revisions of the phylogeny. Students may be understandably frustrated by the lack of consensus among experts and an ever-changing phylogeny for animals. But these disputes highlight the uniqueness of science as a way of knowing the natural world through the process of collecting evidence and rigorously challenging accepted hypotheses. The phylogenetic tree based on molecular sequence data is truly revolutionary, and the dust has yet to settle on the disagreements that these new analyses have provoked.

Study Break

1. Which major groupings of animals defined on the basis of morphological characters have been confirmed by molecular sequence studies?
2. What type of body cavity is ancestral within the Protostomes?

29.4 Animals without Tissues: Parazoa

The Parazoa is a lineage that includes just one group of animals, the sponges.



Sponges Have Simple Body Plans and Lack Tissues

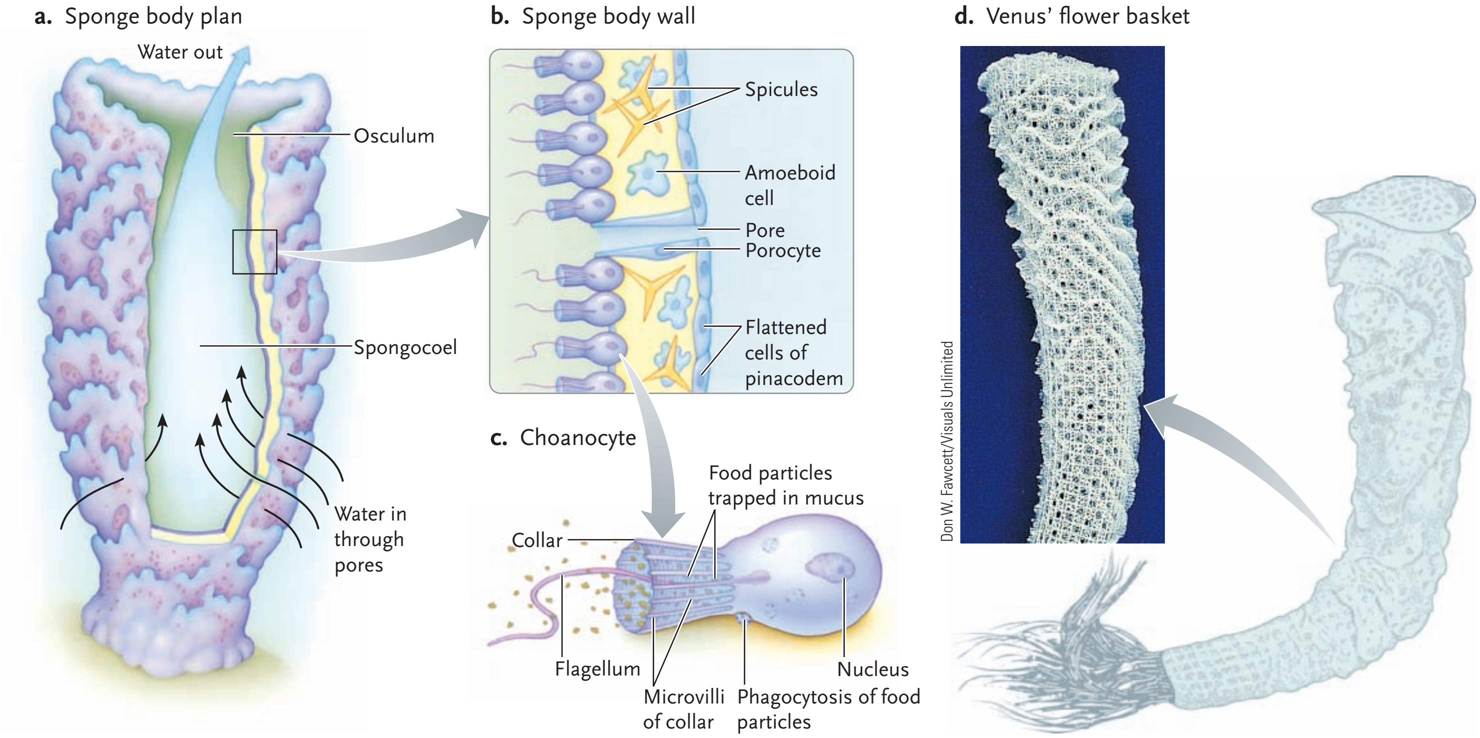
Sponges, phylum Porifera (meaning "pore bearers"), lack true tissues: during development, their cells do not form the layers typical of other phyla. Mature sponges are sessile, and their shapes are less fixed than those of other animals, because mobile cells allow them to change shape in response to local conditions **(Figure 29.7).** Sponges have been abundant since the Cambrian, especially in shallow coastal areas. Most of the 8000 living species are marine. Mature sponges range in size from 1 cm to 2 m.

Sponges have simple body plans **(Figure 29.8).** Flattened cells form an outer layer, the **pinacoderm.** The inner surface of saclike sponges is lined by collar cells, called **choanocytes,** each equipped with a beating flagellum and a surrounding "collar" of modified microvilli. (Choanocytes resemble the cells of choanoflagellates, the hypothesized ancestor of all animals.) Amoeboid cells wander through the gelatinous **mesohyl** between the two layers; they secrete a supporting skeleton of a fibrous protein and *spicules,* small needlelike structures of calcium carbonate or silica (see Figure 29.8d). The natural sponges that we use are the fibrous remains of the bath sponge *(Spongia),* which lacks mineralized parts.


Marty Snyderman/Planet Earth Pictures

Figure 29.7 **Asymmetry in sponges.** The shapes of sponges vary with their habitats. Those that occupy calm waters, such as this stinker vase sponge *(Ircinia campana),* may be lobed, tubular, cuplike, or vaselike.

A sponge's body is an elaborate system for filtering food particles from the surrounding water. Water flows through pores in the pinacoderm into a central chamber, the **spongocoel,** and then out of the sponge through one or more openings called **oscula** (singular, *osculum*). The beating flagellae of the choanocytes maintain a constant flow, and contractile pore cells *(porocytes)* adjust the flow rate. Even a small sponge may filter as much as 20 liters of water per day. The choanocytes capture suspended parti-



Don W. Fawcett/Visuals Unlimited

Figure 29.8

The body plan of sponges. Most sponges have **(a)** simple body plans and **(b)** relatively few cell types. **(c)** Beating flagella on the choanocytes create a flow of water through incurrent pores, into the spongocoel, and out through the osculum. **(d)** Venus' flower basket (*Euplectella* species), a marine sponge, has spicules of silica fused into a rigid framework.

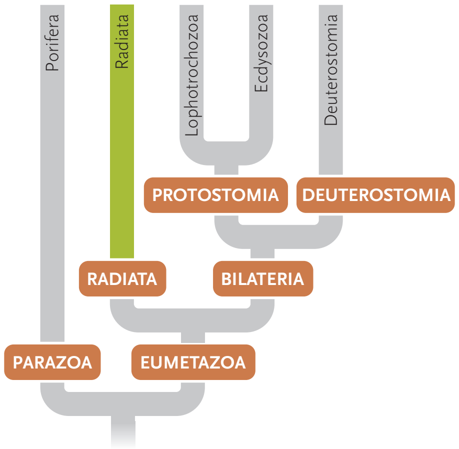
cles and microorganisms from the water and pass this food to mobile amoeboid cells, which carry nutrients to cells of the pinacoderm.

Most sponges are **hermaphroditic:** individuals produce both sperm and eggs. Sperm are released into the spongocoel and then out into the environment through oscula; eggs remain in the mesohyl, where sperm from other sponges, drawn in with water, fertilize them. Zygotes develop into flagellated larvae that are expelled to fend for themselves. Surviving larvae attach to substrates and undergo **metamorphosis** (a reorganization of form) into sessile adults. Some sponges also reproduce asexually; small fragments break off an adult and grow into new sponges. Many species also produce *gemmules,* clusters of cells with a resistant covering that allows them to survive unfavorable conditions; gemmules germinate into new sponges when conditions improve.

Study Break

1. What type of body symmetry do sponges exhibit?
2. How does a sponge gather food from its environment?

29.5 Eumetazoans with Radial Symmetry



Unlike sponges, eumetazoans have true tissues, which develop from distinct layers in the embryo. Working together, the cells of a tissue perform complex functions beyond the capacity of individual cells. For example, nerve tissue transmits information rapidly through an animal's body, and epithelial tissue forms barriers that surround the body and line body cavities. In this section, we describe eumetazoans with radial symmetry, which enables them to sense stimuli from all directions, an effective adaptation for life in open water.

Two phyla of soft-bodied organisms, Cnidaria and Ctenophora, have radial symmetry and tissues, but they lack organ systems and a coelom. Species in both phyla possess a **gastrovascular cavity** that serves both digestive and circulatory functions. It has a single opening, the mouth. Gas exchange and excretion occur by diffusion because no cell is far from a body surface.

The radiate phyla have a diploblastic body plan with only two tissue layers, the inner *gastrodermis* (an endoderm derivative) and the outer *epidermis* (an ectoderm derivative). Most species also possess a gelatinous *mesoglea* (*mesos* = middle; *glia* = glue) between the two layers. The mesoglea contains widely dispersed fibrous and amoeboid cells.

Cnidarians Use Nematocysts to Stun or Kill Prey

Nearly all of the 8900 species in the phylum Cnidaria (*knide* = stinging nettle, a plant with irritating surface hairs) live in the sea **(Figure 29.9).** Their body plan is organized around a saclike gastrovascular cavity; the mouth is ringed with tentacles, which push food into it. Cnidarians may be vase-shaped, upward-pointing **polyps** or bell-shaped, downward-pointing **medusae** (see Figure 29.9a). Most polyps attach to a substrate at the *aboral* (opposite the mouth) end; medusae are unattached and float.

Cnidarians are the simplest animals that exhibit a division of labor among specialized tissues (see Figure 29.9b, c). (Sponges have specialized cells, but no tissues.) The gastrodermis includes gland cells and phagocytic nutritive cells. Gland cells secrete enzymes for the extracellular digestion of food, which is then engulfed by nutritive cells and exposed to intracellular digestion. The epidermis includes nerve cells, sensory cells, contractile cells, and cells specialized for prey capture. A layer of acellular mesoglea separates the gastrodermis from the epidermis.

Cnidarians prey on crustaceans, fishes, and other animals. The epidermis includes unique cells, **cnidocytes**, each armed with a stinging **nematocyst (Figure 29.10).** The nematocyst is an encapsulated, coiled thread that is fired at prey or predators, sometimes releasing a toxin through its tip. Discharge of nematocysts may be triggered by touch, vibrations, or chemical stimuli. The toxin can paralyze small prey by disrupting nerve cell membranes. The painful stings of some jellyfishes and corals result from the discharge of nematocysts.

Cnidarians engage in directed movements by contracting specialized cells in the epidermis. In medusae, the mesogleal jelly serves as a deformable skeleton against which contractile cells act. Rapid contractions narrow the bell, forcing out jets of water that propel the animal. Polyps use their water-filled gastrovascular cavity as a hydrostatic skeleton. When some cells contract, fluid within the chamber is shunted about,

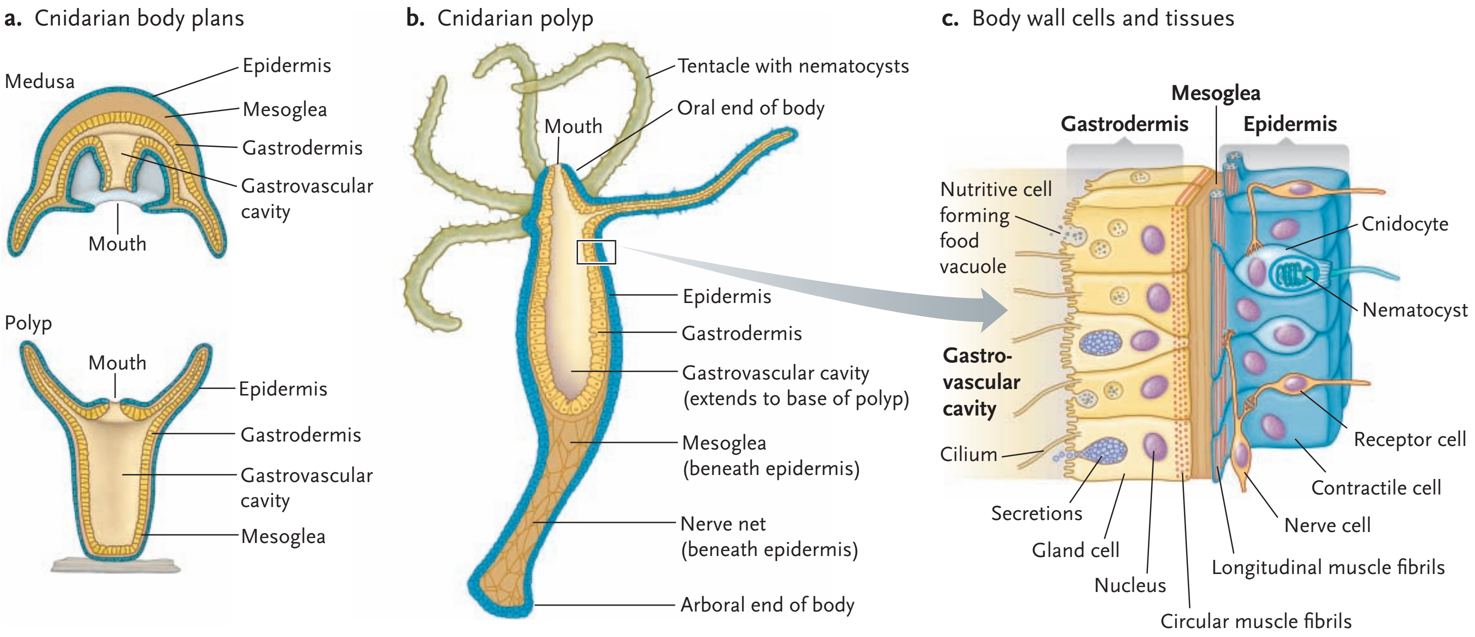
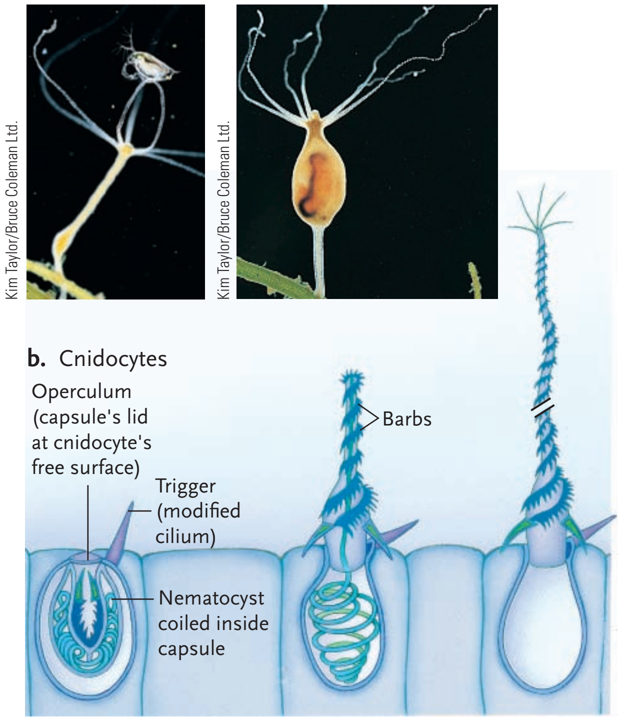


Figure 29.9
The cnidarian body plan. **(a)** Cnidarians exist as either polyps or medusae. **(b)** The body of both forms is organized around a gastrovascular cavity, which extends all the way to the aboral end of the animal. **(c)** The two tissue layers in the body wall, the gastrodermis and the epidermis, include a variety of cell types.



a. *Hydra* consuming a crustacean

Kim Taylor/Bruce Coleman Ltd.

Kim Taylor/Bruce Coleman Ltd.

b. Cnidocytes

Figure 29.10
Predation by cnidarians. **(a)** A polyp of a freshwater *Hydra* captures a small crustacean with its tentacles and swallows it whole. **(b)** Cnidocytes, special cells on the tentacles, encapsulate nematocysts, which are discharged at prey.

changing the body's shape and moving it in a particular direction.

The **nerve net,** which threads through both tissue layers, is a simple nervous system that coordinates responses to stimuli but has no central control organ or brain. Impulses initiated by sensory cells are transmitted in all directions from the site of stimulation.

Many cnidarians exist in only the polyp or the medusa form, but some have a life cycle that alternates between them **(Figure 29.11).** In the latter type, the polyp often produces new individuals asexually from buds that break free of the parent (see Figure 47.2). The medusa is often the sexual stage, producing sperm and eggs, which are released into the water. The four lineages of Cnidaria differ in the form that predominates in the life cycle.

Hydrozoa. Most of the 2700 species in the Hydrozoa have both polyp and medusa stages in their life cycles (see Figure 29.11). The polyps form sessile colonies that develop asexually from one individual. A colony can include thousands of polyps, which may be specialized for feeding, defense, or reproduction. They share food through their connected gastrovascular cavities.

Unlike most hydrozoans, freshwater species of *Hydra* (see Figure 29.10a) live as solitary polyps that attach temporarily to rocks, twigs, and leaves. Under favorable conditions hydras reproduce by budding. Under adverse conditions they produce eggs and sperm; the zygotes, which are encapsulated in a protective coating, develop and grow when conditions improve.

Scyphozoa. The medusa stage predominates in the 200 species of the Scyphozoa **(Figure 29.12a),** or jellyfishes. They range from 2 cm to more than 2 m in diameter. Nerve cells near the margin of the bell control their tentacles and coordinate the rhythmic activity of contractile cells, which move the animal. Specialized sensory cells are clustered at the edge of the bell: **statocysts** sense gravity and **ocelli** are sensitive to light. Scyphozoan medusae are either male or female; they release gametes into the water where fertilization takes place.

Cubozoa. The 20 known species of box jellyfish, the Cubozoa **(Figure 29.12b),** exist primarily as cube-shaped medusas only a few centimeters tall; the largest species grows to 25 cm in height. Nematocyst-rich tentacles grow in clusters from the four corners of the boxlike medusa, and groups of light receptors and image-forming eyes occur on the four sides of the bell. Unlike the true jellyfish, cubozoans are active swimmers. They feed on small fishes and invertebrates, immobilizing their prey with one of the deadliest toxins produced by animals. Cubozoans live in tropical and subtropical coastal waters, where they sometimes pose a serious threat to swimmers.

Anthozoa. The Anthozoa includes 6000 species of corals and sea anemones **(Figure 29.13).** Anthozoans exist only as polyps, and often reproduce by budding or fission; most also reproduce sexually. Corals are always sessile and usually colonial. Most species build calcium carbonate skeletons, which sometimes accumulate into gigantic underwater reefs. The energy needs of many corals are partly fulfilled by the photosynthetic activity of symbiotic protists that live within the corals' cells. For this reason, corals are restricted to shallow water where sunlight can penetrate. Sea anemones, by contrast, are soft-bodied, solitary polyps, ranging from 1 cm to 10 cm in diameter. They occupy shallow coastal waters. Most species are essentially sessile, but some move by crawling slowly or by using the gastrovascular cavity as a hydrostatic skeleton.

