Part **XII**

Animal Diversity

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44

The Noncoelomate Animals

Concept Outline

44.1 Animals are multicellular heterotrophs without cell walls.

Some General Features of Animals. Animals lack cell walls and move more rapidly and in more complex ways than other organisms. The animal kingdom is divided into animals without symmetry and tissues, and animals with symmetry and tissues.

Five Key Transitions in Body Plan. Over the course of animal evolution, the animal body plan has undergone many changes, five of them significant.

44.2 The simplest animals are not bilaterally symmetrical.

Parazoa. Sponges are the most primitive animals, without either tissues or, for the most part, symmetry.

Eumetazoa: The Radiata. Cnidarians and ctenophorans have distinct tissues and radial symmetry.

44.3 Acoelomates are solid worms that lack a body cavity.

Eumetazoa: The Bilaterian Acoelomates. Flatworms are the simplest bilaterally symmetrical animals; they lack a body cavity, but possess true organs.

44.4 Pseudocoelomates have a simple body cavity.

The Pseudocoelomates. Nematodes and rotifers possess a simple body cavity.

44.5 The coming revolution in animal taxonomy will likely alter traditional phylogenies.

Reevaluating How the Animal Body Plan Evolved. The use of molecular data will most likely generate changes to traditional animal phylogenies.

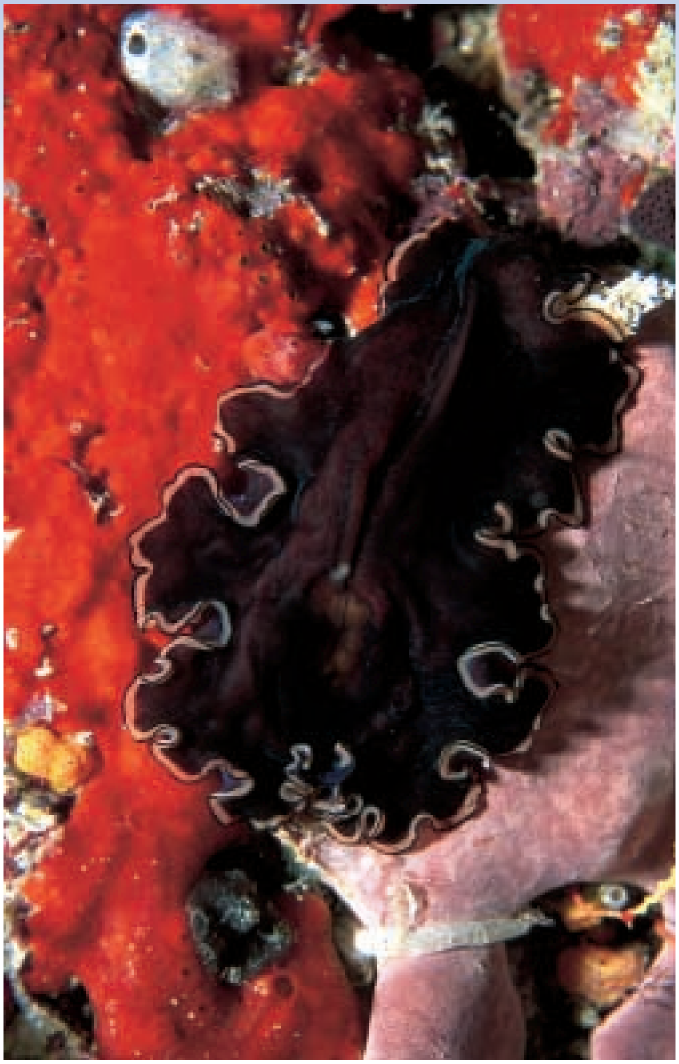


FIGURE 44.1
A noncoelomate: a marine flatworm. Some of the earliest invertebrates to evolve, marine flatworms possess internal organs but lack a true cavity called a coelom.

We will now explore the great diversity of animals, the result of a long evolutionary history. Animals, constituting millions of species, are among the most abundant living things. Found in every conceivable habitat, they bewilder us with their diversity. We will start with the simplest members of the animal kingdom—sponges, jellyfish, and simple worms. These animals lack a body cavity called a coelom, and are thus called noncoelomates (figure 44.1). The major organization of the animal body first evolved in these animals, a basic body plan upon which all the rest of animal evolution has depended. In chapters 45 through 48, we will consider the more complex animals. Despite their great diversity, you will see that all animals have much in common.

44.1 Animals are multicellular heterotrophs without cell walls.

Some General Features of Animals

Animals are the eaters or consumers of the earth. They are heterotrophs and depend directly or indirectly on plants, photosynthetic protists (algae), or autotrophic bacteria for nourishment. Animals are able to move from place to place in search of food. In most, ingestion of food is followed by digestion in an internal cavity.

Multicellular Heterotrophs. All animals are multicellular heterotrophs. The unicellular heterotrophic organisms called Protozoa, which were at one time regarded as simple animals, are now considered to be members of the kingdom Protista, the large and diverse group we discussed in chapter 35.

Diverse in Form. Almost all animals (99%) are **invertebrates,** lacking a backbone. Of the estimated 10 million living animal species, only 42,500 have a backbone and are referred to as **vertebrates.** Animals are very diverse in form, ranging in size from ones too small to see with the naked eye to enormous whales and giant squids. The animal kingdom includes about 35 phyla, most of which occur in the sea. Far fewer phyla occur in fresh water and fewer still occur on land. Members of three phyla, Arthropoda (spiders and insects), Mollusca (snails), and Chordata (vertebrates), dominate animal life on land.

No Cell Walls. Animal cells are distinct among multicellular organisms because they lack rigid cell walls and are usually quite flexible. The cells of all animals but sponges are organized into structural and functional units called **tissues,** collections of cells that have joined together and are specialized to perform a specific function; muscles and nerves are tissues types, for example.

Active Movement. The ability of animals to move more rapidly and in more complex ways than members of other kingdoms is perhaps their most striking characteristic and one that is directly related to the flexibility of their cells and the evolution of nerve and muscle tissues. A remarkable form of movement unique to animals is flying, an ability that is well developed among both insects and vertebrates. Among vertebrates, birds, bats, and pterosaurs (now-extinct flying reptiles) were or are all strong fliers. The only terrestrial vertebrate group never to have had flying representatives is amphibians.

Sexual Reproduction. Most animals reproduce sexually. Animal eggs, which are nonmotile, are much larger than the small, usually flagellated sperm. In animals, cells formed in meiosis function directly as gametes. The haploid cells do not divide by mitosis first, as they do in plants and fungi, but rather fuse directly with each other to form the zygote. Consequently, with a few exceptions, there is no counterpart among animals to the alternation of haploid (gametophyte) and diploid (sporophyte) generations characteristic of plants (see chapter 32).