Ctenophores Use Tentacles to Feed on Microscopic Plankton

Like the cnidarians, the 100 species of comb jellies in the phylum Ctenophora (*kteis* = comb; *-phoros* = bearing) have radial symmetry, mesoglea, and feeding tentacles. However, they differ from cnidarians in signifi-

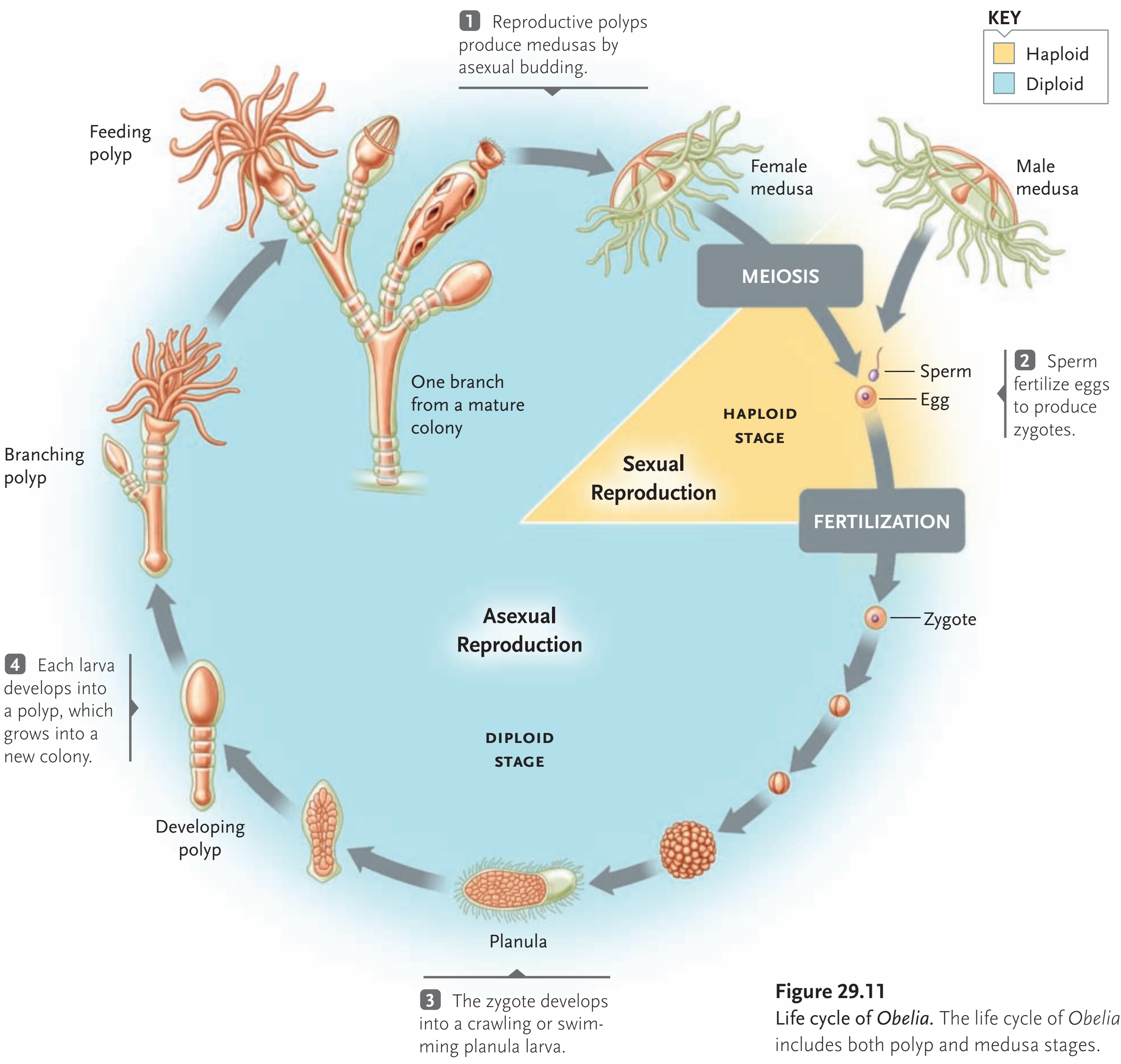


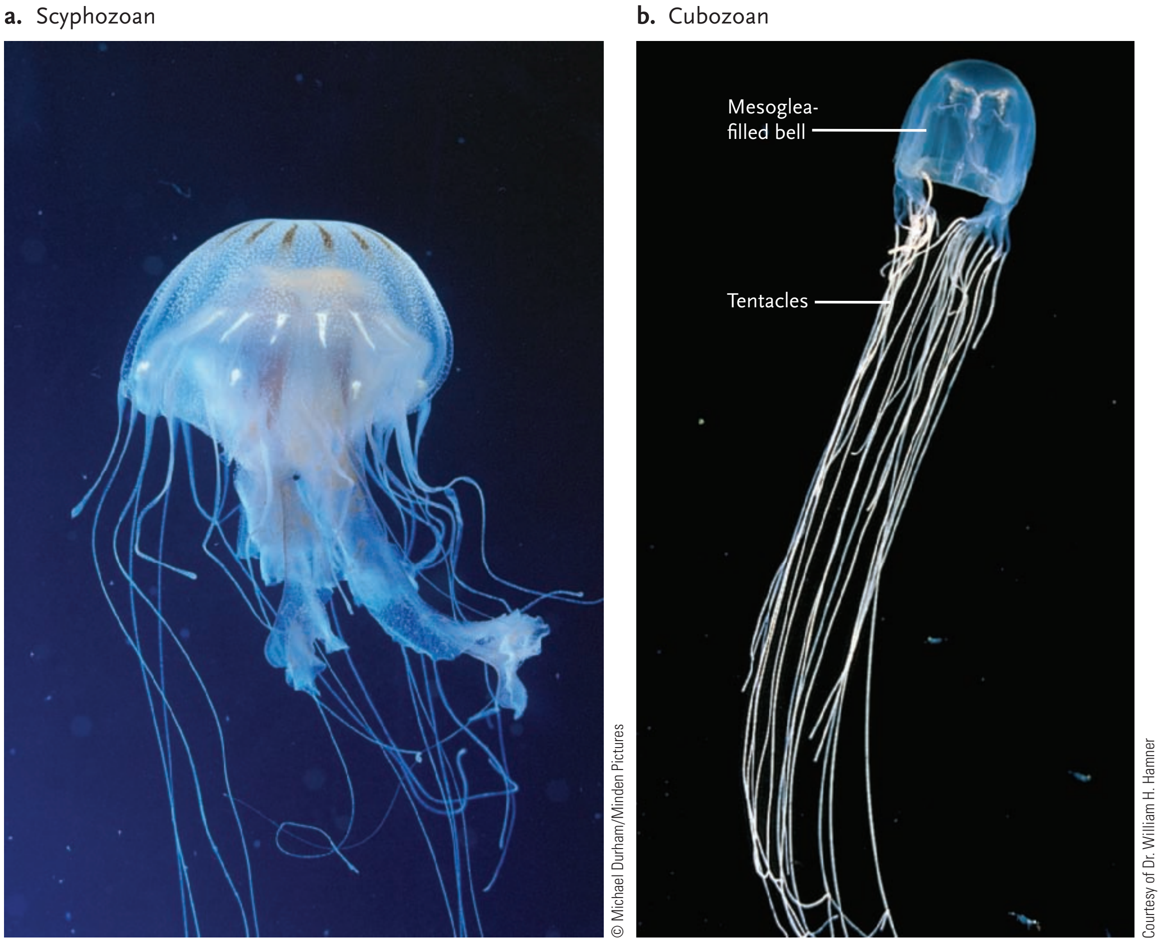
Figure 29.11
Life cycle of *Obelia*. The life cycle of *Obelia*, a colonial hydrozoan, includes both polyp and medusa stages.

cant ways: they lack nematocysts; they expel some waste through anal pores opposite the mouth; and certain tissues appear to be of mesodermal origin. These transparent, and often luminescent, animals range in size from a few millimeters to a few meters **(Figure 29.14).** They live primarily in coastal regions of the oceans.

Ctenophores move by beating cilia arranged on eight longitudinal plates that resemble combs. They are the largest animals to use cilia for locomotion, but they are feeble swimmers. Nerve cells connected to the cilia coordinate the animals' movements, and a gravity-sensing statocyst helps them maintain an upright position. They capture microscopic plankton with their two tentacles, which have specialized cells that discharge sticky filaments; the food-laden tentacles are drawn across the mouth. Ctenophores are hermaphroditic, producing gametes in cells that line the gastrovascular cavity. Eggs and sperm are expelled through the mouth or from special pores, and fertilization occurs in the open water.

STUDY BREAK

1. How do cnidarians capture, consume, and digest their prey?
2. Which group of cnidarians has only a polyp stage in its life cycle?
3. What do ctenophores eat, and how do they collect their food?

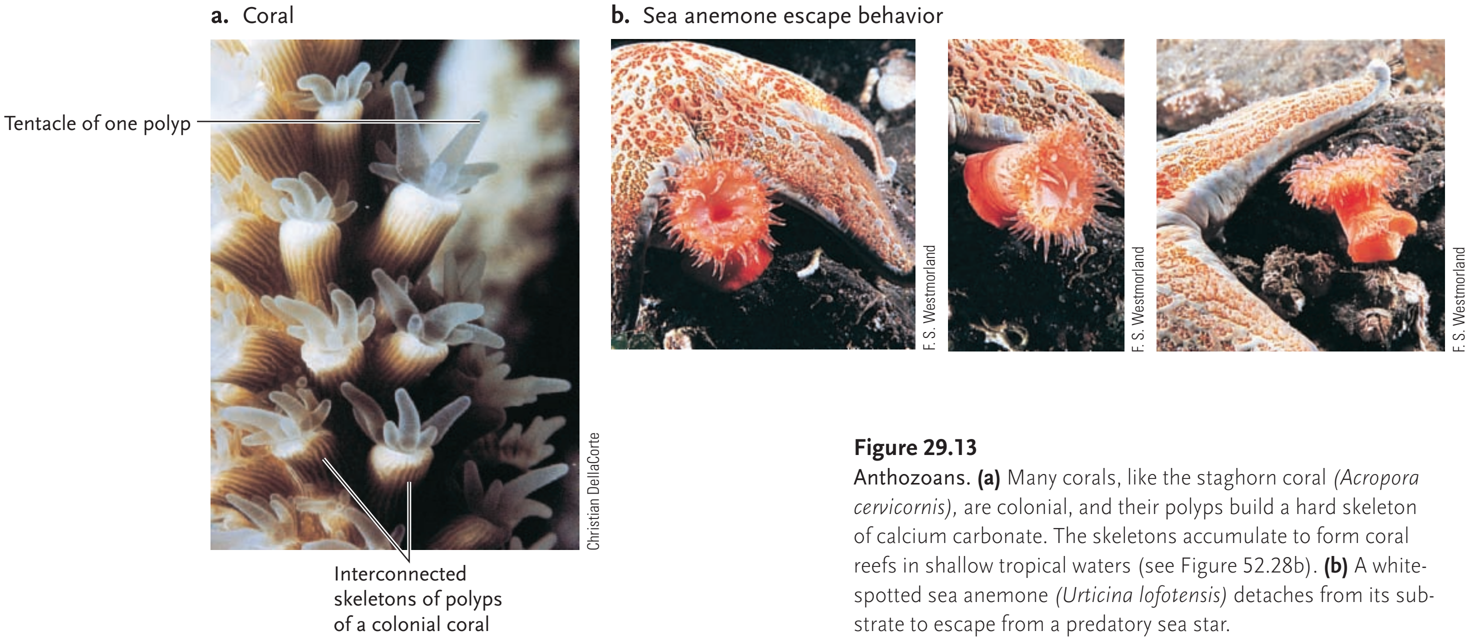

a. Scyphozoan

b. Cubozoan

© Michael Durham/Minden Pictures

Courtesy of Dr. William H. Hamner

Figure 29.12
Scyphozoans and cubozoans. (a) Most scyphozoans, like the sea nettle *(Chrysaora quinquecirrha)*, live as floating medusae. Their tentacles trap prey, and the long oral arms transfer it to the mouth on the underside of the bell. **(b)** Cubozoans, like the sea wasp *(Chironex fleckeri)*, are strong swimmers that actively pursue small fishes and invertebrates.


a. Coral

b. Sea anemone escape behavior

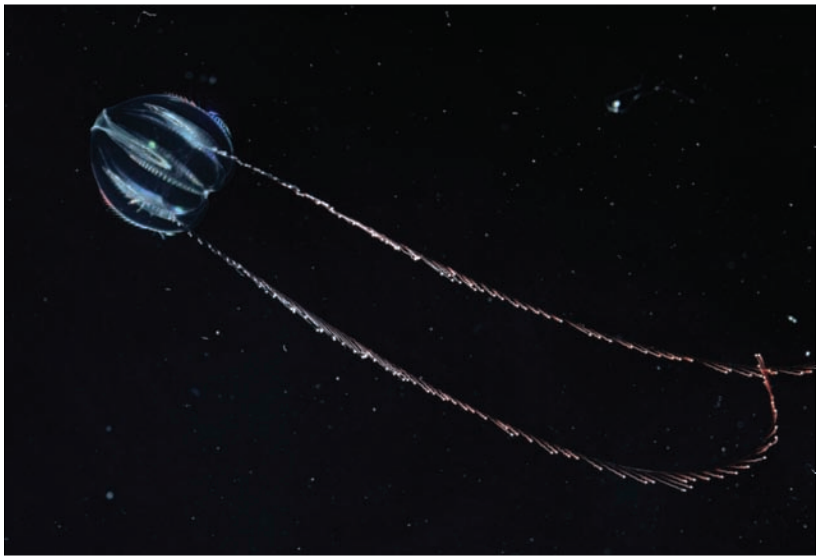
Christian DellaCorte

F. S. Westmorland

F. S. Westmorland

F. S. Westmorland

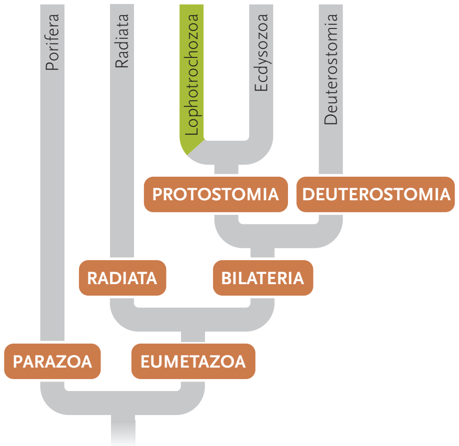
Figure 29.13
Anthozoans. (a) Many corals, like the staghorn coral *(Acropora cervicornis)*, are colonial, and their polyps build a hard skeleton of calcium carbonate. The skeletons accumulate to form coral reefs in shallow tropical waters (see Figure 52.28b). **(b)** A white-spotted sea anemone *(Urticina lofotensis)* detaches from its substrate to escape from a predatory sea star.



© Norbert Wu/Minden Pictures

Figure 29.14
Ctenophores. The comb jelly *Mertensia ovum* collects microscopic prey on its two long sticky tentacles and then wipes the food-laden tentacles across its mouth.

29.6 Lophotrochozoan Protostomes

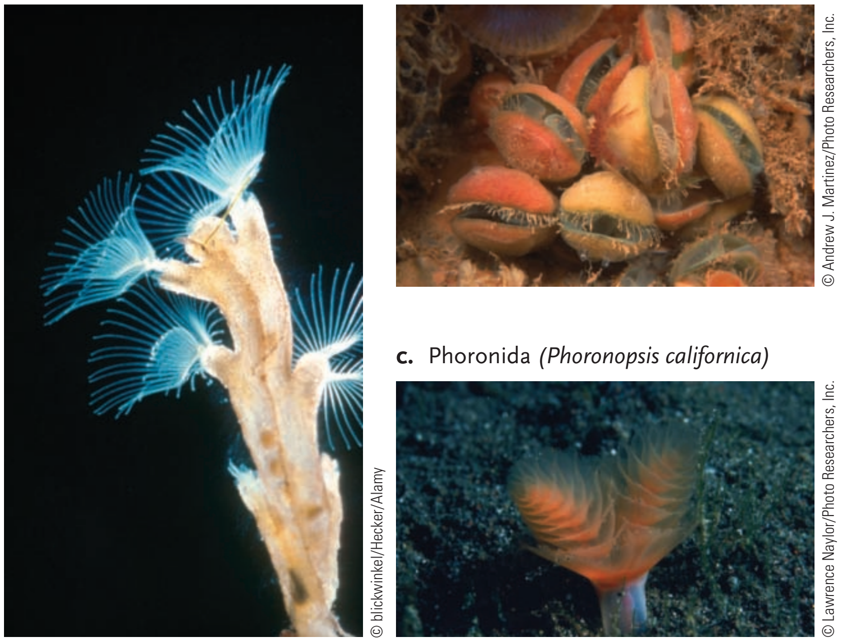


The remaining organisms described in this chapter fall within the group Bilateria: they have bilateral symmetry and a greater variety of tissues than do the Radiata. Bilaterians also have organ systems, structures that include two or more tissue types organized to perform specific functions; most of them also possess a coelom or pseudocoelom. With bilateral symmetry and sensory organs concentrated at the anterior end of the body, most bilaterians engage in highly directed, often rapid movements in pursuit of food or mates or to escape danger. And their complex organ systems accomplish tasks more efficiently than simple tissues. For example, animals that have a tubular digestive system surrounded by a space (the coelom or pseudocoelom) use muscular contractions of the digestive system to move ingested food past specialized epithelia that break it down and absorb the breakdown products.

Molecular analyses group eight of the phyla that we consider into the Lophotrochozoa, one of the two main protostome lineages (see Figure 29.6).

The Lophophorate Phyla Share a Distinctive Feeding Structure

Three small groups of aquatic, coelomate animals—the phyla Ectoprocta, Brachiopoda, and Phoronida—possess a **lophophore,** a circular or U-shaped fold with one or two rows of hollow, ciliated tentacles surrounding the mouth **(Figure 29.15).** Molecular sequence data as well as the lophophore suggest that these phyla share a common ancestry.



a. Ectoprocta *(Plumatella repens)*

b. Brachiopoda *(Terebraulina septentrionalis)*

c. Phoronida *(Phoronopsis californica)*

© blickwinkel/Hecker/Alamy

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© Lawrence Naylor/Photo Researchers, Inc.

Figure 29.15
Lophophorate animals. Although the lophophorate animals differ markedly in appearance, they all use a lophophore—the feathery structures in the photos—to acquire food.

The lophophore, which looks like a crown of tentacles at the anterior end of the animal, serves as a site for gas exchange and waste elimination as well as for food capture. Most lophophorates are sessile suspension-feeders as adults: movement of cilia on the tentacles brings food-laden water toward the lophophore, the tentacles capture small organisms and debris, and the cilia transport them to the mouth. The lophophorates have a complete digestive system, which is U-shaped in most species, with the anus lying outside the ring of tentacles.

Phylum Ectoprocta. The Ectoprocta (sometimes called Bryozoa) are tiny colonial animals that mainly occupy marine habitats (see Figure 29.15a). They secrete a hard covering over their soft bodies and feed by extending the lophophore through a hole. Each colony, which may include more than a million individuals, is produced asexually by a single animal. Ectoproct colonies are permanently attached to solid substrates, where they form encrusting mats, bushy upright growths, or jellylike blobs. Nearly 4000 living species are known.

Phylum Brachiopoda. The Brachiopoda, or lampshells, have two calcified shells that develop on the animal's dorsal and ventral sides (see Figure 29.15b). Most species attach to substrates with a stalk that protrudes through one of the shells. The lophophore is held within the two shells, and the animal feeds by opening its shell and drawing water over its tentacles. Although only 250 species of brachiopods live today, more than 30,000 extinct species are known as fossils, mostly from Paleozoic seas.

Phylum Phoronida. The 18 or so species of phoronid worms vary in length from a few millimeters to 25 cm (see Figure 29.15c). They usually build tubes in soft ocean sediments or on hard substrates, and feed by protruding the lophophore from the top of the tube. The animal can withdraw into the tube when disturbed. Phoronida reproduce both sexually and by budding.

Flatworms Have Digestive, Excretory, Nervous, and Reproductive Systems, but Lack a Coelom

The 13,000 flatworm species in the phylum Platyhelminthes (*platys* = flat; *helmis* = worm) live in aquatic and moist terrestrial habitats. Like cnidarians, flatworms can swim or float in water, but they are also able to crawl over surfaces. They range from less than 1 mm to more than 20 m in length, but most are just a few millimeters thick. Free-living species eat live prey or decomposing carcasses, whereas parasitic species consume the tissues of living hosts.

Like the radiate phyla, flatworms are acoelomate, but they have a complex structural organization that reflects their triploblastic construction **(Figure 29.16).** Endoderm lines the digestive cavity with cells specialized for the chemical breakdown and absorption of ingested food. Mesoderm, the middle tissue layer, produces muscles and reproductive organs. Ectoderm produces a ciliated epidermis, the nervous system, and the *flame cell system,* a simple excretory system; flame cells regulate the concentrations of salts and water within body fluids, allowing free-living flatworms to live in freshwater habitats. Flatworms do not have circulatory or respiratory systems, but, because all cells of their dorsoventrally (top-to-bottom) flattened bodies are near an interior or exterior surface, diffusion supplies them with nutrients and oxygen.