Embryonic Development. Most animals have a similar pattern of embryonic development. The zygote first undergoes a series of mitotic divisions, called *cleavage*, and becomes a solid ball of cells, the **morula,** then a hollow ball of cells, the **blastula.** In most animals, the blastula folds inward at one point to form a hollow sac with an opening at one end called the **blastopore.** An embryo at this stage is called a **gastrula.** The subsequent growth and movement of the cells of the gastrula produce the digestive system, also called the gut or intestine. The details of embryonic development differ widely from one phylum of animals to another and often provide important clues to the evolutionary relationships among them.

The Classification of Animals

Two subkingdoms are generally recognized within the kingdom Animalia: **Parazoa**—animals that for the most part lack a definite symmetry and possess neither tissues nor organs, mostly comprised of the sponges, phylum Porifera; and **Eumetazoa**—animals that have a definite shape and symmetry and, in most cases, tissues organized into organs and organ systems. Although very different in structure, both types evolved from a common ancestral form (figure 44.2) and possess the most fundamental animal traits.

All eumetazoans form distinct embryonic layers during development that differentiate into the tissues of the adult animal. Eumetazoans of the subgroup Radiata (having radial symmetry) have two layers, an outer **ectoderm** and an inner **endoderm,** and thus are called **diploblastic.** All other eumetazoans, the Bilateria (having bilateral symmetry), are **triploblastic** and produce a third layer, the **mesoderm,** between the ectoderm and endoderm. No such layers are present in sponges.

The major phyla of animals are listed in table 44.1. The simplest invertebrates make up about 14 phyla. In this chapter, we will discuss 8 of these 14 phyla and focus in detail on 4 major phyla: phylum Porifera (sponges), which lacks any tissue organization; phylum Cnidaria (radially symmetrical jellyfish, hydroids, sea anemones, and corals); phylum Platyhelminthes (bilaterally symmetrical flatworms); and phylum Nematoda (nematodes), a phylum that includes both free-living and parasitic roundworms.

Animals are complex multicellular organisms typically characterized by high mobility and heterotrophy. Most animals also possess internal tissues and organs and reproduce sexually.

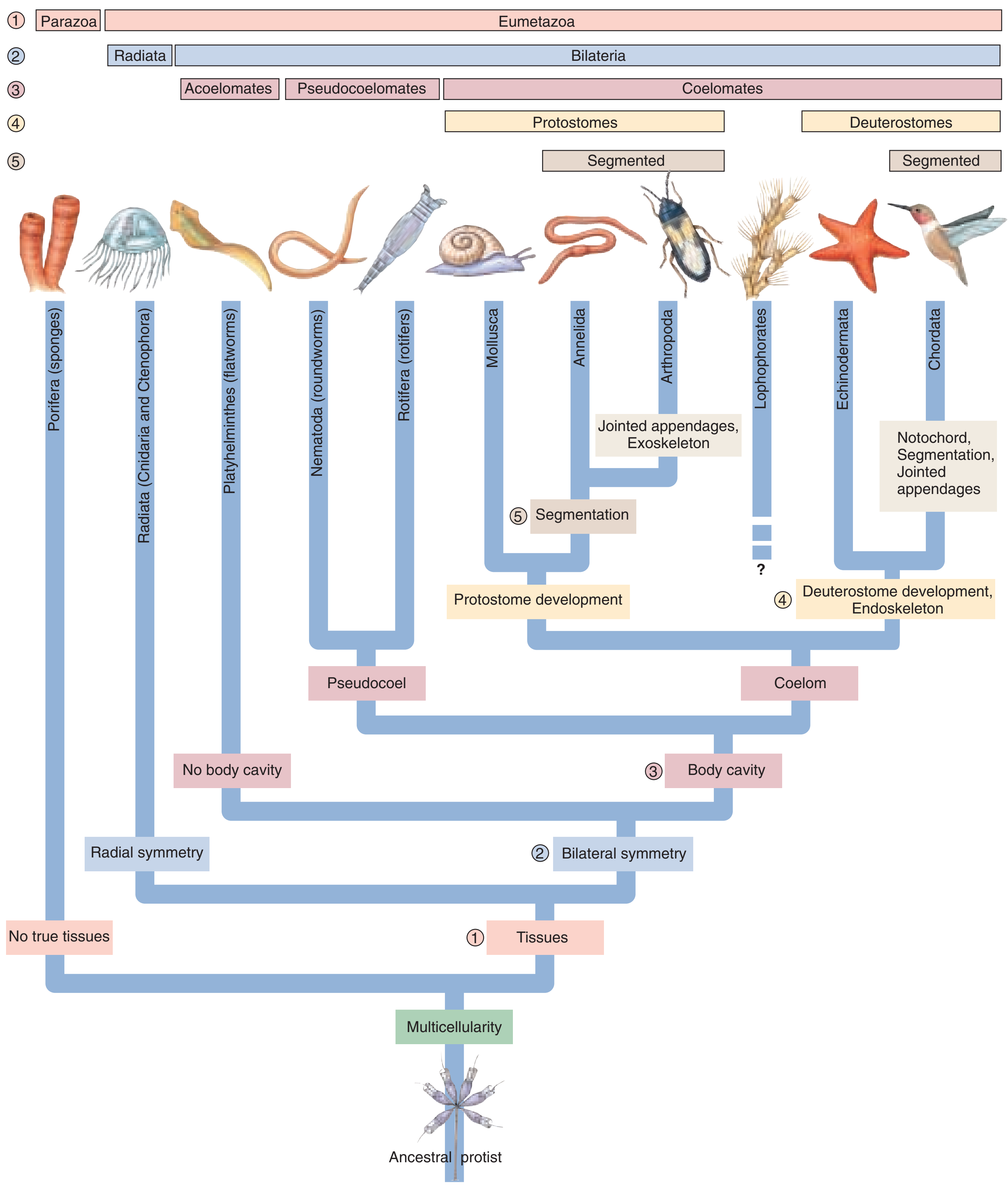


FIGURE 44.2
A possible phylogeny of the major groups of the kingdom Animalia. Transitions in the animal body plan are identified along the branches; the five key advances are the evolution of tissues, bilateral symmetry, a body cavity, protostome and deuterostome development, and segmentation.

Table 44.1 The Major Animal Phyla

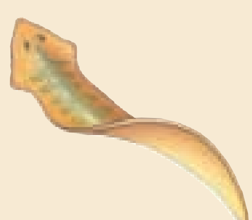
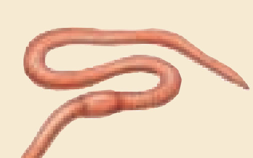
Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Arthropoda (arthropods)	Beetles, other insects, crabs, spiders		Most successful of all animal phyla; chitinous exoskeleton covering segmented bodies with paired, jointed appendages; many insect groups have wings	1,000,000
Mollusca (mollusks)	Snails, oysters, octopuses, nudibranchs		Soft-bodied coelomates whose bodies are divided into three parts: head-foot, visceral mass, and mantle; many have shells; almost all possess a unique rasping tongue, called a radula; 35,000 species are terrestrial	110,000
Chordata (chordates)	Mammals, fish, reptiles, birds, amphibians		Segmented coelomates with a notochord; possess a dorsal nerve cord, pharyngeal slits, and a tail at some stage of life; in vertebrates, the notochord is replaced during development by the spinal column; 20,000 species are terrestrial	42,500
Platyhelminthes (flatworms)	*Planaria*, tapeworms, liver flukes		Solid, unsegmented, bilaterally symmetrical worms; no body cavity; digestive cavity, if present, has only one opening	20,000
Nematoda (roundworms)	*Ascaris*, pinworms, hookworms, *Filaria*		Pseudocoelomate, unsegmented, bilaterally symmetrical worms; tubular digestive tract passing from mouth to anus; tiny; without cilia; live in great numbers in soil and aquatic sediments; some are important animal parasites	12,000+
Annelida (segmented worms)	Earthworms, polychaetes, beach tube worms, leeches		Coelomate, serially segmented, bilaterally symmetrical worms; complete digestive tract; most have bristles called setae on each segment that anchor them during crawling	12,000

Table 44.1 The Major Animal Phyla (continued)

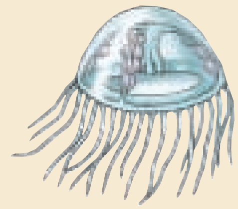
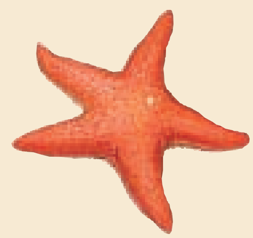
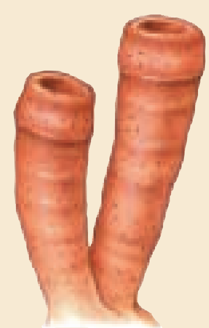
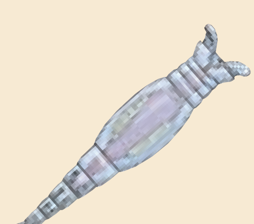
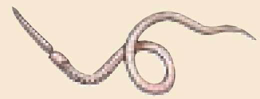
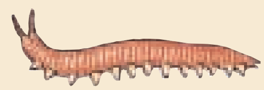
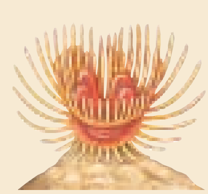
Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Cnidaria (cnidarians)	Jellyfish, hydra, corals, sea anemones		Soft, gelatinous, radially symmetrical bodies whose digestive cavity has a single opening; possess tentacles armed with stinging cells called cnidocytes that shoot sharp harpoons called nematocysts; almost entirely marine	10,000
Echinodermata (echinoderms)	Sea stars, sea urchins, sand dollars, sea cucumbers		Deuterostomes with radially symmetrical adult bodies; endoskeleton of calcium plates; five-part body plan and unique water vascular system with tube feet; able to regenerate lost body parts; marine	6,000
Porifera (sponges)	Barrel sponges, boring sponges, basket sponges, vase sponges		Asymmetrical bodies without distinct tissues or organs; saclike body consists of two layers breached by many pores; internal cavity lined with food-filtering cells called choanocytes; most marine (150 species live in fresh water)	5,150
Bryozoa (moss animals)	*Bowerbankia*, *Plumatella*, sea mats, sea moss		Microscopic, aquatic deuterostomes that form branching colonies, possess circular or U-shaped row of ciliated tentacles for feeding called a lophophore that usually protrudes through pores in a hard exoskeleton; also called Ectoprocta because the anus or proct is external to the lophophore; marine or freshwater	4,000
Rotifera (wheel animals)	Rotifers		Small, aquatic pseudocoelomates with a crown of cilia around the mouth resembling a wheel; almost all live in fresh water	2,000

Table 44.1 The Major Animal Phyla (continued)				
Phylum	**Typical Examples**		**Key Characteristics**	**Approximate Number of Named Species**
Five phyla of minor worms	Velvet worms, acorn worms, arrow worms, giant tube worms	 	**Chaetognatha** (arrow worms): coelomate deuterostomes; bilaterally symmetrical; large eyes (some) and powerful jaws **Hemichordata** (acorn worms): marine worms with dorsal *and* ventral nerve cords **Onychophora** (velvet worms): protostomes with a chitinous exoskeleton; evolutionary relics **Pogonophora** (tube worms): sessile deep-sea worms with long tentacles; live within chitinous tubes attached to the ocean floor **Nemertea** (ribbon worms): acoelomate, bilaterally symmetrical marine worms with long extendable proboscis	980
Brachiopoda (lamp shells)	*Lingula*		Like bryozoans, possess a lophophore, but within two clamlike shells; more than 30,000 species known as fossils	250
Ctenophora (sea walnuts)	Comb jellies, sea walnuts		Gelatinous, almost transparent, often bioluminescent marine animals; eight bands of cilia; largest animals that use cilia for locomotion; complete digestive tract with anal pore	100
Phoronida (phoronids)	*Phoronis*		Lophophorate tube worms; often live in dense populations; unique U-shaped gut, instead of the straight digestive tube of other tube worms	12
Loricifera (loriciferans)	*Nanaloricus mysticus*		Tiny, bilaterally symmetrical, marine pseudocoelomates that live in spaces between grains of sand; mouthparts include a unique flexible tube; a recently discovered animal phylum (1983)	6

Five Key Transitions in Body Plan

1. Evolution of Tissues

The simplest animals, the Parazoa, lack both defined tissues and organs. Characterized by the sponges, these animals exist as aggregates of cells with minimal intercellular coordination. All other animals, the Eumetazoa, have distinct tissues with highly specialized cells. The evolution of tissues is the first key transition in the animal body plan.

2. Evolution of Bilateral Symmetry

Sponges also lack any definite symmetry, growing asymmetrically as irregular masses. Virtually all other animals have a definite shape and symmetry that can be defined along an imaginary axis drawn through the animal's body. Animals with symmetry belong to either the Radiata, animals with radial symmetry, or the Bilateria, animals with bilateral symmetry.

Radial Symmetry. Symmetrical bodies first evolved in marine animals belonging to two phyla: Cnidaria (jellyfish, sea anemones, and corals) and Ctenophora (comb jellies). The bodies of members of these two phyla, the Radiata, exhibit **radial symmetry,** a body design in which the parts of the body are arranged around a central axis in such a way that any plane passing through the central axis divides the organism into halves that are approximate mirror images (figure 44.3*a*).