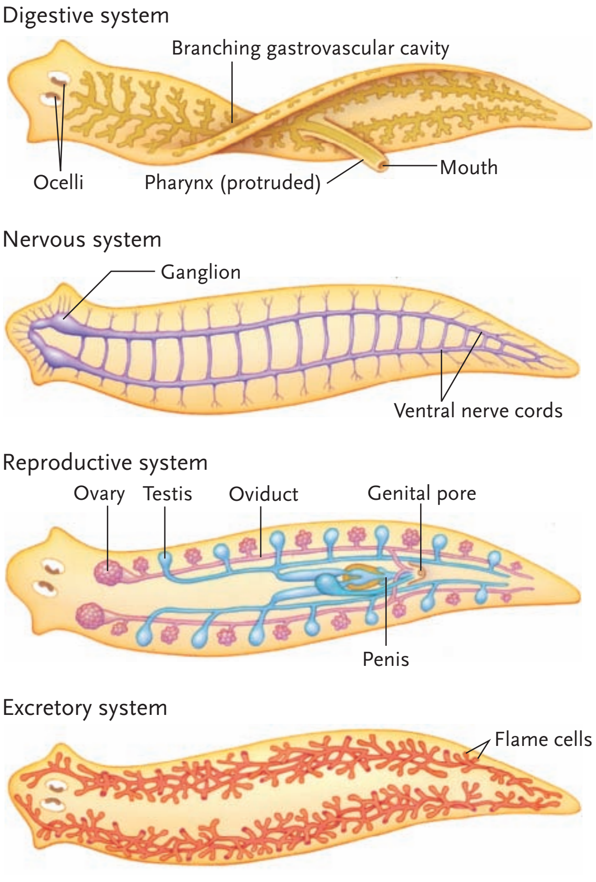

Figure 29.16
Flatworms. The phylum Platyhelminthes, exemplified by a freshwater planarian, have well-developed digestive, excretory, nervous, and reproductive systems. Because flatworms are acoelomate, their organ systems are embedded in a solid mass of tissue between the gut and the epidermis.

The flatworm nervous system includes two or more longitudinal ventral nerve cords interconnected by numerous smaller nerve fibers, like rungs on a ladder. An anterior **ganglion,** a concentration of nervous system tissue that serves as a primitive brain, integrates their behavior. Most free-living species have *ocelli,* or eye spots, that distinguish light from dark and tiny chemoreceptor organs that sense chemical cues.

© Cory Gray

Figure 29.17

Turbellaria. A few turbellarians, such as *Pseudoceros dimidiatus*, are colorful marine worms.

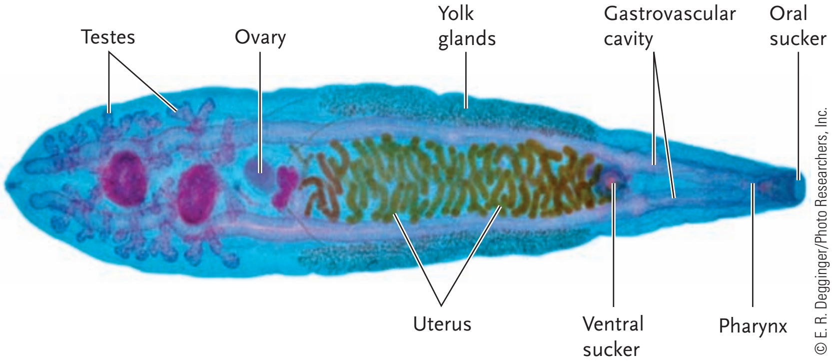

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Figure 29.18

Trematoda. The hermaphroditic Chinese liver fluke *(Opisthorchis sinensis)* uses a well-developed reproductive system to produce thousands of eggs.

The phylum Platyhelminthes includes four lineages, defined largely by their anatomical adaptations to free-living or parasitic habits.

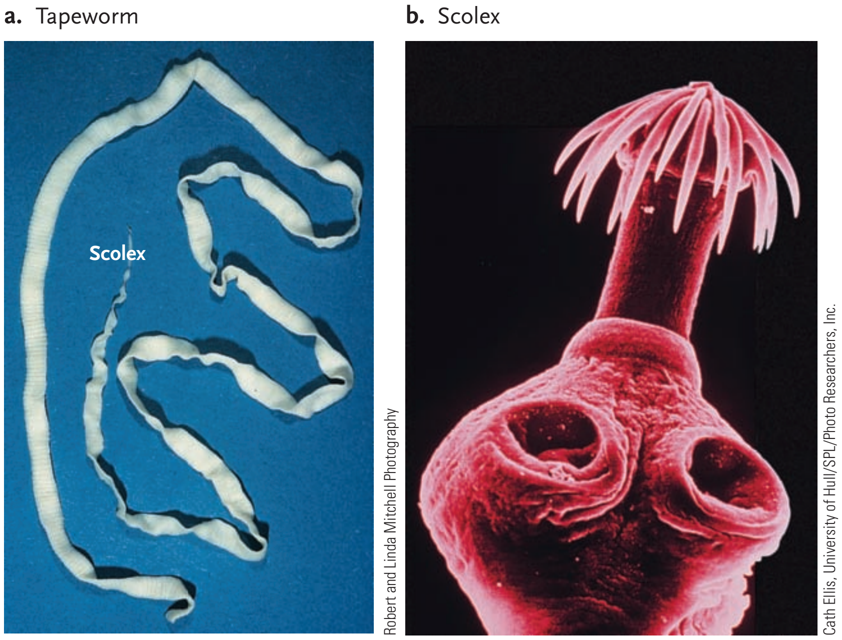
Turbellaria. Most free-living flatworms (Turbellaria) live in the sea **(Figure 29.17),** but the familiar planarians and a few others live in fresh water or on land. Turbellarians swim by undulating the body wall musculature, or they crawl across surfaces by using muscles and cilia to glide on mucous trails produced by the ventral epidermis.

The gastrovascular cavity in free-living flatworms is similar to that in cnidarians. Food is ingested and wastes eliminated through a single opening, the mouth, located on the ventral surface. Most turbellarians also acquire food with a muscular **pharynx** that connects the mouth to the digestive cavity (see Figure 29.16). Chemicals secreted into the saclike cavity digest the food into particles; then cells throughout the gastrovascular surface engulf the particles and subject them to intracellular digestion. In some species, the digestive cavity is highly branched, increasing the surface area for digestion and absorption.

Nearly all turbellarians are hermaphroditic, with complex reproductive systems (see Figure 29.16). When they mate, each partner functions simultaneously as a male and a female. Many free-living species also reproduce asexually by simply separating the anterior half of the animal from the posterior half. Both halves subsequently regenerate the missing parts.

Trematoda and Monogenoidea. Flukes (Trematoda and Monogenoidea) are parasites that obtain nutrients from host tissues **(Figure 29.18).** Most adult trematodes are **endoparasites,** living in the gut, liver, lungs, bladder, or blood vessels of vertebrates. Monogenes are **ectoparasites,** attaching to the gills or skin of aquatic vertebrates. Flukes are structurally specialized for a parasitic existence. They use suckers or hooks to attach to hosts, and a tough outer covering protects them from chemical attack. They produce large numbers of eggs that can readily infect new hosts. Monogene flukes usually have simple life cycles with a single host species. Trematodes, by contrast, have complex life cycles and multiple hosts. Humans suffer potentially fatal infections by many flukes, as discussed in *Focus on Applied Research*.

Cestoda. Tapeworms (Cestoda) develop, grow, and reproduce within the intestines of vertebrates **(Figure 29.19).** Through evolution, they have lost their mouths


a. Tapeworm

b. Scolex

Robert and Linda Mitchell Photography

Cath Ellis, University of Hull/SPL/Photo Researchers, Inc.

Figure 29.19

Cestoda. **(a)** Tapeworms have long bodies comprised of a series of proglottids that each produce thousands of fertilized eggs. **(b)** The anterior end is a scolex with hooks and suckers that attach to the host's intestinal wall.

FOCUS ON RESEARCH

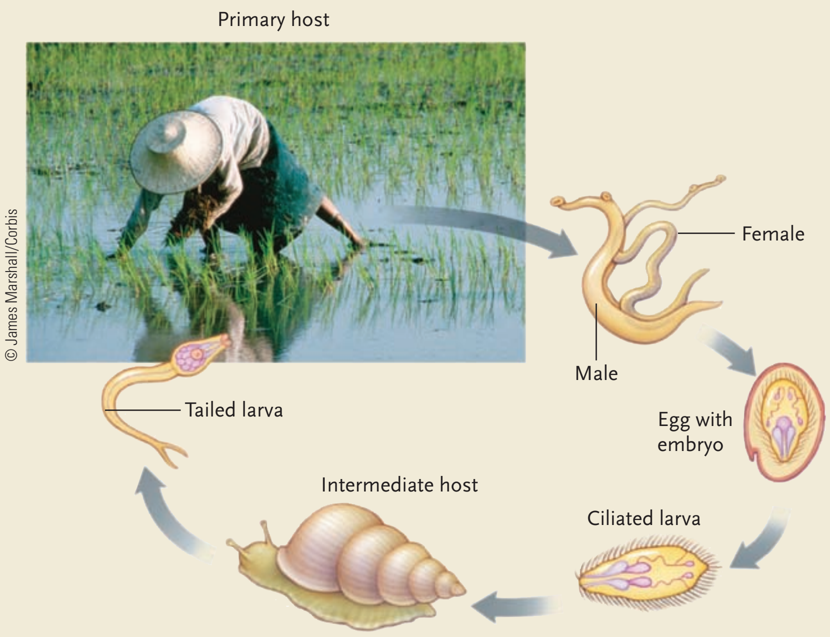
Applied Research: A Rogue's Gallery of Parasitic Worms

Many parasitic flatworms (phylum Platyhelminthes) and roundworms (phylum Nematoda) call the human body home, frequently causing disfiguring or life-threatening infections. The effort to control or eliminate these infections often begins when parasitologists or public health researchers study the worms' life cycles and ecology. This approach is successful because the worms often have more than one host: humans may be the *primary host,* harboring the sexually mature stage of the parasites' life cycles, but other animals serve as *intermediate hosts* to the larval stages. If researchers can learn the details of a parasite's life cycle, they can identify ways to cut it short before the parasite infects a human host.

More than 200 million people in tropical and subtropical regions suffer from *schistosomiasis,* a disease caused by three species of flatworms called blood flukes (Trematoda). Japanese blood flukes *(Schistosoma japonicum)* mature and mate in blood vessels of the human intestine **(Figure a).** Sharp spines on their eggs rupture the blood vessels, releasing the eggs into the lumen of the gut, from which they are passed with feces. When the infected human waste enters standing fresh water, the eggs hatch into ciliated larvae, which burrow into certain aquatic snails. The larvae feed on the snail's tissues and reproduce asexually. Their tailed offspring leave the snail and, when they contact human skin, bore inward to a blood vessel. They eventually reach the intestine, where they complete their complex life cycle and produce fertilized eggs. Infected humans mount an immune response against flukes, but it is always a losing battle. Severe infections cause coughs, rashes, pain, and eventually diarrhea, anemia, and permanent damage to the intestines, liver, spleen, bladder, and kidneys. Death often results. Drug therapy can reduce the symptoms, but schistosomiasis is most common in less-developed countries with limited access to medical care. Research has demonstrated that the disease is best controlled by proper sanitation and the elimination of snails that serve as intermediate hosts.

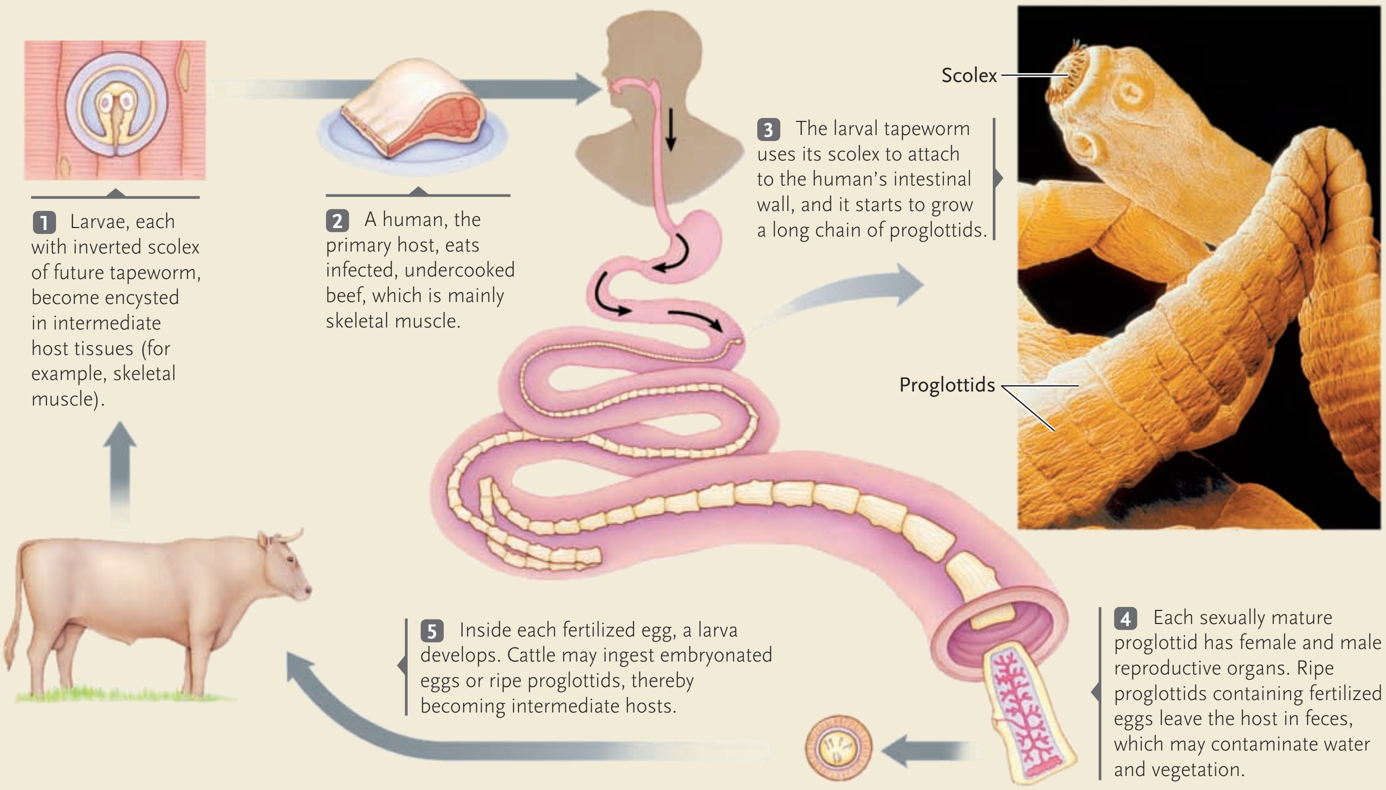
Tapeworms (Cestoda), another group of flatworms, rely primarily on vertebrate hosts. Fishes, hogs, or cattle become intermediate hosts by inadvertently eating tapeworm eggs **(Figure b).** When the host's digestive enzymes dissolve the protective covering on the eggs, the newly freed larvae bore through the intestinal wall and travel through the bloodstream to muscles or other tissues, where they *encyst* (produce a protective covering and enter a resting stage). Humans and other carnivores ingest living cysts when they eat the undercooked flesh of these animals. The scolex of the tapeworm larva then attaches to the primary host's intestinal wall, and the worm begins to grow. When mature, its proglottids produce huge numbers of eggs, which are released with feces to begin the next generation. Tapeworm infection can result in malnutrition of the host, because tapeworms consume much of the nutrients that the host ingests. They can also grow large enough to cause intestinal blockage. A full understanding of the tapeworm life cycle suggests that careful inspection and adequate cooking of meat can prevent infection.

The roundworm *Trichinella spiralis* causes the painful and sometimes fatal symptoms of *trichinosis.* Adult trichinas breed in the small intestine of their hosts, including hogs and some game animals. Female worms release juveniles, which burrow into blood vessels and travel to various organs, where they become encysted **(Figure c).** Humans become infected when they consume insufficiently cooked pork or other meat that contains encysted larvae. Once in the human digestive tract, the encysted worms complete their development, mate, and produce larvae. Most of the



© James Marshall/Corbis

Figure a
Life cycle of the Japanese blood fluke *(Schistosoma japonicum).*



1 Larvae, each with inverted scolex of future tapeworm, become encysted in intermediate host tissues (for example, skeletal muscle).

2 A human, the primary host, eats infected, undercooked beef, which is mainly skeletal muscle.

3 The larval tapeworm uses its scolex to attach to the human's intestinal wall, and it starts to grow a long chain of proglottids.

4 Each sexually mature proglottid has female and male reproductive organs. Ripe proglottids containing fertilized eggs leave the host in feces, which may contaminate water and vegetation.

5 Inside each fertilized egg, a larva develops. Cattle may ingest embryonated eggs or ripe proglottids, thereby becoming intermediate hosts.

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Figure b
Life cycle of the beef tapeworm.

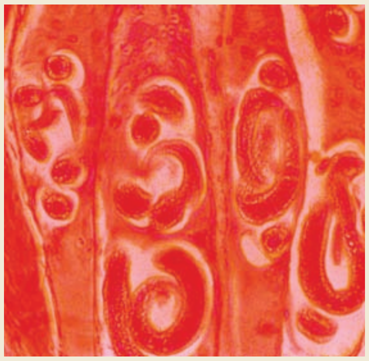
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Figure c
Trichinella spiralis juveniles in muscle tissue.

awful symptoms of trichinosis, including severe pain, high fever, and debilitating anemia, are produced by the migration of millions of larvae throughout the primary host's tissues. Once begun, the infection is difficult or impossible to control, but, as with tapeworms, thorough cooking of meat can prevent infection.

Filarial worms (*Wuchereria* and *Brugia*) cause another debilitating nematode infection. These large roundworms (up to 10 cm long) live in the lymphatic system, where they obstruct the normal flow of lymphatic fluid to the bloodstream. Female worms release first-stage larvae, which are acquired by mosquitoes, the intermediate host, when they feed on human blood. The larvae develop into second-stage larvae in mosquitoes, and when a mosquito bites another human, it may transmit those larvae to a new host. If victims experience severe filarial worm infection, their lymphatic vessels can be so obstructed that surrounding tissues swell grotesquely, a condition know as *elephantiasis* **(Figure d).** Public health programs that reduce or eliminate mosquito populations lower the incidence of this disease.


Dianora Niccolin

Figure d
Elephantiasis caused by *Wuchereria bancrofti.*

and digestive systems and absorb nutrients through their body wall. Tapeworms have a specialized structure, the *scolex,* with hooks and suckers that attach to the host's intestine; like the flukes, they also have a protective covering resistant to digestive enzymes.

Most of a tapeworm's body, which may be up to 20 m long, consists of a series of identical structures, *proglottids,* that contain little more than male and female reproductive systems. New proglottids are generated near the scolex; older proglottids, each carrying as many as 80,000 fertilized eggs, break off from the tapeworm's posterior end and leave the host's body in feces. As described in *Focus on Applied Research,* tapeworms are important parasites on humans, pets, and livestock.

Rotifers Are Tiny Pseudocoelomates with a Jawlike Feeding Apparatus

Most of the 1800 species in the phylum Rotifera (*rota* = wheel; *ferre* = to carry) live in fresh water **(Figure 29.20).** All are microscopic—about the size of a ciliate protist—but they have well-developed digestive, reproductive, excretory, and nervous systems as well as a pseudocoelom. In some habitats, rotifers make up a large part of the zooplankton, tiny animals that float in open water.

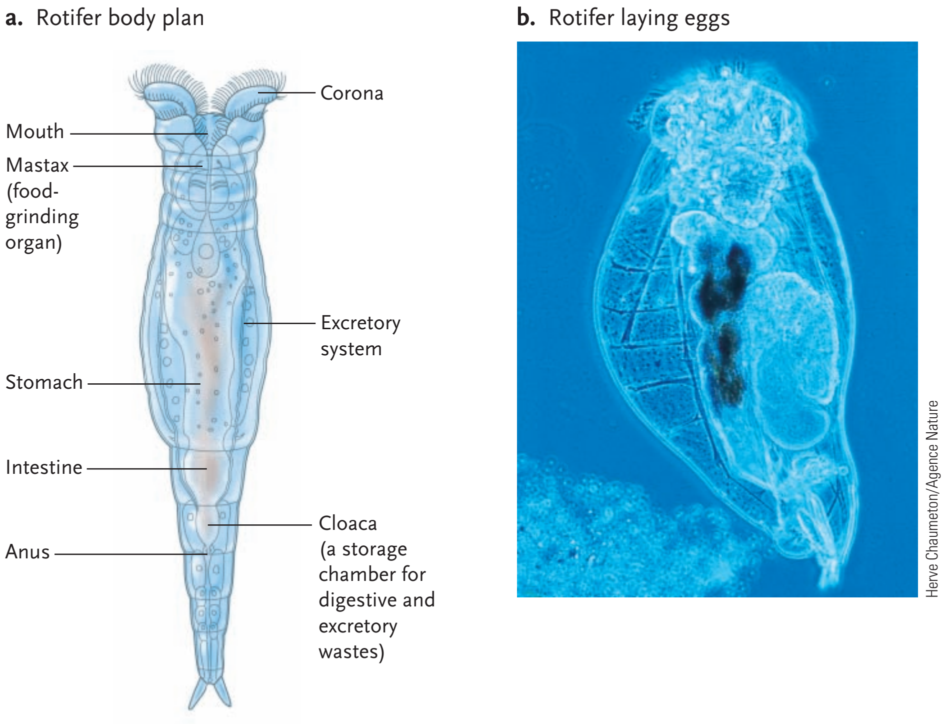
Rotifers use coordinated movements of cilia, arranged in a wheel-like *corona* around the head, to propel themselves in the environment. Cilia also bring food-laden water to their mouths. Ingested microorganisms are conveyed to the *mastax,* a toothed grinding organ, and then passed to the stomach and intestine. Rotifers have a **complete digestive tract:** food enters through the mouth, and undigested waste is voided through the anus.

The life history patterns of some rotifers are adapted to the ever-changing environments in small bodies of water. During most months, rotifer populations include only females that reproduce by **parthenogenesis,** a form of asexual reproduction in which unfertilized eggs develop into diploid females (see Section 47.1). When environmental conditions deteriorate, females produce eggs that develop into haploid males. The males fertilize haploid eggs to produce diploid female zygotes. The fertilized eggs have durable shells and food reserves to survive drying or freezing.

Ribbon Worms Use a Proboscis to Capture Food

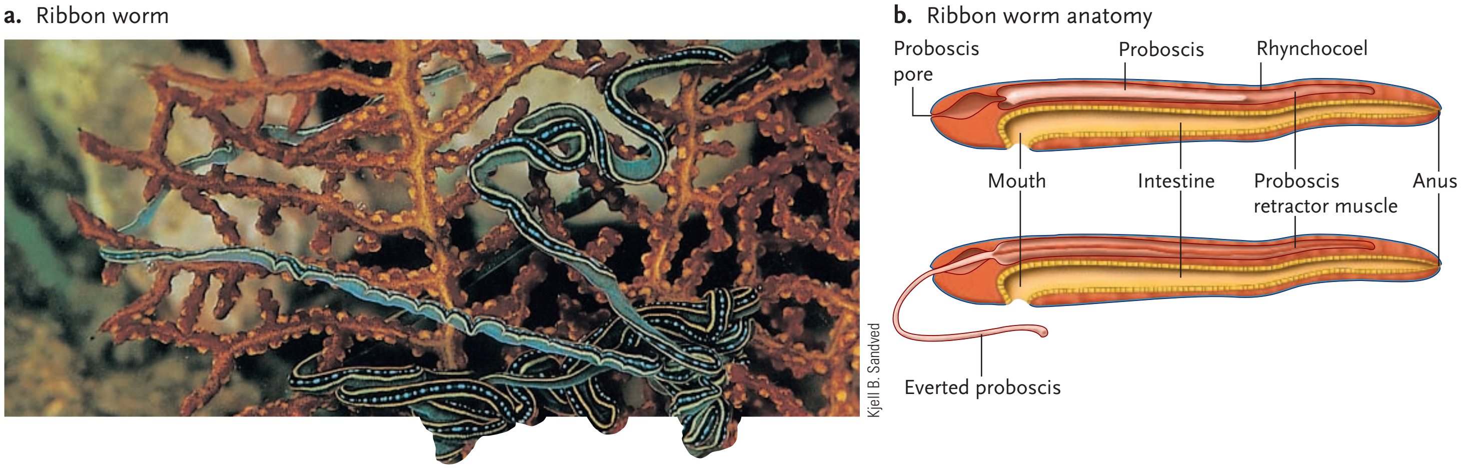
The 650 species of ribbon worms or proboscis worms (phylum Nemertea) vary from less than 1 cm to 30 m in length **(Figure 29.21).** Most species are marine, but a few occupy moist terrestrial habitats. Although the often brightly colored ribbon worms superficially resemble free-living flatworms, their body plans are more complex. First, they possess both a mouth and an anus; thus, they have a complete digestive tract. Second, nemerteans have a circulatory system in which fluid flows through **circulatory vessels** that carry nutrients and oxygen to tissues and remove wastes (see Section 42.1). Finally, they have a muscular, mucus-covered proboscis, a tube that can be everted (turned inside out) through the mouth or a separate pore to capture prey. The proboscis is housed within a chamber, the *rhynchocoel,* which is unique to this phylum.

Figure 29.20
Phylum Rotifera. **(a)** Despite their small size, rotifers such as *Philodina roseola* have complex body plans and organ systems. **(b)** This rotifer, another *Philodina* species, is laying eggs.


a. Rotifer body plan

b. Rotifer laying eggs

Herve Chaumeton/Agence Nature



a. Ribbon worm

b. Ribbon worm anatomy

Kjell B. Sandved

Figure 29.21
Phylum Nemertea. **(a)** The flattened, elongated bodies of ribbon worms, such as this species in the genus *Lineus*, are often brightly colored. **(b)** Ribbon worms have a complete digestive system and a specialized cavity, the rhynchocoel, that houses a protrusible proboscis.

Mollusks Have a Muscular Foot and a Mantle That Secretes a Shell or Aids in Locomotion

Most of the 100,000 species in the phylum Mollusca (*mollis* = soft)—including clams, snails, octopuses, and their relatives—are marine. However, many clams and snails occupy freshwater habitats, and some snails live on land. Mollusks vary in length from clams less than 1 mm to the giant squids, which can exceed 18 m.

In mollusks, the body is divided into three regions: the visceral mass, the head–foot, and the mantle **(Figure 29.22).** The **visceral mass** contains the digestive, excretory, reproductive systems, and heart. The muscular **head–foot** often provides the major means of locomotion. In the more active groups, the head region is well

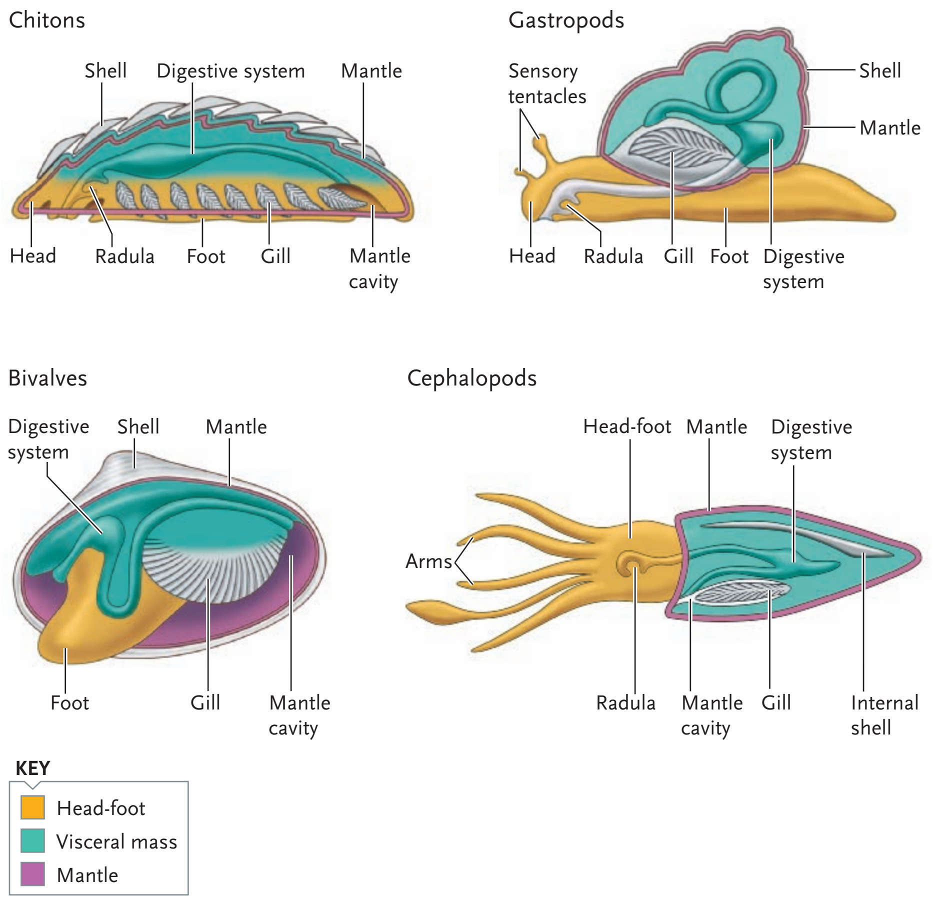


Figure 29.22
Molluskan body plans. The bilaterally symmetrical body plans of mollusks include a muscular head–foot, a visceral mass, and a mantle.

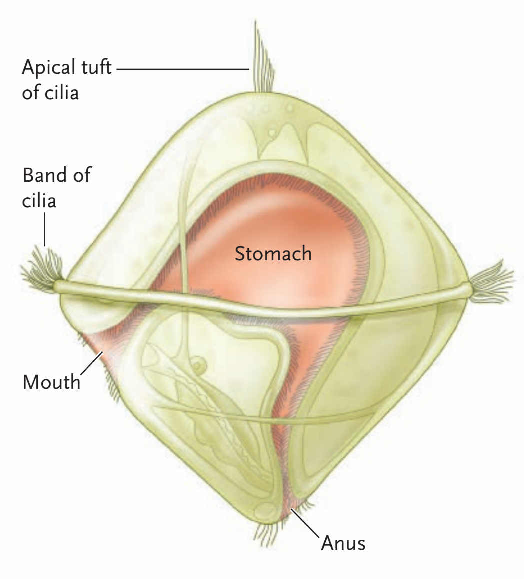


Figure 29.23
Trochophore larva. At the conclusion of their embryological development, both mollusks and annelids typically pass through a trochophore stage. The top-shaped trochophore larva has a band of cilia just anterior to its mouth.

defined and carries sensory organs and a brain. The mouth often includes a toothed **radula,** which scrapes food into small particles or drills through the shells of prey. Many mollusks are covered by a protective shell of calcium carbonate secreted by the **mantle,** one or two folds of the body wall that often enclose the visceral mass. The mantle also defines a space, the *mantle cavity,* that houses the *gills,* delicate respiratory structures with enormous surface area. In most mollusks, cilia on the mantle and gills generate a steady flow of water into the mantle cavity.

The large size of mollusks—as well as their possession of a true coelom—requires a circulatory system to maintain cells that are far from the body surface. Most mollusks have an **open circulatory system** in which **hemolymph,** a bloodlike fluid, leaves the circulatory vessels and bathes tissues directly (see Figure 42.3a). Hemolymph pools in spaces called *sinuses,* and then drains into vessels that carry it back to the heart.

The sexes are usually separate, although many snails are hermaphroditic. Fertilization may be internal or external. The zygotes of marine species often develop into free-swimming, ciliated **trochophore** larvae **(Figure 29.23),** typical of both this phylum and the phylum Annelida, which we describe next. In some mollusks, the trochophore develops into a second larval stage, called a *veliger,* before metamorphosing into an adult. Some snails as well as octopuses and squids have direct development: embryos develop into miniature replicas of the adults.


Jeff Foott/Tom Stack & Associates

Figure 29.24
Polyplacophora. Chitons live on rocky shores, where they use their foot and mantle to grip rocks and other hard substrates. This bristled chiton *(Mopalia ciliata)* lives in Monterey Bay, California.

Mollusca includes eight lineages. In the following sections, we examine the four that are most commonly encountered.

Polyplacophora. The 600 species of chitons (Polyplacophora: *poly* = many; *plax* = flat surface) are sedentary mollusks that graze on algae along rocky marine coasts. The oval, bilaterally symmetrical body has a dorsal shell divided into eight plates that allow it to conform to irregularly shaped surfaces **(Figure 29.24).** When a chiton is disturbed or exposed to strong wave action, the muscles of its broad foot maintain a tenacious grip, and the mantle's edge functions like a suction cup to hold fast to the substrate.

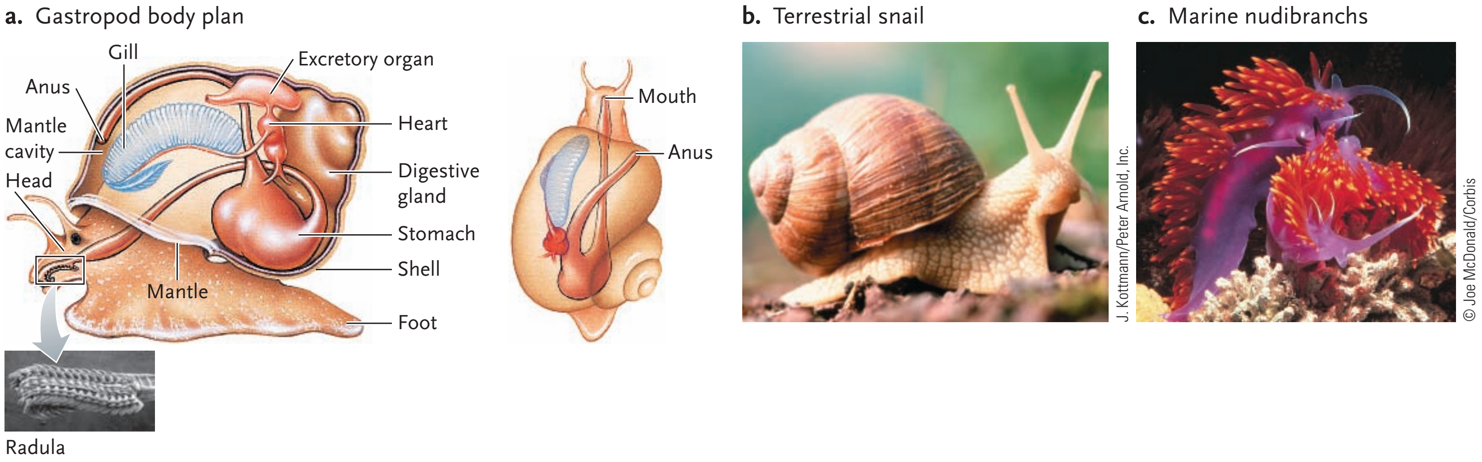
Gastropoda. Snails and slugs (Gastropoda: *gaster* = belly; *pod* = foot) are the largest molluskan group, numbering 40,000 species **(Figure 29.25).** Aquatic species use gills to acquire oxygen, but in terrestrial species a modified mantle cavity functions as an air-breathing lung. Gastropods feed on algae, vascular plants, or animal prey. Some are scavengers, and a few are parasites.

The visceral mass of most snails is housed in a coiled or cone-shaped shell that is balanced above the rest of the body, much as you balance a backpack full of books (see Figure 29.25a, b). Most shelled snails undergo **torsion,** a curious realignment of body parts that is independent of shell coiling. Muscle contractions and differential growth twist the visceral mass and mantle 180° relative to the head–foot. This rearrangement moves the mantle cavity forward so that the head can be withdrawn into the shell in times of danger. But it also brings the gills, anus, and excretory openings above the head—a potentially messy configuration, were it not for cilia that sweep away wastes.

Some gastropods, including terrestrial slugs and colorful nudibranchs (sea slugs), are shell-less, a condition that leaves them somewhat vulnerable to predators (see Figure 29.25c). Some nudibranchs consume cnidarians and then transfer undischarged nematocysts to projections on their dorsal surface, where these "borrowed" stinging capsules provide protection.

The nervous and sensory systems of gastropods are well developed. Tentacles on the head include chemical and touch receptors; the eyes detect changes in light intensity but don't form images.

Bivalvia. The 8000 species of clams, scallops, oysters, and mussels (Bivalvia: *bi* = two; *valva* = folding door) are restricted to aquatic habitats. They are enclosed within a pair of shells, hinged together dorsally by a ligament **(Figure 29.26).** Contraction of the ligament


a. Gastropod body plan

b. Terrestrial snail

c. Marine nudibranchs

J. Kottmann/Peter Arnold, Inc.

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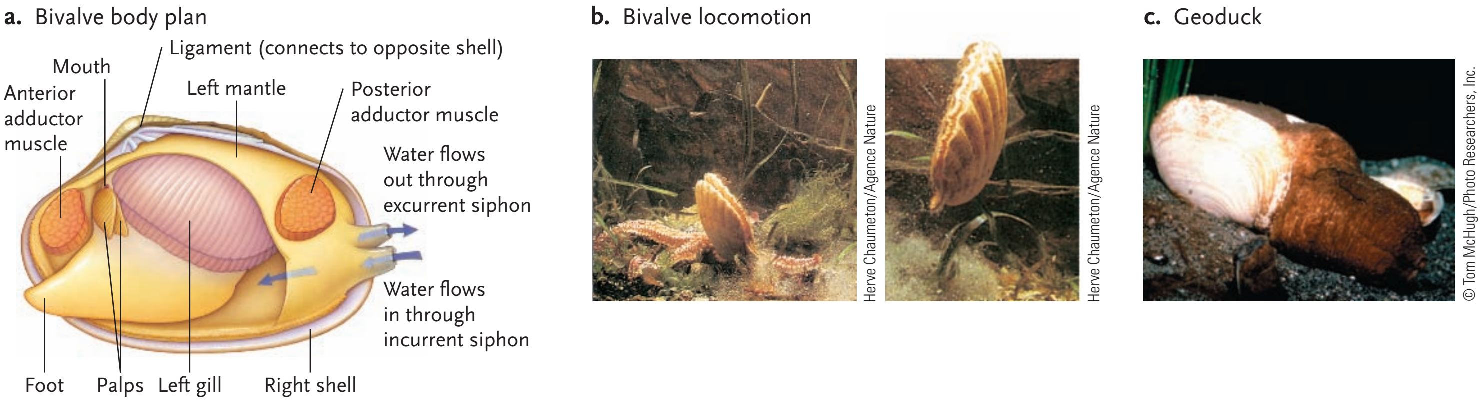
Figure 29.25
Gastropoda. **(a)** Most gastropods have a coiled shell that houses the visceral mass. A developmental process called torsion causes the digestive and excretory systems to eliminate wastes into the mantle cavity, near the animal's head. **(b)** The edible snail *(Helix pomatia)* is a terrestrial gastropod. **(c)** Nudibranchs, like these Spanish shawl nudibranchs *(Flabellina iodinea)*, are shell-less marine snails.
(Micrograph: Danielle C. Zacherl with John McNulty.)

opens the shell by pulling the two sides apart, and contraction of one or two **adductor muscles** closes it by pulling them together (see Figure 29.26a). Although some bivalves are tiny, giant clams of the South Pacific can be more than 1 m across and weigh 225 kg.

Adult mussels and oysters are sessile and permanently attached to hard substrates, but many clams are mobile and use their muscular foot to burrow in sand or mud. Some bivalves, such as young scallops, swim by rhythmically clapping their valves together, forcing a current of water out of the mantle cavity (see Figure 29.26b). The "scallops" that we eat are their well-developed adductor muscles.

Bivalves have a reduced head, and they lack a radula. Part of the mantle forms two tubes called *siphons* (see Figure 29.26c). Beating of cilia on the gills and mantle carry water into the mantle cavity through the incurrent siphon and out through the excurrent siphon. Incurrent water carries dissolved oxygen and food particles to the gills, where oxygen is absorbed. Mucus strands on the gills trap the food, which is then transported by cilia to *palps,* where final sorting takes place; acceptable bits are carried to the mouth. The excurrent water carries away metabolic wastes and feces.

Despite their sedentary existence, bivalves have moderately well developed nervous systems; sensory organs that detect chemicals, touch, and light; and statocysts to sense their orientation. When they encounter pollutants, many bivalves stop pumping water and close their shells. When confronted by a predator, some burrow into sediments or swim away.


a. Bivalve body plan

b. Bivalve locomotion

c. Geoduck

Herve Chaumeton/Agence Nature

Herve Chaumeton/Agence Nature

© Tom McHugh/Photo Researchers, Inc.

Figure 29.26
Bivalvia. **(a)** Bivalves are enclosed in a hinged two-part shell. Part of the mantle forms a pair of water-transporting siphons. **(b)** When threatened by a predator (in this case a sea star), some scallops clap their shells together rapidly, propelling the animal away from danger. **(c)** The geoduck *(Panope generosa)* is a clam with enormous muscular siphons.