Bilateral Symmetry. The bodies of all other animals, the Bilateria, are marked by a fundamental **bilateral symmetry,** a body design in which the body has a right and a left half that are mirror images of each other (figure 44.3*b*). A bilaterally symmetrical body plan has a top and a bottom, better known respectively as the *dorsal* and *ventral* portions of the body. It also has a front, or *anterior* end, and a back, or *posterior* end. In some higher animals like echinoderms (starfish), the adults are radially symmetrical, but even in them the larvae are bilaterally symmetrical.

Bilateral symmetry constitutes the second major evolutionary advance in the animal body plan. This unique form of organization allows parts of the body to evolve in different ways, permitting different organs to be located in different parts of the body. Also, bilaterally symmetrical animals move from place to place more efficiently than radially symmetrical ones, which, in general, lead a sessile or passively floating existence. Due to their increased mobility, bilaterally symmetrical animals are efficient in seeking food, locating mates, and avoiding predators.

During the early evolution of bilaterally symmetrical animals, structures that were important to the organism in monitoring its environment, and thereby capturing prey or avoiding enemies, came to be grouped at the anterior end. Other functions tended to be located farther back in the body. The number and complexity of sense organs are much greater in bilaterally symmetrical animals than they are in radially symmetrical ones.

Much of the nervous system in bilaterally symmetrical animals is in the form of major longitudinal nerve cords. In a very early evolutionary advance, nerve cells became grouped around the anterior end of the body. These nerve cells probably first functioned mainly to transmit impulses from the anterior sense organs to the rest of the nervous system. This trend ultimately led to the evolution of a definite head and brain area, a process called **cephalization,** as well as to the increasing dominance and specialization of these organs in the more advanced animal phyla.

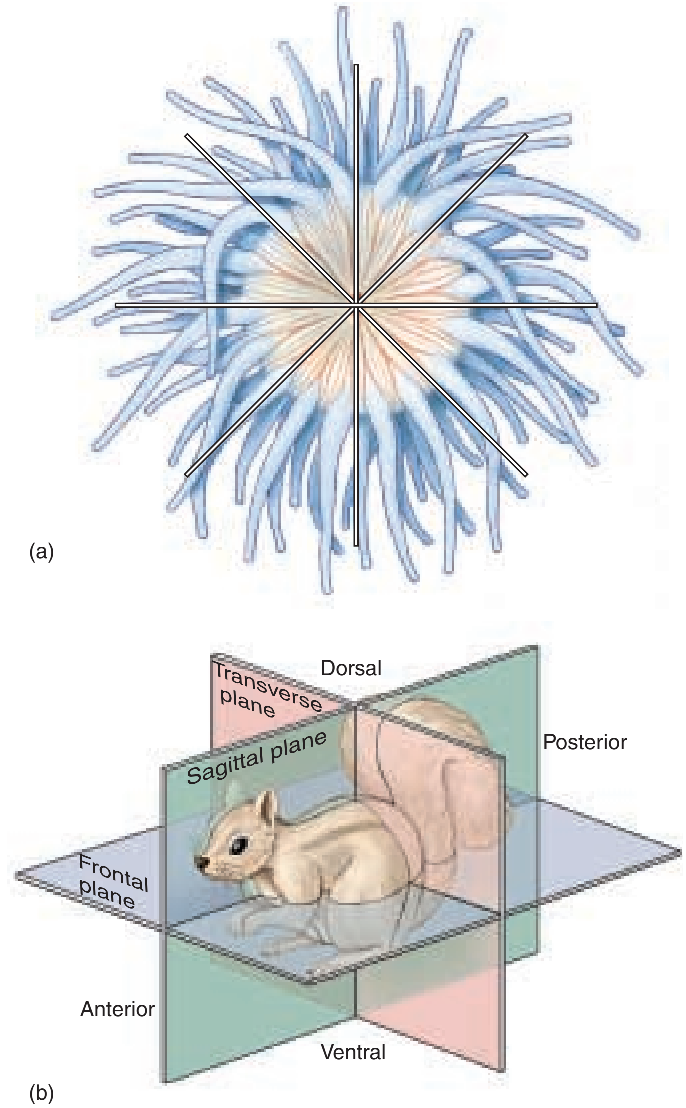


FIGURE 44.3
A comparison of radial and bilateral symmetry. (*a*) Radially symmetrical animals, such as this sea anemone, can be bisected into equal halves in any two-dimensional plane. (*b*) Bilaterally symmetrical animals, such as this squirrel, can only be bisected into equal halves in one plane (the sagittal plane).

3. Evolution of a Body Cavity

A third key transition in the evolution of the animal body plan was the evolution of the body cavity. The evolution of efficient organ systems within the animal body was not possible until a body cavity evolved for supporting organs, distributing materials, and fostering complex developmental interactions.

The presence of a body cavity allows the digestive tract to be larger and longer. This longer passage allows for storage of undigested food, longer exposure to enzymes for more complete digestion, and even storage and final processing of food remnants. Such an arrangement allows an animal to eat a great deal when it is safe to do so and then to hide during the digestive process, thus limiting the animal's exposure to predators. The tube within the body cavity architecture is also more flexible, thus allowing the animal greater freedom to move.

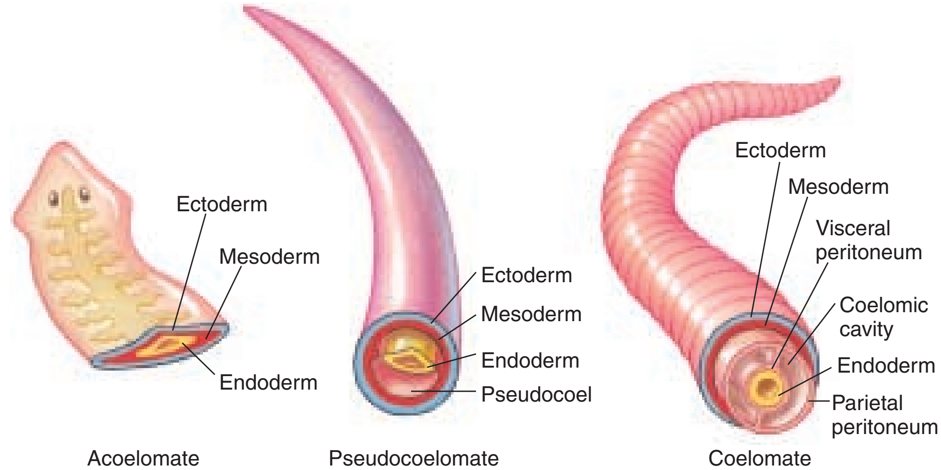


FIGURE 44.4
Three body plans for bilaterally symmetrical animals.

An internal body cavity also provides space within which the gonads (ovaries and testes) can expand, allowing the accumulation of large numbers of eggs and sperm. Such storage capacity allows the diverse modifications of breeding strategy that characterize the more advanced phyla of animals. Furthermore, large numbers of gametes can be stored and released when the conditions are as favorable as possible for the survival of the young animals.