Cephalopoda. The 600 species of octopuses, squids, and nautiluses (Cephalopoda: *kephale* = head) are active marine predators, including the fastest and most intelligent invertebrates **(Figure 29.27).** They vary in length from a few centimeters to 18 m. Giant squids, the largest invertebrates known, may be the source of "sea monster" stories.

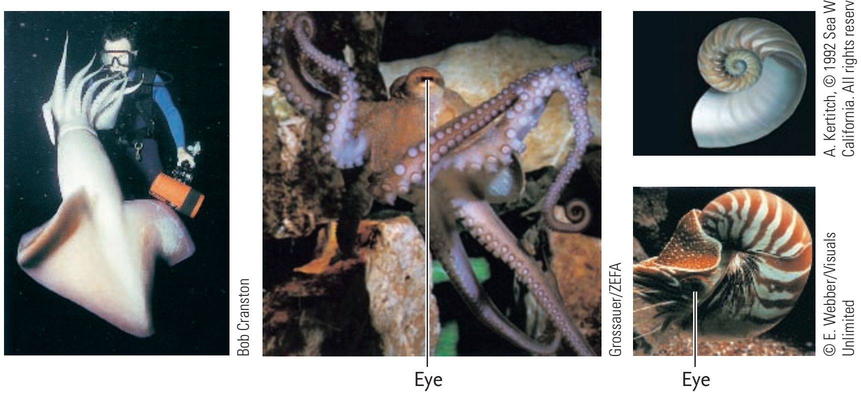
The cephalopod body has a fused head and foot (see Figure 29.27d). The head comprises the mouth and eyes. The ancestral "foot" forms a set of arms and tentacles, equipped with suction pads, adhesive structures, or hooks. Cephalopods use these structures to capture prey and a pair of beaklike jaws to bite or crush it. Venomous secretions often speed the captive's death. Some species use their radula to drill through the shells of other mollusks.

Cephalopods have a highly modified shell. Octopuses have no remnant of a shell at all. In squids and cuttlefishes, it is reduced to a stiff internal support. Only the chambered nautilus and its relatives retain an external shell.

a. Squid

b. Octopus

c. Chambered nautilus



Bob Cranston

Grossauer/ZEFA

A. Kerstitch, © 1992 Sea World of California. All rights reserved

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d. Internal anatomy of squid

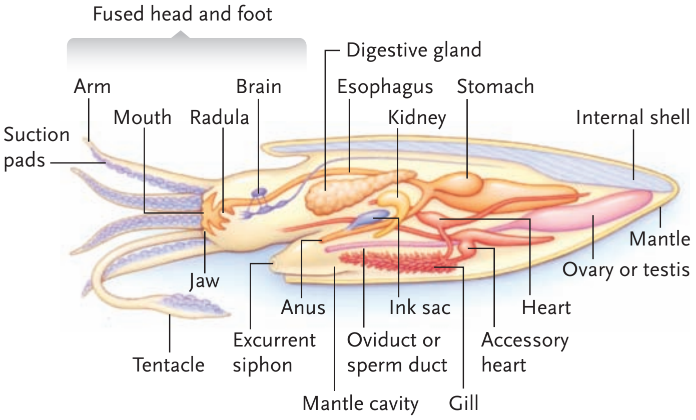


Figure 29.27
Cephalopoda. **(a)** Squids, such as *Dosidicus gigas,* and **(b)** octopuses, such as *Octopus vulgaris,* are the most familiar cephalopods. **(c)** The chambered nautilus *(Nautilus macromphalus)* and its relatives retain an external shell. **(d)** Like other cephalopods, the squid body includes a fused head and foot; most organ systems are enclosed by the mantle.

Squids are the most mobile cephalopods, moving rapidly by a kind of jet propulsion. When muscles in the mantle relax, water is drawn into the mantle cavity. When they contract, a jet of water is squeezed out through a funnel-shaped excurrent siphon. By manipulating the position of the mantle and siphon, the animal can control the rate and direction of its locomotion. When threatened, a squid can make a speedy escape. Many species simultaneously release a dark fluid, commonly called "ink," that obscures their direction of movement. Being highly active, cephalopods need lots of oxygen, and they alone among the mollusks have a **closed circulatory system:** hemolymph is confined within the walls of hearts and blood vessels, providing increased pressure to the vascular fluid. Moreover, accessory hearts speed the flow of hemolymph through the gills, enhancing the uptake of oxygen and release of carbon dioxide.

Compared with other mollusks, cephalopods have large and complex brains. Giant nerve fibers connect the brain with the muscles of the mantle, enabling quick responses to food or danger. Their image-forming eyes are similar to those of vertebrates. Cephalopods are also highly intelligent. Octopuses, for example, learn to recognize objects with distinctive shapes or colors, and they can be trained to approach or avoid them.

Cephalopods have separate sexes and elaborate courtship rituals. Males store sperm within the mantle cavity and use a specialized tentacle to transfer packets of sperm into the female's mantle cavity, where fertilization occurs. Fertilized eggs, wrapped in a protective jelly, are attached to objects in the environment. The young hatch with an adult body form.

Annelids Exhibit a Serial Division of the Body Wall and Some Organ Systems

The 15,000 species of segmented worms (phylum Annelida: *anellus* = ring) occupy marine, freshwater, and moist terrestrial habitats. Terrestrial annelids eat organic debris; aquatic species consume algae, microscopic organisms, detritus, or other animals. They range from a few millimeters to several meters in length.

The annelid body is highly segmented: the body wall muscles and some organs—including respiratory surfaces, parts of the nervous, circulatory, and excretory systems, and the coelom itself—are divided into similar repeating units **(Figure 29.28).** Body segments are separated by transverse partitions called **septa.** The digestive system and major blood vessels are not segmented and run the length of the animal.

The body wall muscles of annelids have both circular and longitudinal layers. Alternate contractions of these muscle groups allow annelids to make directed movements, using the pressure of the fluid in the coe-

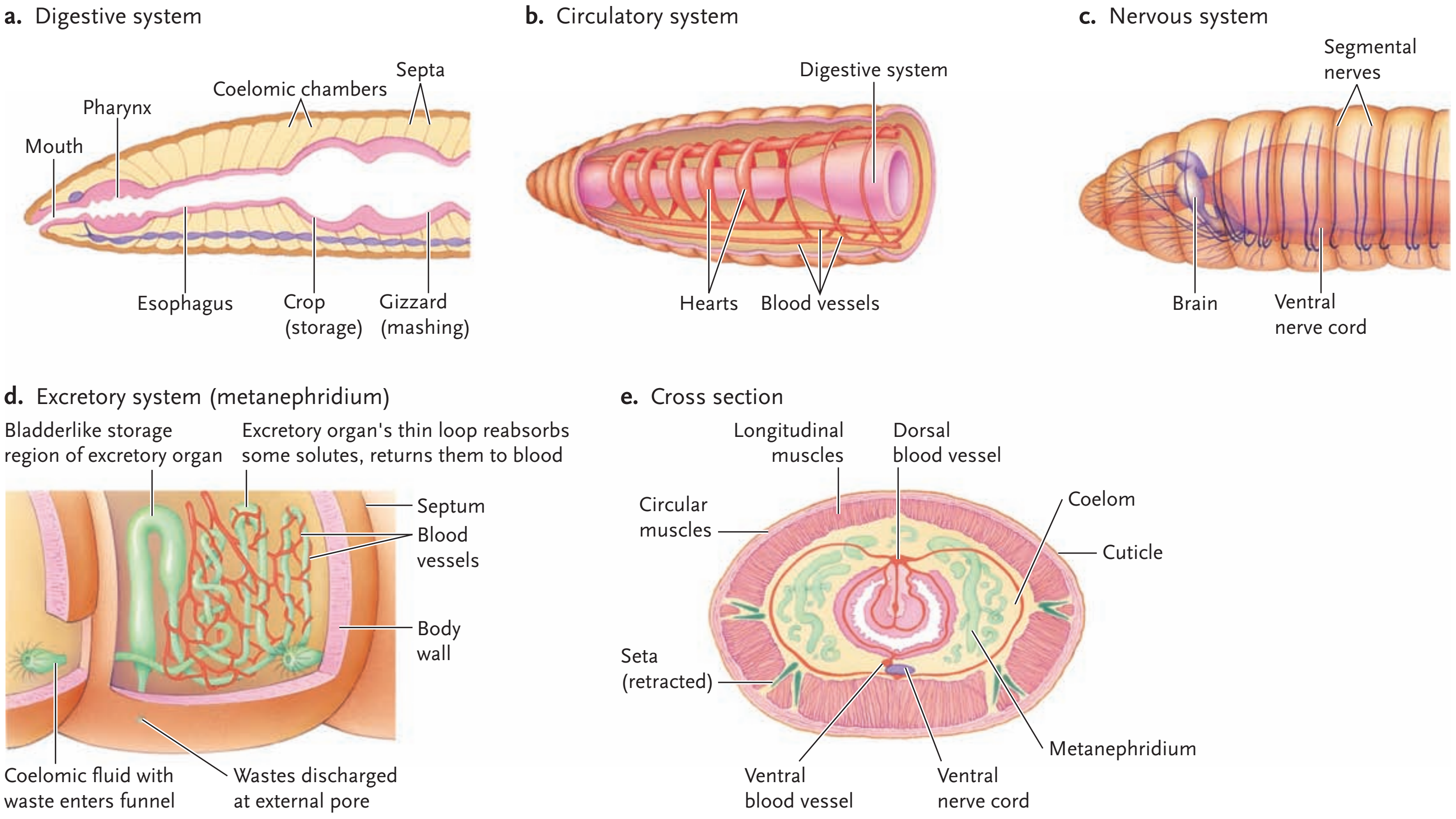


Figure 29.28

Segmentation in the phylum Annelida. Although the digestive system **(a),** the longitudinal blood vessels **(b),** and the ventral nerve cord **(c)** are not segmented, the coelom **(a),** blood vessels **(b),** nerves **(c),** and excretory organs **(d)** appear as repeating structures in most segments. The body musculature **(e)** includes both circular and longitudinal layers that allow these animals to use the coelomic chambers as a hydrostatic skeleton.

lom as a hydrostatic skeleton. All annelids except leeches also have chitin-reinforced bristles, called **setae** (sometimes written *chaetae*), which protrude outward from the body wall. Setae anchor the worm against the substrate, providing traction.

Annelids have a complete digestive system and a closed circulatory system. However, they lack a discrete respiratory system; oxygen and carbon dioxide diffuse through the skin. The excretory system is composed of paired **metanephridia,** which usually occur in all body segments posterior to the head. The nervous system is highly developed, with ganglia (local control centers) in every segment, a simple brain in the head, and sensory organs that detect chemicals, moisture, light, and touch.

Most freshwater and terrestrial annelids are hermaphroditic, and worms exchange sperm when they mate. Newly hatched worms have an adult morphology. Some terrestrial annelids also reproduce asexually by fragmenting and regenerating missing parts. Marine annelids usually have separate sexes, and release gametes into the sea for fertilization. The zygotes develop into trochophore larvae that add segments, gradually assuming an adult form.

Annelida includes three lineages, each of which is largely restricted to one environment.

Polychaeta. The 10,000 species of bristle worms (Polychaeta: *chaite* = bristles) are primarily marine **(Figure 29.29).** Many live under rocks or in tubes constructed from mucus, calcium carbonate secretions, grains of sand, and small shell fragments. Their setae project from well-developed **parapodia** (singular, *parapodium* = closely resembling a foot), fleshy lateral extensions of the body wall used for locomotion and gas exchange. Sense organs are concentrated on a well-developed head.

Crawling or swimming polychaetes are often predatory; they use sharp jaws in a protrusible muscular pharynx to grab small invertebrate prey. Other species graze on algae or scavenge organic matter. A few tube dwellers draw food-laden water into the tube by beating their parapodia; most others collect food by extending feathery, ciliated, mucus-coated tentacles.

Oligochaeta. Most of the 3500 species of oligochaete worms (Oligochaeta: *oligos* = few) are terrestrial **(Figure 29.30),** but they are restricted to moist habitats because

a. Fan worm


Kjell B. Sandved@sandved.com

b. Polychaete feeding structures **c.** Polychaete setae

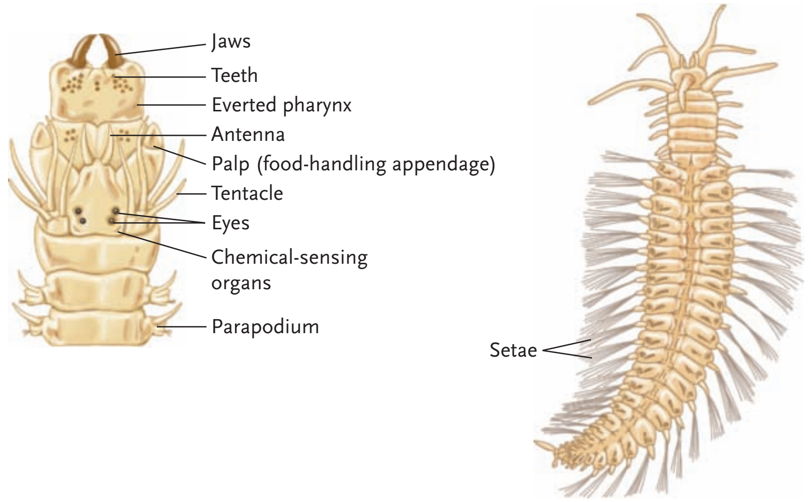


Figure 29.29
Polychaeta. **(a)** The tube-dwelling fan worm *(Sabella melanostigma)* has mucus-covered tentacles that trap small food particles. **(b)** Some polychaetes, like *Nereis,* actively seek food; when they encounter a suitable tidbit, they evert their pharynx, exposing sharp jaws that grab the prey and pull it into the digestive system. **(c)** Many marine polychaetes (such as *Proceraea cornuta*, shown here) have numerous setae, which they use for locomotion.


Duncan Mcewan/npl/Minden Pictures

Figure 29.30
Oligochaeta. Earthworms *(Lumbricus terrestris)* generally move across the ground surface at night.

they quickly dehydrate in dry air or soil. They range in length from a few millimeters to more than 3 m. Terrestrial oligochaetes, the earthworms, are nocturnal, spending their days in burrows that they excavate. Aquatic species live in mud or detritus at the bottom of lakes, rivers, and estuaries.

Earthworms are scavengers on decomposing organic matter. In his book *The Formation of Vegetable Mould through the Action of Worms,* Darwin noted that earthworms can ingest their own weight in soil every day. He calculated that a typical population of 16,000 worms per hectare (10,000 sq m) consumes more than 20 tons of soil in a year. This impressive activity aerates soil and makes nutrients available to plants by mixing the subsoil with the topsoil. Earthworms have complex organ systems (see Figure 29.28), and they sense light and touch at both ends of the body. In addition, they have moisture receptors, an important adaptation in organisms that must stay wet to allow gas exchange across the skin.

Hirudinea. The 500 species of leeches (Hirudinea: *hirudo* = leech) are mostly freshwater parasites. They have dorsoventrally flattened, tapered bodies with a sucker at each end. Although the body wall is segmented, the coelom is reduced and not partitioned. Many leeches are ectoparasites of vertebrates, but some attack small invertebrate prey.

Parasitic leeches feed on the blood of their hosts. Most attach to the host with the posterior sucker, and then use their sharp jaws to make a small, often painless, triangular incision. A sucking apparatus draws blood from the prey, while a special secretion, *hirudin,* maintains the flow by preventing the host's blood from coagulating. Leeches have a highly branched gut that allows them to consume huge blood meals **(Figure 29.31).** For centuries, doctors used medicinal leeches *(Hirudo medicinalis)* to "bleed" patients; today, surgeons use them to drain excess fluid from tissues after recon-

Leech before feeding Leech after feeding


J. A. L. Cooke/Oxford Scientific Films
J. A. L. Cooke/Oxford Scientific Films

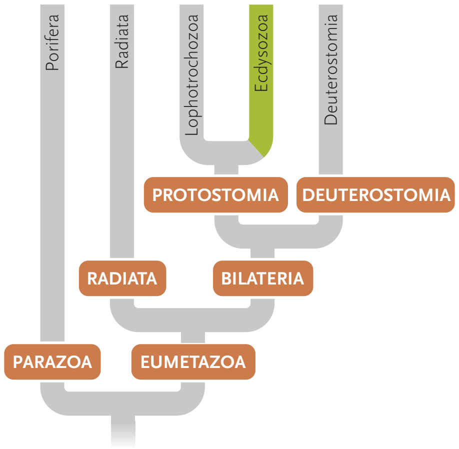
Figure 29.31
Hirudinea. Parasitic leeches consume huge blood meals, as shown by these before and after photos of a medicinal leech *(Hirudo medicinalis).* Because suitable hosts are often hard to locate, gorging allows a leech to take advantage of any host it finds.

structive surgery, reducing swelling until the patient's blood vessels regenerate and resume this function.

Study Break

1. What organs systems are present in free-living flatworms (Turbellaria)? Which of these organ systems is absent in tapeworms (Cestoda)?
2. What characteristic reveals the close evolutionary relationship of ectoprocts, brachiopods, and phoronid worms?
3. What anatomical structures and physiological systems allow squids and other cephalopods to be much more active than other types of mollusks?
4. Which organs systems exhibit segmentation in most annelid worms?

29.7 Ecdysozoan Protostomes



The three phyla in the protostome group Ecdysozoa all have an external covering that they shed periodically. The outer covering protects these animals from harsh environmental conditions, and it helps parasitic species resist host defenses. Although many of these animals live in either aquatic or moist terrestrial habitats, a tough exoskeleton allows one group, the insects, to thrive on dry land and in the air.

Nematodes Are Unsegmented Worms Covered by a Flexible Cuticle

Roundworms (phylum Nematoda: *nema* = thread) are perhaps the most abundant animals on Earth. A cupful of rich soil, a dead earthworm, or a rotting fruit may contain thousands of them. Although 80,000 species have been described, experts estimate that more than half a million exist. Many nematodes are almost microscopically small, but some species are a meter or more long. They occupy nearly every freshwater, marine, and terrestrial habitat on Earth, consuming detritus, microorganisms, plants, or animals.

The roundworm body is cylindrical and usually tapered at both ends **(Figure 29.32).** None of the cells have cilia or flagella. Roundworms are covered in a tough but flexible, water-resistant **cuticle,** which is replaced by the underlying epidermis as the worm grows. The cuticle prevents the animal from dehydrating in dry environments, and, in parasitic species, it resists attack by acids and enzymes in a host's digestive system. Beneath the cuticle and epidermis, a layer of longitudinal muscles extends the length of the body. Nematodes use alternating muscle contractions to push against the substrate and propel themselves forward, usually with a thrashing motion.

The adults of one soil-dwelling species, *Caenorhabditis elegans,* are transparent and contain fewer than 1000 cells. As *Focus on Model Research Organisms* explains, biologists have studied this worm inside and out.

Nematodes reproduce sexually, and the sexes are separate in most species. In some, internal fertilization produces many thousands of fertile eggs per day. The eggs of many species can remain dormant if environmental conditions are unsuitable.

Because of their great numbers, nematodes have enormous ecological, agricultural, and medical significance. Free-living species are responsible for decomposition and nutrient recycling in many habitats. Parasitic nematodes attack the roots of plants, causing tremendous crop damage. Roundworms also parasitize animals, including humans. Although some, like pinworms *(Enterobius),* are more of a nuisance than a danger, others, like trichinas or filarial worms, can cause serious disease, disfigurement, or even death (see *Focus on Applied Research* on pages 644–645). More than 1 billion people worldwide suffer from debilitating and life-threatening nematode infections.


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Figure 29.32
Phylum Nematoda. Some roundworms, like these *Anguillicola crassus* in the swim bladder of an eel, are parasites of plants or animals. Others are important consumers of dead organisms in most ecosystems.

FOCUS ON RESEARCH

Model Research Organisms: *Caenorhabditis elegans*

Researchers studying the tiny, free-living nematode *Caenorhabditis elegans* have made many recent advances in molecular genetics, animal development, and neurobiology. It is so popular as a model research organisms that most workers simply refer to it as "the worm."

Several attributes make *C. elegans* a model research organism. It has an adult size of about 1 mm and thrives on cultures of *E. coli* or other bacteria; thus, thousands can be raised in a culture dish. It is hermaphroditic and often self-fertilizing, which allows researchers to maintain pure genetic strains. It completes its life cycle from egg to reproductive adult within 3 days at room temperature. Furthermore, stock cultures can be kept alive indefinitely by freezing them in liquid nitrogen or in an ultra-cold freezer set to −80°C. Researchers can therefore store new mutants for later research without having to clean, feed, and maintain active cultures.

Best of all, the worm is anatomically simple (see **figure**); an adult contains just 959 cells (excluding the gonads). Having a fixed cell number is relatively uncommon among animals, and developmental biologists have made good use of this trait. The eggs, juveniles, and adults of the worm are completely transparent, and researchers can observe cell divisions and cell movements in living animals with straightforward microscopy techniques. There is no need to kill, fix, and stain specimens for study. And virtually every cell in the worm's body is accessible for manipulation by laser microsurgery, microinjection, and similar approaches.

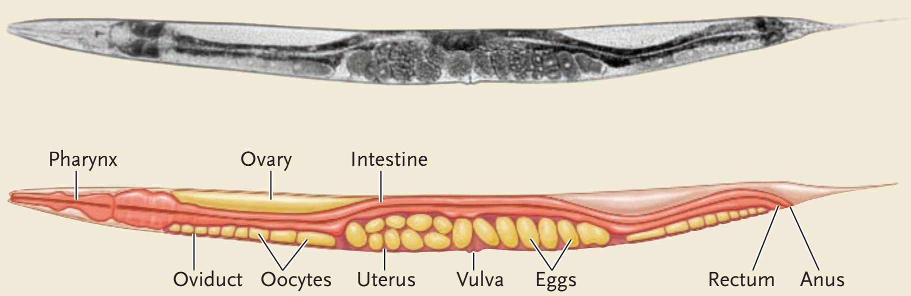
The genome of *C. elegans,* which was sequenced in 1998, is also simple, consisting of 100 million base pairs organized into roughly 17,000 genes on six pairs of chromosomes. The genome, which is about the same size as one human chromosome, specifies the amino acid sequences of about 10,000 protein molecules, far fewer than are found in more complex animals.

The worm entered the biological limelight in 1965 when Sidney Brenner of the Medical Research Council's Laboratory of Molecular Biology in Cambridge, England, identified it as an ideal organism for research on the genetic control of development. By 1983 numerous researchers had collectively identified the cell lineage for every one of its 959 cells. We now know the exact patterns of cell divisions, cell migrations, and programmed cell death that generate an adult from a fertilized egg.

Research on *C. elegans* has generated interesting results, some of which contradict old assumptions about animal development. For example, researchers once believed that a particular tissue always arises from the same embryonic germ layer, but in *C. elegans* some muscle cells do not develop from mesoderm and some nervous system cells do not arise from ectoderm. Moreover, the bilaterally symmetrical body of the adult worm does not arise from symmetrical events; matching cells on the left and right sides of the worm sometimes arise from different developmental pathways. Finally, researchers were surprised by the important role of cell death in this organism. Developmental events in the embryo produce 671 cells, but 113 of them are programmed to die before the larva hatches from the egg.

Studies of the worm's nervous system have been equally fruitful. Researchers have mapped the development of all 302 neurons and their 7000 connections. Now they are working to identify the molecules that function in sensory recognition and cell-to-cell signaling. Molecular analyses reveal that some of the proteins that carry messages between nerve cells in the worm are similar to those found in vertebrates.

The knowledge gained from research on *C. elegans* is highly relevant to studies of larger and more complex organisms, including vertebrates. Recent research demonstrates some striking similarities among nematodes, fruit flies, and mice in the genetic control of development, in some of the proteins that govern important events like cell death, and in the molecular signals used for cell-to-cell communication. Using a relatively simple model like *C. elegans,* researchers can answer research questions more quickly and more efficiently than they could if they studied larger and more complex animals.



J. Sulston, MRC Laboratory of Molecular Biology

Velvet Worms Have Segmented Bodies and Numerous Unjointed Legs

The 65 living species of velvet worms (phylum Onychophora: *onyx* = claw) live under stones, logs, and forest litter in the tropics and in moist temperate habitats in the southern hemisphere. They range in size from 15 mm to 15 cm and feed on small invertebrates.

Onychophorans have a flexible cuticle, segmented bodies, and numerous pairs of unjointed legs **(Figure 29.33).** Like the annelids, they have pairs of excretory organs in most segments. But unlike annelids, they


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Figure 29.33
Phylum Onychophora. Members of the small phylum Onychophora, such as species in the genus *Dnycophor,* have segmented bodies and unjointed appendages.

have an open circulatory system, a specialized respiratory system, relatively large brains, jaws, and tiny claws on their feet. Many produce live young, which, in some species, are nourished within a uterus. Fossil evidence indicates that the onychophoran body plan has not changed much over the last 500 million years.

Arthropods Are Segmented Animals with a Hard Exoskeleton and Jointed Appendages

The more than 1 million known species of arthropods (phylum Arthropoda: *arthron* = joint) include more than half the animal species on Earth—and only a fraction of the living arthropods have been described. This huge lineage includes insects, spiders, crustaceans, millipedes, centipedes, the extinct trilobites, and their relatives.

Arthropods have a segmented body encased in a rigid **exoskeleton.** This external covering is made of chitin, a mix of polysaccharide fibers glued together with glycoproteins, as well as waxes and lipids that block the passage of water. In some marine groups, such as crabs and lobsters, it is hardened with calcium carbonate. The exoskeleton probably first evolved in marine species, providing protection against predators. In terrestrial habitats, it provides support against gravity and protection from dehydration, contributing to the success of insects in even the driest places on Earth. The exoskeleton is especially thin and flexible at the joints between body segments and in the appendages. Contractions of muscles attached to the inside of the exoskeleton move individual body parts like levers, allowing highly coordinated movements and patterns of locomotion that are more precise than those in soft-bodied animals with hydrostatic skeletons.

Although the exoskeleton has obvious advantages, it is nonexpandable and therefore could limit growth of the animal. But, like other Ecdysozoa, arthropods grow and periodically develop a soft, new exoskeleton beneath the old one, which they shed in the complex process of ecdysis **(Figure 29.34).** After shedding the old exoskeleton, aquatic species swell with water and terrestrial species swell with air before the new one hardens. They are especially vulnerable to predators at these times. “Soft-shelled” crabs, prized as food in many countries, are ones that have recently molted.

As arthropods evolved, body segments became fused in various ways, reducing their overall number. Each region, along with its highly modified paired appendages, is specialized, but the structure and function vary greatly among groups. In insects (see Figure 29.43), which have three body regions, the **head** includes a brain, sensory structures, and some sort of feeding apparatus. The segments of the **thorax** bear walking legs and, in some insects, wings. The **abdomen** includes much of the digestive system and sometimes part of the reproductive system.

The coelom of arthropods is greatly reduced, but another cavity, the *hemocoel,* is filled with bloodlike hemolymph. The heart pumps the hemolymph through an open circulatory system, bathing tissues directly.

Arthropods are active animals and require substantial quantities of oxygen. Different groups have distinctive mechanisms for gas exchange, because oxygen cannot cross the impermeable exoskeleton. Marine and freshwater species, like crabs and lobsters, rely on diffusion across gills. The terrestrial groups—


Mitsuhiko Imamori/Minden Pictures

Figure 29.34
Ecdysis in insects. Like all other arthropods, this cicada *(Graptopsaltsia nigrofusca)* sheds its old exoskeleton as it grows and when it undergoes metamorphosis into a winged adult.

Insights from the Molecular Revolution

Unscrambling the Arthropods

This book follows a classification that divides arthropods into five subphyla—trilobites (now extinct), chelicerates, crustaceans, myriapods, and hexapods. In the past, biologists grouped hexapods and myriapods together **(figure, left)** because they share certain morphological characteristics, which may indicate a common ancestry: unbranched appendages, a tracheal system for gas exchange, Malpighian tubules for excretion, and one pair of antennae. Some biologists have argued, however, that these traits may have been produced by convergent evolution. Furthermore, the comparison of other morphological traits suggests that hexapods are more closely related to crustaceans than to myriapods. For example, both hexapods and crustaceans have jawlike mandibles on the fourth head segment, similar compound eyes, comparable development of the nervous system, and similarities in the structure of thoracic appendages.

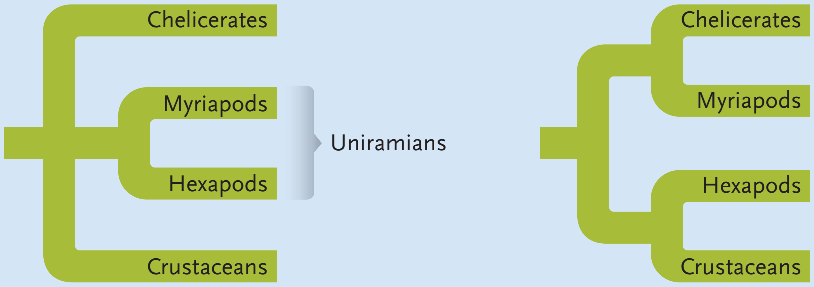
A molecular study by Jeffry L. Boore and his colleagues at the University of Michigan lends support to the hypothesis that hexapods may indeed be more closely related to crustaceans than to myriapods. For their study, Boore and his coworkers compared the arrangement of genes in the mitochondrial DNA of representative arthropod species. Mitochondrial DNA (mtDNA) was chosen for study because it has been subject to many random rearrangements during the evolutionary history of the arthropods, producing wide variations in the order and placement of the 36 or 37 genes typically present. As long as the rearrangements do not disrupt gene function, they may have little or no effect on fitness; therefore, they may not be affected by natural selection. As Boore and his colleagues noted, the large number of possible rearrangements of the mtDNA genes makes it unlikely that the same gene order would appear by chance in any two groups; thus, groups with the same arrangement are likely to share a common ancestor in which the rearrangement first appeared.

The investigators sequenced the mtDNA of a chelicerate, two crustaceans, and a myriapod (listed in the figure caption). They also sequenced the mtDNAs of a mollusk and an annelid, animals that are only distantly related to arthropods, to provide outgroup comparisons. They compared these sequences with those in 14 other invertebrates, including four hexapods and one crustacean, already obtained by other workers.

The locations of two genes encoding leucine-carrying tRNAs provide the strongest clue to the evolutionary relationships of these organisms. These genes are positioned next to each other in the mtDNA of the chelicerate, the mollusk, and the annelid. This arrangement appears to reflect the ancient gene order present in the common ancestor of annelids, mollusks, and arthropods. However, in the hexapods and the crustaceans studied, one of the leucine tRNA genes is located at a different position, between two genes coding for electron transfer proteins. Moreover, this rearrangement does not appear in the myriapod examined. It is extremely unlikely that the same translocation of the leucine tRNA gene occurred independently in hexapods and crustaceans. Instead, this gene rearrangement probably occurred in an ancestor shared by hexapods and crustaceans after this ancestor diverged from the lineage that includes the chelicerates and myriapods.

The shared gene arrangement in insects and crustaceans and the absence of a matching arrangement in myriapods suggests that hexapods and crustaceans are closely related, and that hexapods and myriapods are not, in spite of their morphological similarities **(figure, right).** Other investigators, who compared the sequences of ribosomal RNA genes in a variety of arthropod species, reached the same conclusions independently.

Because the molecular research studied a relatively few characteristics, it cannot yet be accepted as the definitive answer to questions about arthropod lineages. However, the results give strong support to the idea that hexapods and crustaceans are more closely related than the traditional family tree suggested.



The traditional phylogenetic tree for arthropods (left) differs from that suggested by the research described in this box. The DNA sequences used to construct the new phylogenetic tree (right) were obtained from the chelicerate *Limulus,* the myriapod *Thyrophygus,* the hexapod *Drosophila,* and the crustaceans *Daphnia* and *Homarus.*

insects and spiders—have developed unique and specialized respiratory systems.

High levels of activity also require intricate sensory structures. Many arthropods are equipped with a highly organized central nervous system, touch receptors, chemical sensors, **compound eyes** that include multiple image-forming units, and in some, hearing organs.

Arthropod systematics is an active area of research, and scientists are currently using molecular, morpho-

Dr. Chip Clark

Figure 29.35

Subphylum Trilobita. Trilobites, like *Olenellus gilberti,* bore many pairs of relatively undifferentiated appendages.

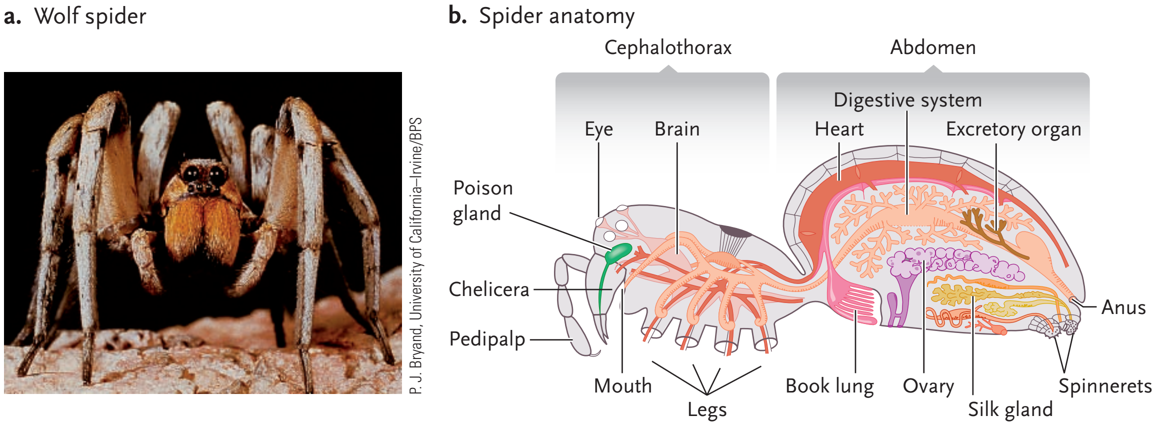
logical, and developmental data to reexamine relationships within this immense group. As *Insights from the Molecular Revolution* explains, hypotheses about the phylogeny and classification of arthropods are in a state of flux. Some researchers even argue for splitting them into four or more phyla. We follow the traditional definition of five *subphyla,* partly because this classification adequately reflects arthropod diversity and partly because no alternative hypothesis has been widely adopted by experts.

Subphylum Trilobita. The trilobites (subphylum Trilobita: *tri* = three; *lobos* = lobe), now extinct, were among the most numerous animals in shallow Paleozoic seas. They disappeared in the Permian mass extinction, but the cause of their demise is unknown. Most trilobites were ovoid, dorsoventrally flattened, and heavily armored, with two deep longitudinal grooves that divided the body into the one median and two lateral lobes for which the group is named **(Figure 29.35).** Their segmented bodies were organized into a head, which included a pair of sensory **antennae** (chemosensory organs) and two compound eyes, and a thorax and an abdomen, both of which bore pairs of walking legs.

The position of trilobites in the fossil record indicates that they were among the earliest arthropods. Thus, biologists are confident that their three body regions and numerous unspecialized appendages—one pair per segment—represent ancestral traits within the phylum. As you will learn as you read about the other four subphyla, the subsequent evolution of the different arthropod groups included dramatic remodeling of the major body regions as well as modifications of the ancestral, unspecialized paired appendages into structures specialized for different functions.

Subphylum Chelicerata. In spiders, ticks, mites, scorpions, and horseshoe crabs (subphylum Chelicerata: *chela* = claw; *keras* = horn), the first pair of appendages, the **chelicerae,** are fanglike structures used for biting prey. The second pair of appendages, the *pedipalps,* serve as grasping organs, sensory organs, or walking legs. All chelicerates have two major body regions, the **cephalothorax** (a fused head and thorax) and the abdomen. The group originated in shallow Paleozoic seas, but most living species are terrestrial. They vary in size from less than a millimeter to 20 cm; all are predators or parasites.

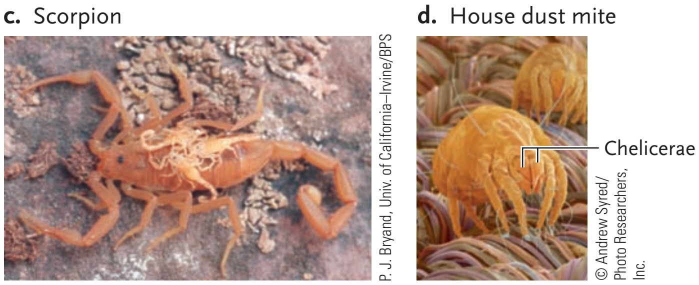
The 60,000 species of spiders, scorpions, mites, and ticks (Arachnida) represent the vast majority of chelicerates **(Figure 29.36).** Arachnids have four pairs



a. Wolf spider

P. J. Bryand, University of California–Irvine/BPS

b. Spider anatomy



c. Scorpion

P. J. Bryand, Univ. of California–Irvine/BPS

d. House dust mite

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Figure 29.36

Subphylum Chelicerata, subgroup Arachnida. **(a)** The wolf spider (*Lycosa* species) is harmless to humans. **(b)** The arachnid body plan includes a cephalothorax and abdomen. **(c)** Scorpions have a stinger at the tip of the segmented abdomen. Many, like *Centruroides sculpuratus,* protect their eggs and young. **(d)** House dust mites *(Dermatophagoides pteronyssinus),* shown in a scanning electron micrograph, feed on microscopic debris.

of walking legs on the cephalothorax and highly modified chelicerae and pedipalps. In some spiders, males use their pedipalps to transfer packets of sperm to females. Scorpions use them to shred food and to grasp one another during courtship. Many predatory arachnids have excellent vision, provided by simple eyes on the cephalothorax. Scorpions and some spiders also have unique pocketlike respiratory organs called **book lungs,** derived from abdominal appendages.

Spiders, like most other arachnids, subsist on a liquid diet. They use their chelicerae to inject paralyzing poisons and digestive enzymes into prey and then suck up the partly digested tissues. Many spiders are economically important predators, helping to control insect pests. Only a few are a threat to humans. The toxin of a black widow *(Latrodectus mactans)* causes paralysis, and the toxin of the brown recluse *(Loxosceles reclusa)* destroys tissues around the site of the bite.

Although many spiders hunt actively, others capture prey on silken threads secreted by **spinnerets,** which are modified abdominal appendages. Some species weave the threads into complex, netlike webs. The silk is secreted as a liquid, but quickly hardens on contact with air. Spiders also use silk to make nests, to protect their egg masses, as a safety line when moving through the environment, and to wrap prey for later consumption.

Most mites are tiny, but they have a big impact. Some are serious agricultural pests that feed on the sap of plants. Others cause mange (patchy hair loss) or painful and itchy welts on animals. House dust mites cause allergic reactions in many people. Ticks, which are generally larger than mites, are blood-feeding ectoparasites that often transmit pathogens, such as those causing Rocky Mountain spotted fever and Lyme disease.

The subphylum Chelicerata also includes five species of horseshoe crabs (Merostomata), an ancient lineage that has not changed much during its 350 million year history **(Figure 29.37).** Horseshoe crabs are carnivorous bottom feeders in shallow coastal waters. Beneath their characteristic shell, they have one pair of chelicerae, a pair of pedipalps, four pairs of walking legs, and a set of paperlike gills, derived from ancestral walking legs.

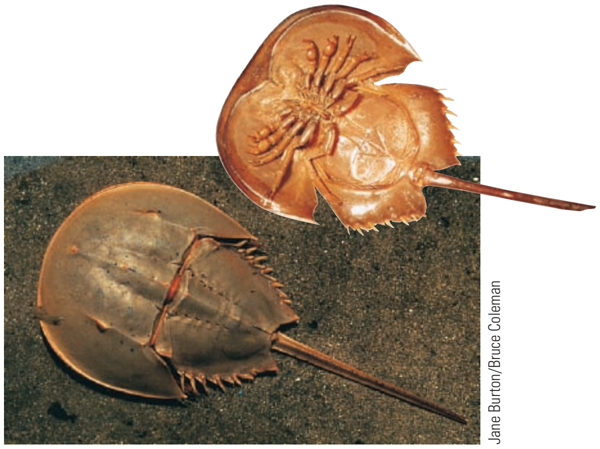


Figure 29.37
Marine chelicerates. Horseshoe crabs, like *Limulus polyphemus*, are included in the Merostomata.