Kinds of Body Cavities. Three basic kinds of body plans evolved in the Bilateria. **Acoelomates** have no body cavity. **Pseudocoelomates** have a body cavity called the **pseudocoel** located between the mesoderm and endoderm. A third way of organizing the body is one in which the fluid-filled body cavity develops not between endoderm and mesoderm, but rather entirely within the mesoderm. Such a body cavity is called a **coelom,** and animals that possess such a cavity are called **coelomates.** In coelomates, the gut is suspended, along with other organ systems of the animal, within the coelom; the coelom, in turn, is surrounded by a layer of epithelial cells entirely derived from the mesoderm. The portion of the epithelium that lines the outer wall of the coelom is called the **parietal peritoneum,** and the portion that covers the internal organs suspended within the cavity is called the **visceral peritoneum** (figure 44.4).

The development of the coelom poses a problem—circulation—solved in pseudocoelomates by churning the fluid within the body cavity. In coelomates, the gut is again surrounded by tissue that presents a barrier to diffusion, just as it was in solid worms. This problem is solved among coelomates by the development of a **circulatory system,** a network of vessels that carries fluids to parts of the body. The circulating fluid, or blood, carries nutrients and oxygen to the tissues and removes wastes and carbon dioxide. Blood is usually pushed through the circulatory system by contraction of one or more muscular hearts. In an **open circulatory system,** the blood passes from vessels into sinuses, mixes with body fluid, and then reenters the vessels later in another location. In a **closed circulatory system,** the blood is physically separated from other body fluids and can be separately controlled. Also, blood moves through a closed circulatory system faster and more efficiently than it does through an open system.

The evolutionary relationship among coelomates, pseudocoelomates, and acoelomates is not clear. Acoelomates, for example, could have given rise to coelomates, but scientists also cannot rule out the possibility that acoelomates were derived from coelomates. The different phyla of pseudocoelomates form two groups that do not appear to be closely related.

Advantages of a Coelom. What is the functional difference between a pseudocoel and a coelom? The answer has to do with the nature of animal embryonic development. In animals, development of specialized tissues involves a process called **primary induction** in which one of the three primary tissues (endoderm, mesoderm, and ectoderm) interacts with another. The interaction requires physical contact. A major advantage of the coelomate body plan is that it allows contact between mesoderm and endoderm, so that primary induction can occur during development. For example, contact between mesoderm and endoderm permits localized portions of the digestive tract to develop into complex, highly specialized regions like the stomach. In pseudocoelomates, mesoderm and endoderm are separated by the body cavity, limiting developmental interactions between these tissues that ultimately limits tissue specialization and development.

4. The Evolution of Protostome and Deuterostome Development

Two outwardly dissimilar large phyla, Echinodermata (starfish) and Chordata (vertebrates), together with two smaller phyla, have a series of key embryological features different from those shared by the other animal phyla. Because it is extremely unlikely that these features evolved more than once, it is believed that these four phyla share a common ancestry. They are the members of a group called the **deuterostomes.** Members of the other coelomate animal phyla are called **protostomes.** Deuterostomes evolved from protostomes more than 630 million years ago.

Deuterostomes, like protostomes, are coelomates. They differ fundamentally from protostomes, however, in the way in which the embryo grows. Early in embryonic growth, when the embryo is a hollow ball of cells, a portion invaginates inward to form an opening called the blastopore. The blastopore of a protostome becomes the animal's mouth, and the anus develops at the other end. In a deuterostome, by contrast, the blastopore becomes the animal's anus, and the mouth develops at the other end (figure 44.5).

Deuterostomes differ in many other aspects of embryo growth, including the plane in which the cells divide. Perhaps most importantly, the cells that make up an embryonic protostome each contain a different portion of the regulatory signals present in the egg, so no one cell of the embryo (or adult) can develop into a complete organism. In marked contrast, any of the cells of a deuterostome can develop into a complete organism.

5. The Evolution of Segmentation

The fifth key transition in the animal body plan involved the subdivision of the body into **segments.** Just as it is efficient for workers to construct a tunnel from a series of identical prefabricated parts, so segmented animals are "assembled" from a succession of identical segments. During the animal's early development, these segments become most obvious in the mesoderm but later are reflected in the ectoderm and endoderm as well. Two advantages result from early embryonic segmentation:

1. In annelids and other highly segmented animals, each segment may go on to develop a more or less complete set of adult organ systems. Damage to any one segment need not be fatal to the individual because the other segments duplicate that segment's functions.
2. Locomotion is far more effective when individual segments can move independently because the animal as a whole has more flexibility of movement. Because the separations isolate each segment into an individual skeletal unit, each is able to contract or expand autonomously in response to changes in hydrostatic pressure. Therefore, a long body can move in ways that are often quite complex.

Segmentation, also referred to as *metamerism,* underlies the organization of all advanced animal body plans. In some adult arthropods, the segments are fused, but segmentation is usually apparent in their embryological development. In vertebrates, the backbone and muscular areas are segmented, although segmentation is often disguised in the adult form. True segmentation is found in only three phyla: the annelids, the arthropods, and the chordates, although this trend is evident in many phyla.

Five key transitions in body design are responsible for most of the differences we see among the major animal phyla: the evolution of (1) tissues, (2) bilateral symmetry, (3) a body cavity, (4) protostome and deuterostome development, and (5) segmentation.