Jane Burton/Bruce Coleman

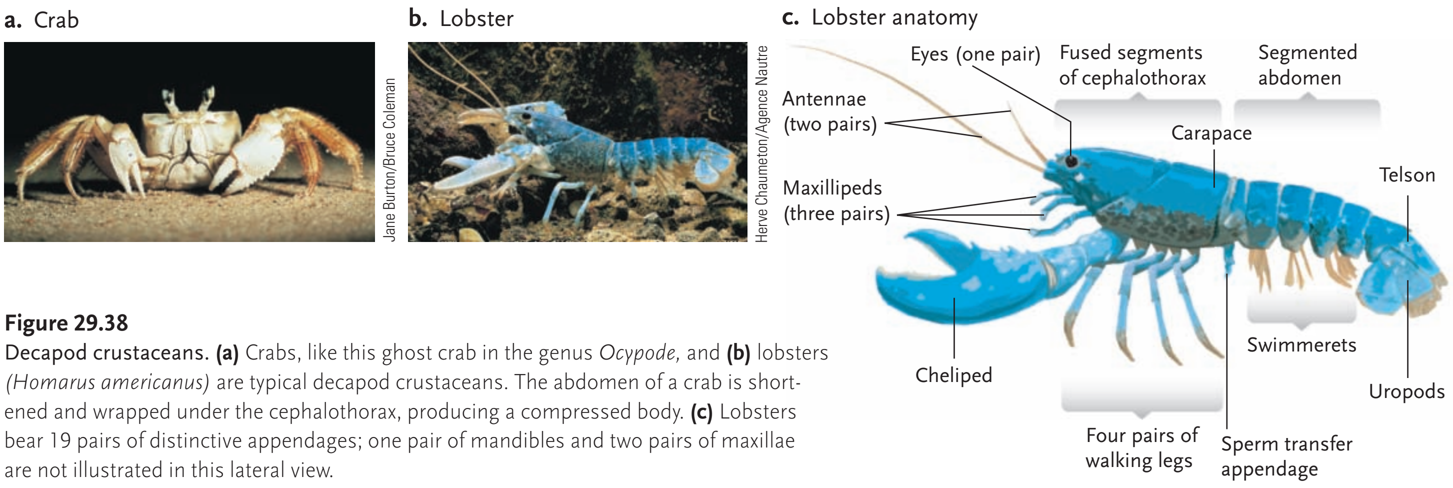
Subphylum Crustacea. The 35,000 species of shrimps, lobsters, crabs, and their relatives (subphylum Crustacea, meaning "encrusted") represent a lineage that emerged more than 500 million years ago. They are abundant in marine and freshwater habitats. A few species, such as sowbugs and pillbugs, live in moist, sheltered terrestrial environments. In many crustaceans two, or even all three, of the arthropod body regions—head, thorax, and abdomen—are fused; a fused cephalothorax and a separate abdomen is an especially common pattern. The edible "tail" of a lobster or crayfish is actually a highly muscularized abdomen. In some, the exoskeleton includes a **carapace,** a protective covering that extends backward from the head. Crustaceans vary in size from water fleas less than 1 mm long to lobsters that can grow to 60 cm in length and weigh as much as 20 kg.

Crustaceans generally have five characteristic pairs of appendages on the head **(Figure 29.38).** Most have two pairs of sensory antennae and three pairs of mouthparts. The latter include one pair of *mandibles,* which move laterally to bite and chew, and two pairs of *maxillae,* which hold and manipulate food. Numerous paired appendages posterior to the mouthparts vary among groups.

Most crustaceans are active animals that exhibit complex patterns of movement. Their activities are coordinated by elaborate sensory and nervous systems, including chemical and touch receptors in the antennae, compound eyes, statocysts on the head, and sensory hairs embedded in the exoskeleton throughout the body. The nervous system is similar to that in annelids, but the ganglia are larger and more complex, allowing a finer level of motor control. High levels of activity require substantial oxygen, and larger species have complex, feathery gills tucked beneath the carapace. Activity also produces abundant metabolic wastes that are excreted by diffusion across the gills or, in larger species, by glands located in the head.

The sexes are typically separate, and courtship rituals are often complex. Eggs are usually brooded on the surface of the female's body or beneath the carapace. Many have free-swimming larvae that, after undergoing a series of molts, gradually assume an adult form.

The subphylum includes so many different body plans that it is usually divided into six major groups with numerous subgroups. The crabs, lobsters, and shrimps (Decapoda, meaning "10 feet," a subgroup of the Malacostraca) number more than 10,000 species. The vast majority of decapods are marine, but a few shrimps, crabs, and crayfishes occupy freshwater habitats. Some crabs also live in moist terrestrial habitats, where they scavenge dead vegetation, clearing the forest floor of debris.



Jane Burton/Bruce Coleman

Herve Chaumeton/Agence Nautre

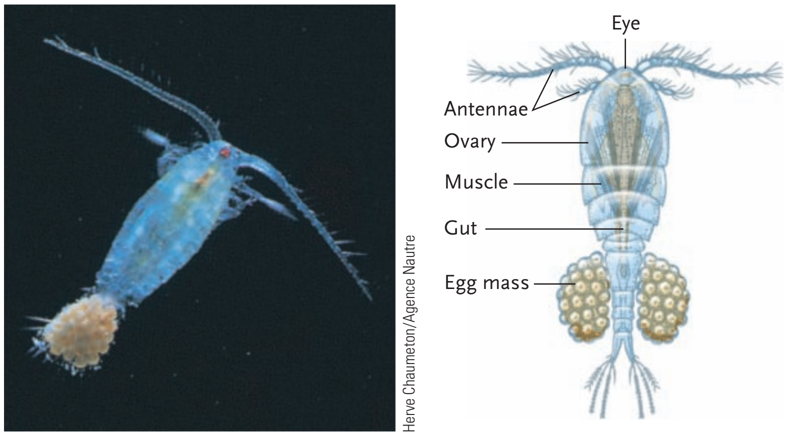
Figure 29.38
Decapod crustaceans. **(a)** Crabs, like this ghost crab in the genus *Ocypode,* and **(b)** lobsters *(Homarus americanus)* are typical decapod crustaceans. The abdomen of a crab is shortened and wrapped under the cephalothorax, producing a compressed body. **(c)** Lobsters bear 19 pairs of distinctive appendages; one pair of mandibles and two pairs of maxillae are not illustrated in this lateral view.

All decapods exhibit extreme specialization of their appendages. In the American lobster, for example, each of the 19 pairs of appendages is different (see Figure 29.38c). Behind the antennae, mandibles, and maxillae, the thoracic segments have three pairs of *maxillipeds,* which shred food and pass it up to the mouth, a pair of large *chelipeds* (pinching claws), and four pairs of walking legs. The abdominal appendages include a pair specialized for sperm transfer (in males only), *swimmerets* for locomotion and for brooding eggs, and *uropods,* a pair of appendages that, combined with the *telson,* the tip of the abdomen, form a fan-shaped tail. If any appendage is damaged, the animal can autotomize (drop) it and begin growing a new one before its next molt.

Representatives of several crustacean groups—fairy shrimps, amphipods, water fleas, krill, ostracods, and copepods **(Figure 29.39)**—live as plankton in the upper waters of oceans and lakes. Most are only a few millimeters long, but are present in huge numbers. They feed on microscopic algae or detritus and are themselves food for larger invertebrates, fishes, and some suspension-feeding marine mammals like the baleen whales. Planktonic crustaceans are among the most abundant animals on Earth.

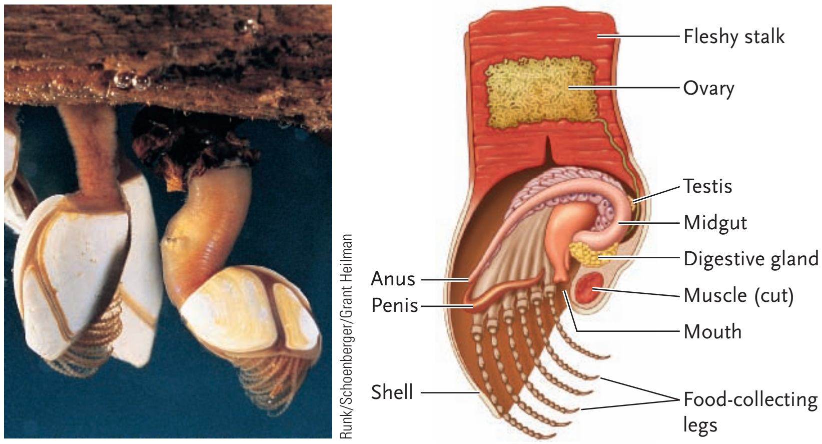
Adult barnacles (Cirripedia, meaning "hairy footed," a subgroup of the Maxillopoda) are sessile, marine crustaceans that live within a strong, calcified cup-shaped shell **(Figure 29.40).** Their free-swimming larvae attach permanently to substrates—rocks, wooden pilings, the hulls of ships, the shells of mollusks, even the skin of whales—and secrete the shell, which is actually a modified exoskeleton. To feed, barnacles open the shell and extend six pairs of feathery legs. The beating legs capture microscopic plankton and transfer it the mouth. Unlike most crustaceans, barnacles are hermaphroditic.

Subphylum Myriapoda. The 3000 species of centipedes (Chilopoda) and 10,000 species of millipedes (Diplopoda) are classified together in the subphylum Myriap-



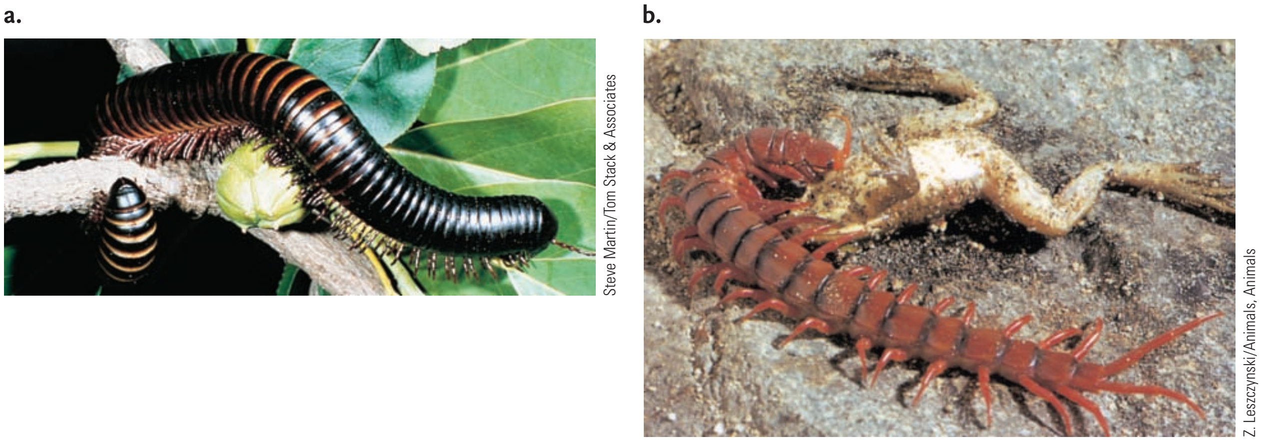
Herve Chaumeton/Agence Nautre

Figure 29.39
Copepods. Tiny crustaceans, like these copepods (*Calanus* species on the left, *Cyclops* species on the right), occur by the billions in freshwater and marine plankton.



Runk/Schoenberger/Grant Heilman

Figure 29.40
Barnacles. Gooseneck barnacles *(Lepas anatifera)* attach to the underside of floating debris. Like other barnacles, they open their shells and extend their feathery legs to collect particulate food from seawater.



Steve Martin/Tom Stack & Associates

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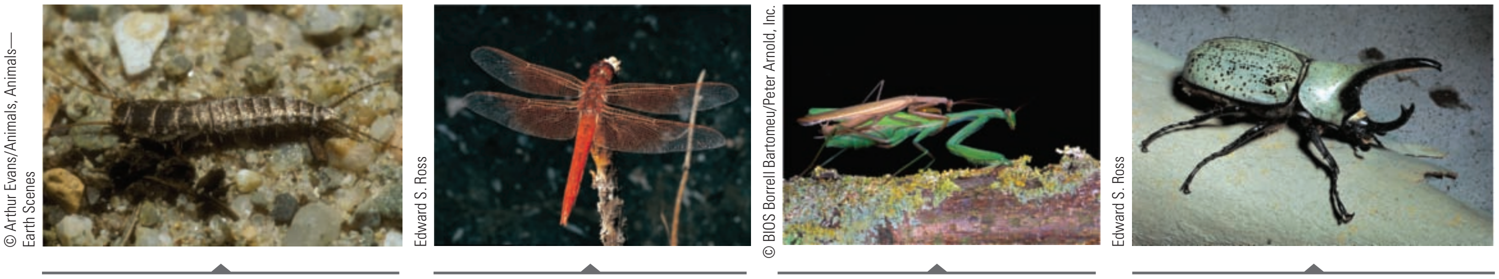
Figure 29.41
Millipedes and centipedes. (a) Millipedes, like *Spirobolus* species, feed on living and decaying vegetation. They have two pairs of walking legs on most segments. **(b)** Like all centipedes, this Southeast Asian species *(Scolopendra subspinipes),* shown feeding on a small frog, is a voracious predator. Centipedes have one pair of walking legs per segment.

oda (meaning "countless feet"). Myriapods have two body regions, a head and a segmented trunk **(Figure 29.41).** The head bears one pair of antennae, and the trunk bears one (centipedes) or two (millipedes) pairs of walking legs on most of its many segments. Myriapods are terrestrial, and many species live under rocks or dead leaves. Centipedes are fast and voracious predators, using powerful toxins to kill their prey; they generally feed on invertebrates, but some eat small vertebrates. The bite of some species is harmful to humans. Although most species are less than 10 cm long, some grow to 25 cm. The millipedes are slow but powerful

Figure 29.42
Insect diversity. Insects are grouped into about 30 orders, 8 of which are illustrated here.



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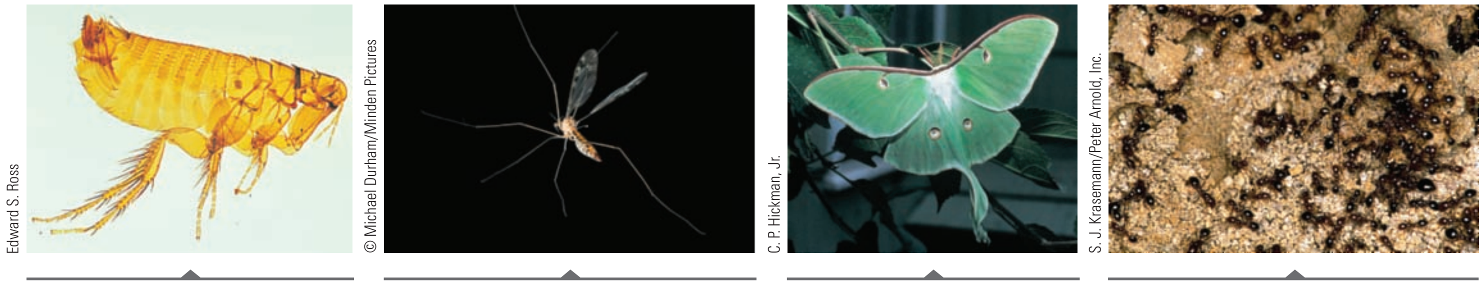
a. Silverfish (Thysanura, *Ctenolepisma longicaudata*) are primitive wingless insects.

b. Dragonflies, like the flame skimmer (Odonata, *Libellula saturata*), have aquatic larvae that are active predators; adults capture other insects in mid-air.

c. Male praying mantids (Mantodea, *Mantis religiosa*) are often eaten by the larger females during or immediately after mating.

d. This rhinoceros beetle (Coleoptera, *Dynastes granti*) is one of more than 250,000 beetle species that have been described.



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e. Fleas (Siphonoptera, *Hystrichopsylla dippiei*) have strong legs with an elastic ligament that allows these parasites to jump on and off their animal hosts.

f. Crane flies (Diptera, *Tipula* species) look like giant mosquitoes, but their mouthparts are not useful for biting other animals; the adults of most species live only a few days and do not feed at all.

g. The luna moth (Lepidoptera, *Actias luna*), like other butterflies and moths, has wings that are covered with colorful microscopic scales.

h. Like many other ant species, fire ants (Hymenoptera, *Solenopsis invicta*) live in large cooperative colonies. Fire ants—named for their painful sting—were introduced into southeastern North America, where they are now serious pests.

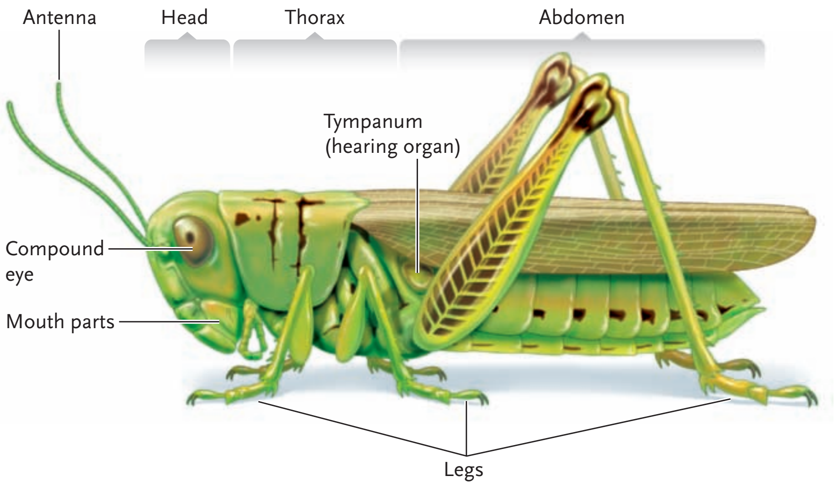
herbivores or scavengers. The largest species attain a length of nearly 30 cm. Although they lack a poisonous bite, they curl into a ball and exude noxious liquids when disturbed.

Subphylum Hexapoda. In terms of sheer numbers, diversity, and the range of habitats they occupy, the 1,000,000 or more species of insects and their closest relatives (subphylum Hexapoda, meaning "six feet") are the most successful animals on Earth. They were among the first animals to colonize terrestrial habitats, where most species still live. The oldest insect fossils date from the Devonian, 380 million years ago. Insects have one pair of antennae on the head, a pair of mandibles for feeding, and unbranched appendages. Insects are generally small, ranging from 0.1 mm to 30 cm in length. The group is divided into about 30 subgroups **(Figure 29.42).** The insect body plan always includes a head, thorax, and abdomen **(Figure 29.43).** The head is equipped with multiple mouthparts, a pair of compound eyes, and one pair of sensory antennae. The thorax has three pairs of walking legs and often one or two pairs of wings. Insects are the only invertebrates capable of flight. Their wings, which are made of lightweight but durable sheets of chitin and sclerotin, arise embryonically from the body wall; unlike the wings of birds and bats, insect wings are not derived from ancestral appendages.

Studies in evolutionary developmental biology have begun to unravel the genetic changes that fostered certain aspects of the insect body plan. For example, the *Distal-less* gene (*Dll* for short) is a highly conserved tool-kit gene (see Section 22.6) that triggers the development of appendages in all sorts of animals—the legs of chickens, the fins of fishes, the parapodia of polychaete worms, and the diverse appendages of arthropods. All arthropods also have a gene called *Ultrabithorax* (*Ubx* for short). It is one of the *Hox* genes that control the overall body plans of animals. In insects, the *Ubx* gene contains a unique mutation, not found in other arthropods, that causes the protein for which it codes to repress *Dll,* thereby preventing the formation of appendages wherever *Ubx* is expressed. And because insects express *Ubx* in their abdomen, they do not grow abdominal appendages. All other arthropods, which have the ancestral, nonrepressing form of the *Ubx* gene, have appendages in the posterior region of their body. Thus, one mutation in a *Hox*-family gene has fostered the evolution of a highly distinctive morphological trait in insects—having legs on the thorax, but not on the abdomen.

Insects exchange gases through a specialized **tracheal system,** a branching network of tubes that carry oxygen from small openings in the exoskeleton to tissues throughout the body. Insects excrete nitrogenous wastes through specialized **Malpighian tubules** that transport wastes to the digestive system for disposal with feces. Both of these organ systems are unique among animals. Insect sensory systems are diverse and complex. Besides image-forming compound eyes, many insects have light-sensing ocelli on their heads. Many also have hairs, sensitive to touch, on their antennae, legs, and other regions of the body. Chemical receptors are particularly common on the legs, allowing the identification of food. And many groups of insects have hearing organs to detect predators and potential mates. The familiar chirping of crickets, for example, is a mating call emitted by males that may repel other males and attract females.

External anatomy of a grasshopper



Internal anatomy of a female grasshopper

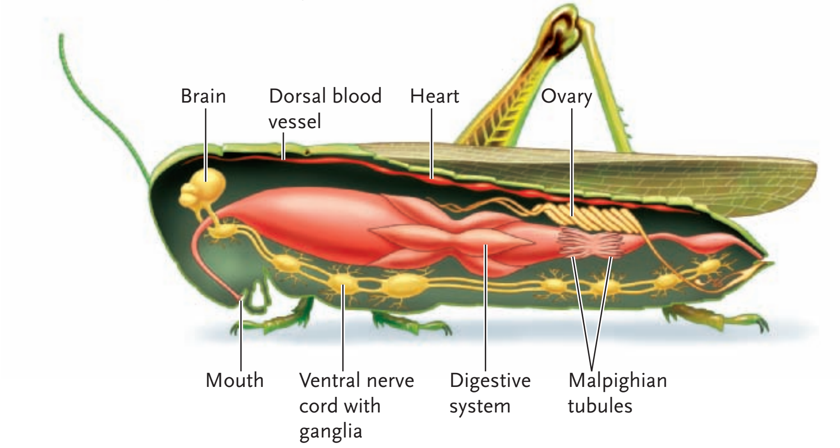


Figure 29.43
The insect body plan. Insects have distinct head, thorax, and abdomen. Of all the internal organ systems, only the dorsal blood vessel, ventral nerve cord, and some muscles are strongly segmented.

As a group, insects feed in every conceivable way and on most other organisms **(Figure 29.44).** Species that eat plants, such as grasshoppers, have a pair of rigid mandibles, which chew food before it is ingested. Behind the mandibles is a pair of maxillae, which may also aid in food acquisition. Insects also have inflexible upper and lower lips, the *labrum* and *labium,* respectively. A tonguelike structure just dorsal to the labium in chewing insects houses the openings of salivary glands. But evolution has modified this ancestral mandibulate pattern in numerous ways. In some biting

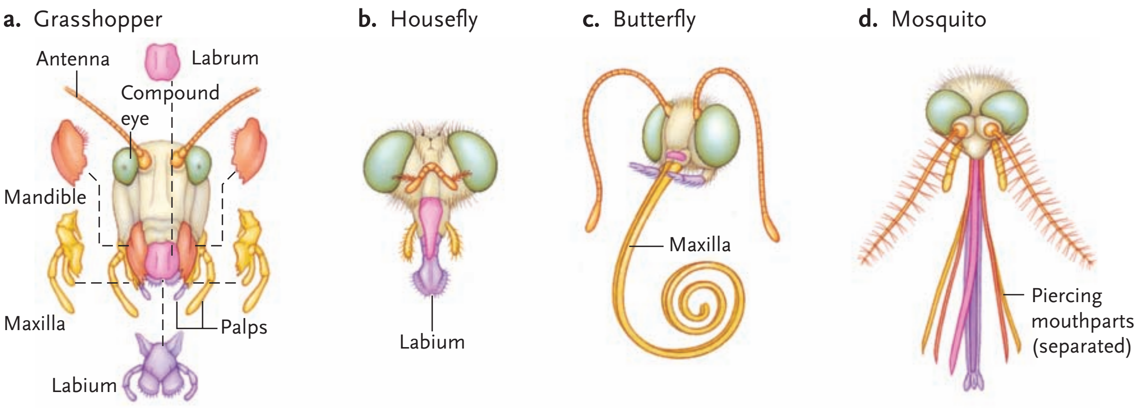


Figure 29.44 Specialized insect mouthparts. The **(a)** ancestral chewing mouthparts have been modified by evolution, allowing different insects to **(b)** sponge up food, **(c)** drink nectar, and **(d)** pierce skin to drink blood.

flies, like mosquitoes and blackflies, the mouthparts have evolved into piercing structures. In butterflies and moths the mouthparts include a long proboscis to drink nectar. And in houseflies, the mouthparts are adapted for sopping up liquid food.

After it hatches from an egg, an insect passes through a series of developmental stages called *instars*. Several hormones control development and ecdysis, which marks the passage from one instar to the next. Insects exhibit one of three basic patterns of postem-

UNANSWERED QUESTIONS

What are the evolutionary relationships among the invertebrate lineages?

If we step back from our vertebrate and terrestrial biases, invertebrates are the dominant form of life on Earth. Many students of natural history are overwhelmed by the sheer numbers of organisms that one encounters, particularly in the aquatic environment, and the challenge of categorizing them taxonomically. Sorting them out in terms of their ecological roles is equally daunting. The problem we face is that invertebrates do it all—they are predators, herbivores, parasites, detritivores, and the primary symbiotic organisms on Earth. This adaptability of form and function is a fascinating hallmark of the animal way of life, but it poses a legion of questions, many still unanswered. Recent advances in genetic technology have advanced our understanding, but there is much left to do.

In the past two decades, our ability to compare genetic information from various invertebrate groups has led to a remarkable reshuffling of the long-established categories used to classify these organisms. The first categories to be eliminated were groups based on superficial phenotypic resemblances, such as the "pseudocoelomates," which had plagued student understanding of diversity. Today, we have a much deeper knowledge of the evolutionary relationships of these organisms. Perhaps the most exciting discovery is that much of the diversity we see is not the product of slow changes in protein-coding gene sequences, but rather the result of variations in the timing and location of the expression of genes that affect development. Evo-devo, the melding of evolutionary and developmental biology—mostly made possible by intensive studies of two model invertebrates, *Caenorhabditis elegans* and *Drosophila melanogaster*—has revealed that changes in the expression of relatively simple sets of genes have brought about the myriad forms of life we see among the invertebrates. As systematists incorporate these new discoveries in their analyses, our understanding of the evolutionary relationships among the invertebrates will surely change.

What is the genetic basis of the diversity of form and function observed among invertebrates?

Because of advances in genetics research, we are on the cusp of being able to answer some fundamental questions. How does an animal's body develop either radial or bilateral symmetry? How does an organism develop a head with a concentration of nervous system tissue, and how do all the exquisite sensory systems associated with a big brain develop? From where do the respiratory pigments, which increase the capacity of the hemolymph or blood to carry oxygen, increasing an organism's capacity for activity, arise? How does the immune system develop, and what genetic change fosters the quantum leap from a nonspecific defense system to one that responds specifically to foreign invaders? More practically, are there genetic switches that we can manipulate? Can we make blood-feeding invertebrates, such as mosquitoes, or parasitic species, like tapeworms or filarial worms, innocuous? Is it possible to use genetic engineering to reduce the ability of the mosquito *Anopheles gambiae* (the "deadliest organism on Earth") to transmit malaria? Will it be possible to forestall or reverse the global decline of coral reefs, one of the richest habitats on Earth?

The answers to these and many more basic and applied questions lie within a deep knowledge and understanding of the invertebrates and the roles they play on our planet. If one looks at invertebrates as dynamic systems, as rich sources of clues to life on Earth, the questions they pose easily provide a lifetime of investigation and reward.

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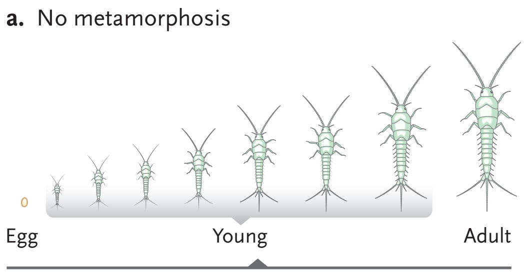
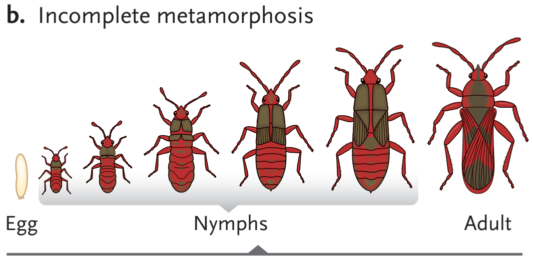
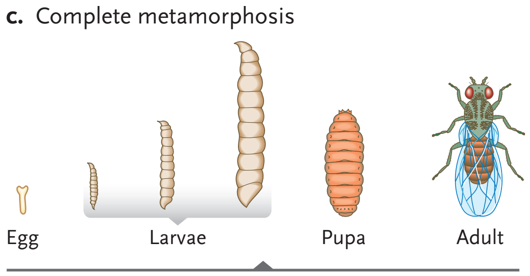


Some wingless insects, like silverfish (order Thysanura), do not undergo a dramatic change in form as they grow.



Other insects, such as true bugs (order Hemiptera), have incomplete metamorphosis; they develop from nymphs into adults with relatively minor changes in form.



Fruit flies (order Diptera) and many other insects have complete metamorphosis; they undergo a total reorganization of their internal and external anatomy when they pass through the pupal stage of the life cycle.

Figure 29.45
Patterns of postembryonic development in insects.

bryonic development **(Figure 29.45).** Primitive, wingless species simply grow and shed their exoskeleton without undergoing major changes in morphology. Other species undergo **incomplete metamorphosis;** they hatch from the egg as a *nymph,* which lacks functional wings. In many species, such as grasshoppers (order Orthoptera), the nymphs resemble the adults. In other insects, such as dragonflies (order Odonata), the aquatic nymphs are morphologically very different from the adults.

Most insects undergo **complete metamorphosis:** the larva that hatches from the egg differs greatly from the adult. Larvae and adults often occupy different habitats and consume different food. The larvae (caterpillars, grubs, or maggots) are often worm-shaped, with chewing mouthparts. They grow and molt several times, retaining their larval morphology. Before they transform into sexually mature adults, they spend a period of time as a sessile **pupa.** During this stage, the larval tissues are drastically reorganized. The adult that emerges is so different from the larva that it is often hard to believe that they are of the same species. Moths, butterflies, beetles, and flies are examples of insects with complete metamorphosis. Their larval stages specialize in feeding and growth, whereas the adults are adapted for dispersal and reproduction. In some species, the adults never feed, relying on the energy stores accumulated during the larval stage.

The 240-million-year-history of insects has been characterized by innovations in morphology, life cycle patterns, locomotion, feeding, and habitat use. Their well-developed nervous systems govern exceptionally complex patterns of behavior, including parental care, a habit that reaches its zenith in the colonial social insects, the ants, bees, and wasps (see Chapter 55). The factors that contribute to the insects' success also make them our most aggressive competitors. They destroy vegetable crops, stored food, wool, paper, and timber. They feed on blood from humans and domesticated animals, sometimes transmitting disease-causing pathogens as they do so. Nevertheless, insects are essential members of terrestrial ecological communities. Many species pollinate flowering plants, including important crops. Many others attack or parasitize species that are harmful to human activities. And most insects are a primary source of food for other animals. Some even make useful products like honey, beeswax, and silk.

In the next chapter we consider the lineage of deuterostomes, which includes the vertebrates and their closest invertebrate relatives.

STUDY BREAK

1. What part of a parasitic nematode's anatomy protects it from the digestive enzymes of its host?
2. If an arthropod's rigid exoskeleton cannot be expanded, how does the animal grow?
3. How do the number of body regions and the appendages on the head differ among the four subphyla of living arthropods?
4. How do the life stages differ between insects that have incomplete metamorphosis and those that have complete metamorphosis?

Review

Go to **ThomsonNOW**™ at www.thomsonedu.com/login to access quizzing, animations, exercises, articles, and personalized homework help.

29.1 What Is an Animal?

- Animals are eukaryotic, multicellular heterotrophs that are motile at some time in their lives.
- Animals probably arose from a colonial flagellated ancestor during the Precambrian era (Figure 29.2).

29.2 Key Innovations in Animal Evolution

- All animals except sponges have tissues, organized into either two or three tissue layers.
- Although some animals exhibit radial symmetry, most exhibit bilateral symmetry (Figure 29.3).
- Acoelomate animals have no body cavity. Pseudocoelomate animals have a body cavity between the derivatives of endoderm and mesoderm. Coelomate animals have a body cavity that is entirely lined by derivatives of mesoderm (Figure 29.4).
- Two lineages of animals differ in developmental patterns (Figure 29.5). Most protostomes exhibit spiral, determinate cleavage, and their coelom forms from a split in a solid mass of mesoderm. Most deuterostomes have radial, indeterminate cleavage, and the coelom usually forms within outpocketings of the primitive gut.
- Four animal phyla exhibit segmentation.

Animation: Types of body symmetry

Animation: Types of body cavities

Animation: Developmental differences between protostomes and deuterostomes

29.3 An Overview of Animal Phylogeny and Classification

- Analyses of molecular sequence data have refined our view of animal evolutionary history (Figure 29.6). The molecular phylogeny recognizes some major lineages that had been identified on the basis of morphological and embryological characters. Sponges are grouped in the Parazoa. All other lineages are grouped in the Eumetazoa. Among the Eumetazoa, the Radiata includes animals with two tissue layers and radial symmetry, and the Bilateria includes animals with three tissue layers and bilateral symmetry.
- Bilateria is further subdivided into Protostomia and Deuterostomia. The new phylogeny divides the Protostomia into the Lophotrochozoa and the Ecdysozoa.
- The molecular phylogeny suggests that ancestral protostomes had a coelom and that segmentation arose independently in three lineages.

29.4 Animals without Tissues: Parazoa

- Sponges (phylum Porifera) are asymmetrical animals with limited integration of cells in their bodies (Figure 29.7).
- The body of many sponges is a water-filtering system (Figure 29.8). Flagellated choanocytes draw water into the body and capture particulate food.

Animation: Body plan of a sponge

29.5 Eumetazoans with Radial Symmetry

- The two major radiate phyla, Cnidaria and Ctenophora, have two well-developed tissue layers with a gelatinous mesoglea between (Figure 29.9). They lack organ systems. All are aquatic.
- Cnidarians capture prey with tentacles and stinging nematocysts (Figures 29.10, 29.12, and 29.13). Their life cycles may include polyps, medusae, or both (Figure 29.11).
- Ctenophores use long tentacles to capture particulate food and use rows of cilia for locomotion (Figure 29.14).

Animation: Cnidarian body plans

Animation: Nematocyst action

Animation: Cnidarian life cycle

29.6 Lophotrochozoan Protostomes

- The taxon Lophotrochozoa includes eight phyla.
- Three small phyla (Ectoprocta, Brachiopoda, and Phoronida) use a lophophore to feed on particulate matter (Figure 29.15).
- Free-living flatworm species (phylum Platyhelminthes) have well-developed digestive, excretory, reproductive, and nervous systems (Figures 29.16 and 29.17). Parasitic species attach to their animal hosts with suckers or hooks (Figures 29.18 and 29.19).
- The rotifers (phylum Rotifera) are tiny and abundant inhabitants of freshwater and marine ecosystems (Figure 29.20). Movements of cilia in the corona control their locomotion and bring food to their mouths.
- The ribbon worms (phylum Nemertea) are elongate and often colorful animals with a proboscis housed in a rhynchocoel (Figure 29.21).
- Mollusks (phylum Mollusca) have fleshy bodies that are often enclosed in a hard shell. The molluskan body plan includes a head–foot, visceral mass, and mantle (Figures 29.22, 29.24–29.27).
- Segmented worms (phylum Annelida) generally exhibit segmentation of the coelom and of the muscular, circulatory, excretory, respiratory, and nervous systems. They use the coelom as a hydrostatic skeleton for locomotion (Figures 29.28–29.31).

Animation: Planarian organ systems

Animation: Blood fluke life cycle

Animation: Tapeworm life cycle

Animation: Earthworm body plan

Animation: Molluscan groups

Animation: Snail body plan

Animation: Torsion in gastropods

Animation: Clam body plan

Animation: Cuttlefish body plan

29.7 Ecdysozoan Protostomes

- The taxon Ecdysozoa includes three phyla that periodically shed their cuticle or exoskeleton.
- Roundworms (phylum Nematoda) feed on decaying organic matter or parasitize plants or animals (Figure 29.32). They move by contracting longitudinal muscles of the body wall.

- The velvet worms (phylum Onychophora) have segmented bodies and unjointed legs (Figure 29.33). Some species bear live young, which develop in a uterus.
- The segmented bodies of the arthropods (phylum Arthropoda) have specialized appendages for feeding, locomotion, or reproduction. Arthropods shed their exoskeleton as they grow or enter a new stage of the life cycle (Figure 29.34). They have an open circulatory system, a complex nervous system, and, in some groups, highly specialized respiratory and excretory systems.
- Arthropods are divided into five subphyla. The extinct trilobites (subphylum Trilobita), with three-lobed bodies and relatively undifferentiated appendages, were abundant in Paleozoic seas (Figure 29.35). Chelicerates have a cephalothorax and abdomen; appendages on the head serve as pincers or fangs and pedipalps (Figures 29.36 and 29.37). Crustaceans have a carapace that covers the cephalothorax as well as highly modified appendages, including antennae and mandibles (Figures 29.38–29.40). Myriapods have a head and an elongate, segmented trunk (Figure 29.41). Hexapods have three body regions, three pairs of walking legs on the thorax, and three pairs of feeding appendages on the head (Figures 29.42–29.44). Insects exhibit three patterns of postembryonic development (Figure 29.45).

Animation: Roundworm body plan

Animation: Crab life cycle

Animation: Chelicerates

Animation: Insect head parts

Animation: Insect development

Questions

Self-Test Questions

1. Which of the following characteristics is *not* typical of most animals?
   a. heterotrophic
   b. sessile
   c. bilaterally symmetrical
   d. multicellular
   e. motile at some stage of life cycle
2. A body cavity that separates the digestive system from the body wall but is *not* completely lined with mesoderm is called a:
   a. schizocoelom.
   b. mesentery.
   c. peritoneum.
   d. pseudocoelom.
   e. hydrostatic skeleton.
3. Protostomes and deuterostomes typically differ in:
   a. their patterns of body symmetry.
   b. the number of germ layers during development.
   c. their cleavage patterns.
   d. the size of their sperm.
   e. the size of their digestive systems.
4. The nematocysts of cnidarians are used primarily for:
   a. capturing prey.
   b. detecting light and dark.
   c. courtship.
   d. sensing chemicals.
   e. gas exchange.
5. Which organ system is absent in flatworms (phylum Platyhelminthes)?
   a. nervous system
   b. reproductive system
   c. circulatory system
   d. digestive system
   e. excretory system
6. Which part of a mollusk secretes the shell?
   a. visceral mass
   b. radula
   c. trochophore
   d. head–foot
   e. mantle
7. What is the major morphological innovation seen in annelid worms?
   a. a complete digestive system
   b. image-forming eyes
   c. a respiratory system
   d. an open circulatory system
   e. body segmentation
8. Which phylum includes the most abundant animals in soil?
   a. Nematoda
   b. Rotifera
   c. Mollusca
   d. Annelida
   e. Brachiopoda
9. Which body region of an insect bears the walking legs?
   a. head
   b. carapace
   c. abdomen
   d. thorax
   e. trunk
10. Ecdysis refers to a process in which:
    a. bivalves use siphons to pass water across their gills.
    b. arthropods shed their old exoskeletons.
    c. cnidarians build skeletons of calcium carbonate.
    d. rotifers produce unfertilized eggs.
    e. squids escape from predators in a cloud of ink.

Questions for Discussion

1. Many invertebrate species are hermaphroditic. What selective advantages might this characteristic offer? In what kinds of environments might it be most useful?
2. People who eat raw clams and oysters harvested from sewage-polluted waters often develop mild to severe gastrointestinal infections. These mollusks are suspension feeders. Develop a hypothesis about why people who eat them raw may be at risk.
3. On a voyage to the ocean bottom, a biologist discovers a worm that appears to be new to science. What characteristics of this animal should the biologist examine to determine whether or not she has discovered a previously undescribed phylum?
4. The phylogenetic tree and classification based on molecular sequence data suggests that segmentation evolved independently in Lophotrochozoa (phylum Annelida), Ecdysozoa (phyla Onychophora and Arthropoda), and Deuterostomia (phylum Chordata). What morphological evidence would you try to collect to confirm that segmentation is not homologous in these three groups?
5. What are the relative advantages and disadvantages of radially symmetrical and bilaterally symmetrical body plans?

Experimental Analysis

Design an experiment to test the hypothesis that the cuticle of parasitic nematodes protects them from the acids and enzymes present in the digestive systems of their hosts. Your design must include both experimental and control treatments.

Evolution Link

Many insects have a larval stage that is morphologically different from the adult and that feeds on different foods. What selection pressures may have fostered the evolution of a life cycle with such distinctive life stages? Your answer should address the different biological activities that characterize each life cycle stage.

How Would You Vote?

Cone snails are diverse, but most kinds have a limited geographic range, which makes them highly vulnerable to extinction. We do not know how many are harvested, because no one monitors the trade. Should the United States push to extend regulations on trade in endangered species to cover any species captured from the wild? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.