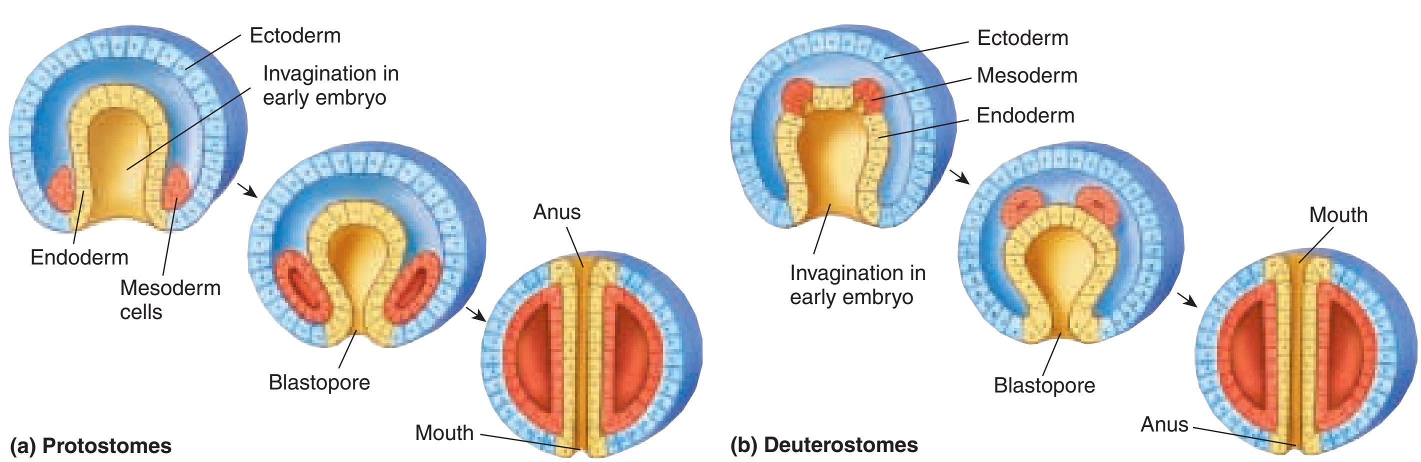
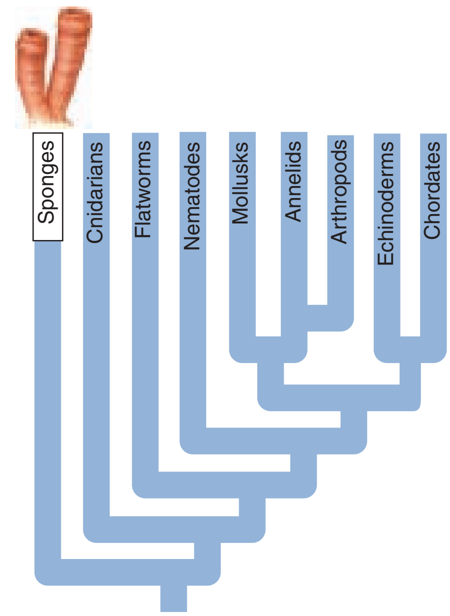


FIGURE 44.5
The fate of the blastopore. (*a*) In protostomes, the blastopore becomes the animal's mouth. (*b*) In deuterostomes, the blastopore becomes the animal's anus.

44.2 The simplest animals are not bilaterally symmetrical.

Parazoa

The sponges are Parazoans, animals that lack tissues and organs and a definite symmetry. However, sponges, like all animals, have true, complex *multicellularity*, unlike their protistan ancestors. The body of a sponge contains several distinctly different types of cells whose activities are loosely coordinated with one another. As we will see, the coordination between cell types in the eumetazoans increases and becomes quite complex.



The Sponges

There are perhaps 5000 species of marine sponges, phylum Porifera, and about 150 species that live in fresh water. In the sea, sponges are abundant at all depths. Although some sponges are tiny, no more than a few millimeters across, some, like the loggerhead sponges, may reach 2 meters or more in diameter. A few small ones are radially symmetrical, but most members of this phylum completely lack symmetry. Many sponges are colonial. Some have a low and encrusting form, while others may be erect and lobed, sometimes in complex patterns. Although larval sponges are free-swimming, adults are **sessile,** or anchored in place to submerged objects.

Sponges, like all animals, are composed of multiple cell types (see figure 44.7), but there is relatively little coordination among sponge cells. A sponge seems to be little more than a mass of cells embedded in a gelatinous matrix, but these cells recognize one another with a high degree of fidelity and are specialized for different functions of the body.

The basic structure of a sponge can best be understood by examining the form of a young individual. A small, anatomically simple sponge first attaches to a substrate and then grows into a vaselike shape. The walls of the "vase" have three functional layers. First, facing into the internal cavity are specialized flagellated cells called **choanocytes,** or collar cells. These cells line either the entire body cavity or, in many large and more complex sponges, specialized chambers. Second, the bodies of sponges are bounded by an outer epithelial layer consisting of flattened cells somewhat like those that make up the epithelia, or outer layers, of other animal phyla. Some portions of this layer contract when touched or exposed to appropriate chemical stimuli, and this contraction may cause some of the pores to close. Third, between these two layers, sponges consist mainly of a gelatinous, protein-rich matrix called the **mesohyl,** within which various types of amoeboid cells occur. In addition, many kinds of sponges have minute needles of calcium carbonate or silica known as **spicules,** or fibers of a tough protein called **spongin,** or both, within this matrix. Spicules and spongin strengthen the bodies of the sponges in which they occur. A spongin skeleton is the model for the bathtub sponge, once the skeleton of a real animal, but now largely known from its cellulose and plastic mimics.

Sponges feed in a unique way. The beating of flagella that line the inside of the sponge draws water in through numerous small pores; the name of the phylum, Porifera, refers to this system of pores. Plankton and other small organisms are filtered from the water, which flows through passageways and eventually is forced out through an **osculum,** a specialized, larger pore (figure 44.6).

FIGURE 44.6
Aplysina longissima. This beautiful, bright blue and yellow elongated sponge is found on deep regions of coral reefs. The oscula are ringed with yellow.

Choanocytes. Each choanocyte closely resembles a protist with a single flagellum (figure 44.7), a similarity that reflects its evolutionary derivation. The beating of the flagella of the many choanocytes that line the body cavity draws water in through the pores and through the sponge, thus bringing in food and oxygen and expelling wastes. Each choanocyte flagellum beats independently, and the pressure they create collectively in the cavity forces water out of the osculum. In some sponges, the inner wall of the body cavity is highly convoluted, increasing the surface area and, therefore, the number of flagella that can drive the water. In such a sponge, 1 cubic centimeter of sponge can propel more than 20 liters of water a day.

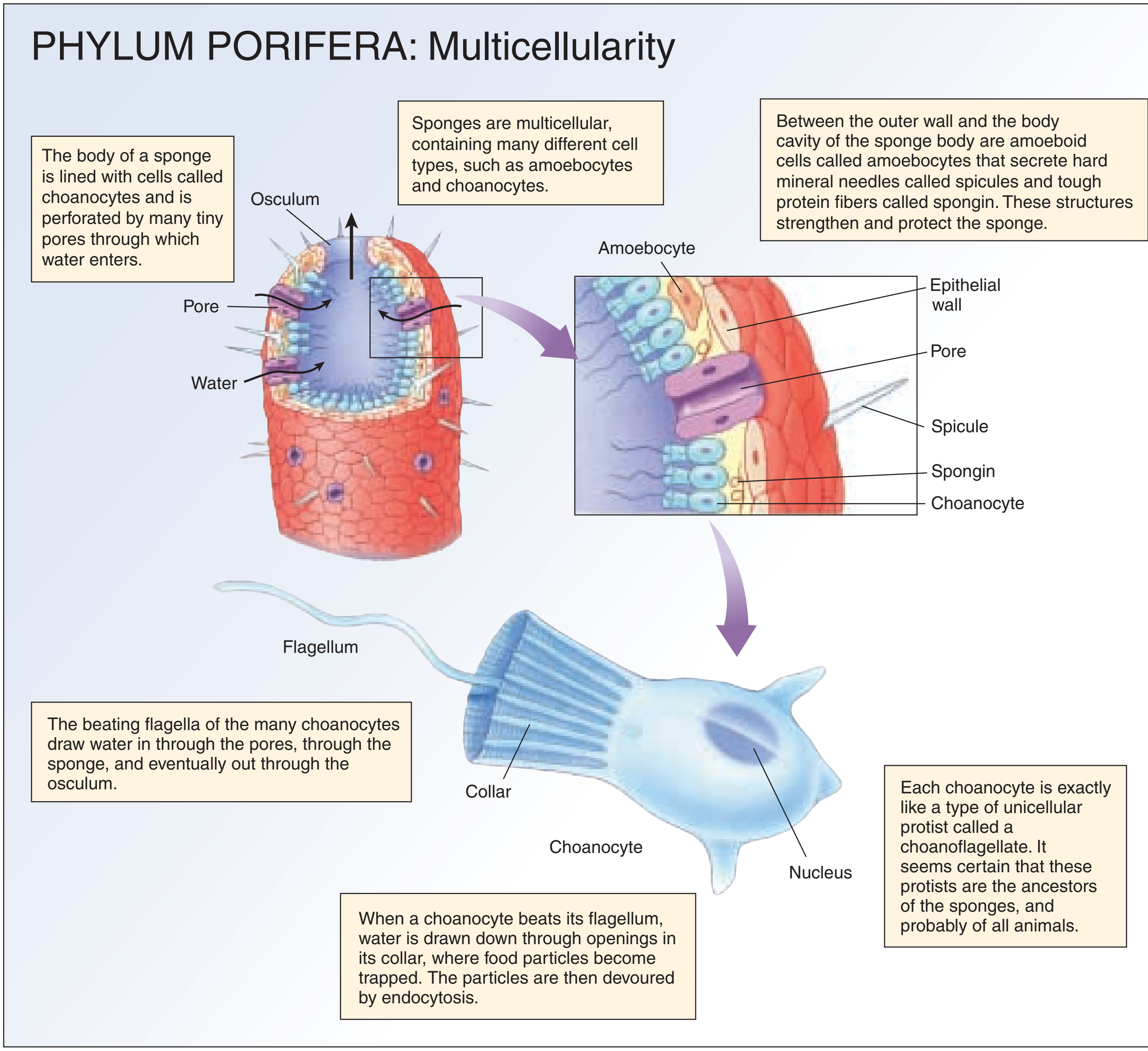


FIGURE 44.7
The body of a sponge is multicellular. The first evolutionary advance seen in animals is complex multicellularity, in which individuals are composed of many highly specialized kinds of cells.

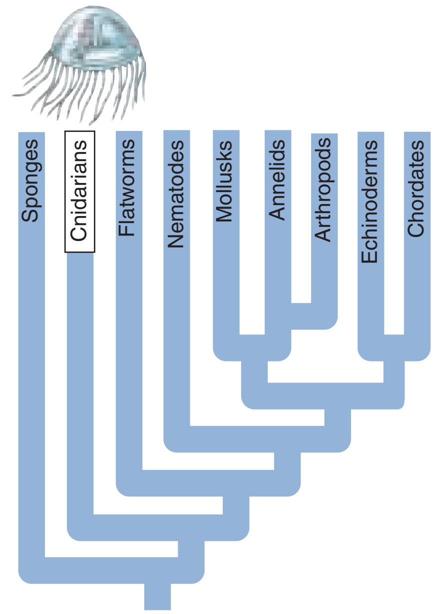
Reproduction in Sponges. Some sponges will re-form themselves once they have passed through a silk mesh. Thus, as you might suspect, sponges frequently reproduce by simply breaking into fragments. If a sponge breaks up, the resulting fragments usually are able to reconstitute whole new individuals. Sexual reproduction is also exhibited by sponges, with some mature individuals producing eggs and sperm. Larval sponges may undergo their initial stages of development within the parent. They have numerous external, flagellated cells and are free-swimming. After a short planktonic stage, they settle down on a suitable substrate, where they begin their transformation into adults.

Sponges probably represent the most primitive animals, possessing multicellularity but neither tissue-level development nor body symmetry. Their cellular organization hints at the evolutionary ties between the unicellular protists and the multicellular animals. Sponges are unique in the animal kingdom in possessing choanocytes, special flagellated cells whose beating drives water through the body cavity.

Eumetazoa: The Radiata

The subkingdom Eumetazoa contains animals that evolved the first key transition in the animal body plan: distinct *tissues*. Two distinct cell layers form in the embryos of these animals: an outer ectoderm and an inner endoderm. These embryonic tissues give rise to the basic body plan, differentiating into the many tissues of the adult body. Typically, the outer covering of the body (called the epidermis) and the nervous system develop from the ectoderm, and the layer of digestive tissue (called the **gastrodermis**) develops from the endoderm. A layer of gelatinous material, called the **mesoglea,** lies between the epidermis and gastrodermis and contains the muscles in most eumetazoans.

Eumetazoans also evolved true body symmetry and are divided into two major groups. The Radiata includes two phyla of radially symmetrical organisms, Cnidaria (pronounced ni-DAH-ree-ah), the cnidarians—hydroids, jellyfish, sea anemones, and corals—and Ctenophora (pronounced tea-NO-fo-rah), the comb jellies, or ctenophores. All other eumetazoans are in the Bilateria and exhibit a fundamental bilateral symmetry.



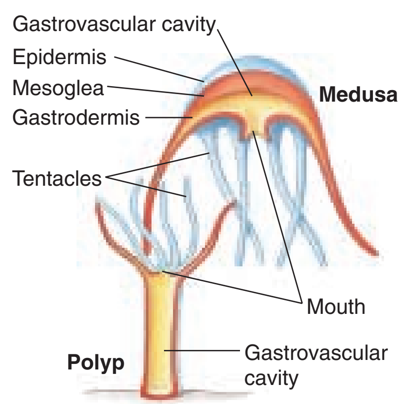


FIGURE 44.8
Two body forms of cnidarians, the medusa and the polyp. These two phases alternate in the life cycles of many cnidarians, but a number—including the corals and sea anemones, for example—exist only as polyps. Both forms have two fundamental layers of cells, separated by a jellylike layer called the mesoglea.

The Cnidarians

Cnidarians are nearly all marine, although a few live in fresh water. These fascinating and simply constructed animals are basically gelatinous in composition. They differ markedly from the sponges in organization; their bodies are made up of distinct tissues, although they have not evolved true organs. These animals are carnivores. For the most part, they do not actively move from place to place, but rather capture their prey (which includes fishes, crustaceans, and many other kinds of animals) with the tentacles that ring their mouths.

Cnidarians may have two basic body forms, polyps and medusae (figure 44.8). Polyps are cylindrical and are usually found attached to a firm substrate. They may be solitary or colonial. In a polyp, the mouth faces away from the substrate on which the animal is growing, and, therefore, often faces upward. Many polyps build up a chitinous or calcareous (made up of calcium carbonate) external or internal skeleton, or both. Only a few polyps are free-floating. In contrast, most medusae are free-floating and are often umbrella-shaped. Their mouths usually point downward, and the tentacles hang down around them. Medusae, particularly those of the class Scyphozoa, are commonly known as jellyfish because their mesoglea is thick and jellylike.

Many cnidarians occur only as polyps, while others exist only as medusae; still others alternate between these two phases during their life cycles. Both phases consist of diploid individuals. Polyps may reproduce asexually by budding; if they do, they may produce either new polyps or medusae. Medusae reproduce sexually. In most cnidarians, fertilized eggs give rise to free-swimming, multicellular, ciliated larvae known as **planulae.** Planulae are common in the plankton at times and may be dispersed widely in the currents.

A major evolutionary innovation in cnidarians, compared with sponges, is the internal extracellular digestion of food (figure 44.9). Digestion takes place within a gut cavity, rather than only within individual cells. Digestive enzymes are released from cells lining the walls of the cavity and partially break down food. Cells lining the gut subsequently engulf food fragments by phagocytosis.

The extracellular fragmentation that precedes phagocytosis and intracellular digestion allows cnidarians to digest animals larger than individual cells, an important improvement over the strictly intracellular digestion of sponges.

Nets of nerve cells coordinate contraction of cnidarian muscles, apparently with little central control. Cnidarians have no blood vessels, respiratory system, or excretory organs.

On their tentacles and sometimes on their body surface, cnidarians bear specialized cells called **cnidocytes.** The name of the phylum Cnidaria refers to these cells, which are highly distinctive and occur in no other group of organisms. Within each cnidocyte is a **nematocyst,** a small but powerful "harpoon." Each nematocyst features a coiled, threadlike tube. Lining the inner wall of the tube is a series of barbed spines.

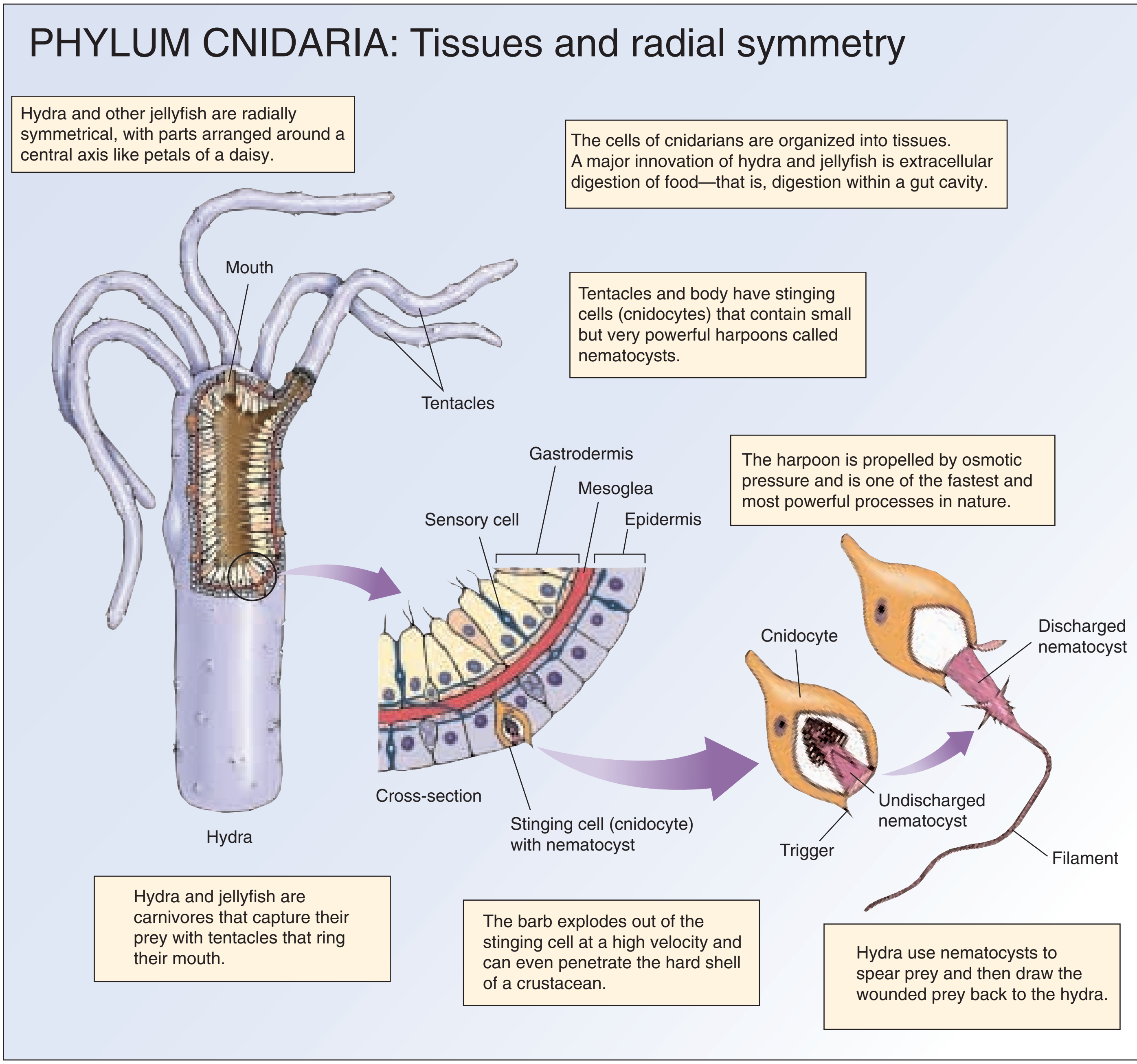


FIGURE 44.9
Eumetazoans all have tissues and symmetry. The cells of a cnidarian like this *Hydra* are organized into specialized tissues. The interior gut cavity is specialized for extracellular digestion—that is, digestion within a gut cavity rather than within individual cells. Cnidarians are also radially symmetrical.

Cnidarians use the threadlike tube to spear their prey and then draw the harpooned prey back with the tentacle containing the cnidocyte. Nematocysts may also serve a defensive purpose. To propel the harpoon, the cnidocyte uses water pressure. Before firing, the cnidocyte builds up a very high internal osmotic pressure. This is done by using active transport to build a high concentration of ions inside, while keeping its wall impermeable to water. Within the undischarged nematocyst, osmotic pressure reaches about 140 atmospheres.

When a flagellum-like trigger on the cnidocyte is stimulated to discharge, its walls become permeable to water, which rushes inside and violently pushes out the barbed filament. Nematocyst discharge is one of the fastest cellular processes in nature. The nematocyst is pushed outward so explosively that the barb can penetrate even the hard shell of a crab. A toxic protein often produced a stinging sensation, causing some cnidarians to be called "stinging nettles."

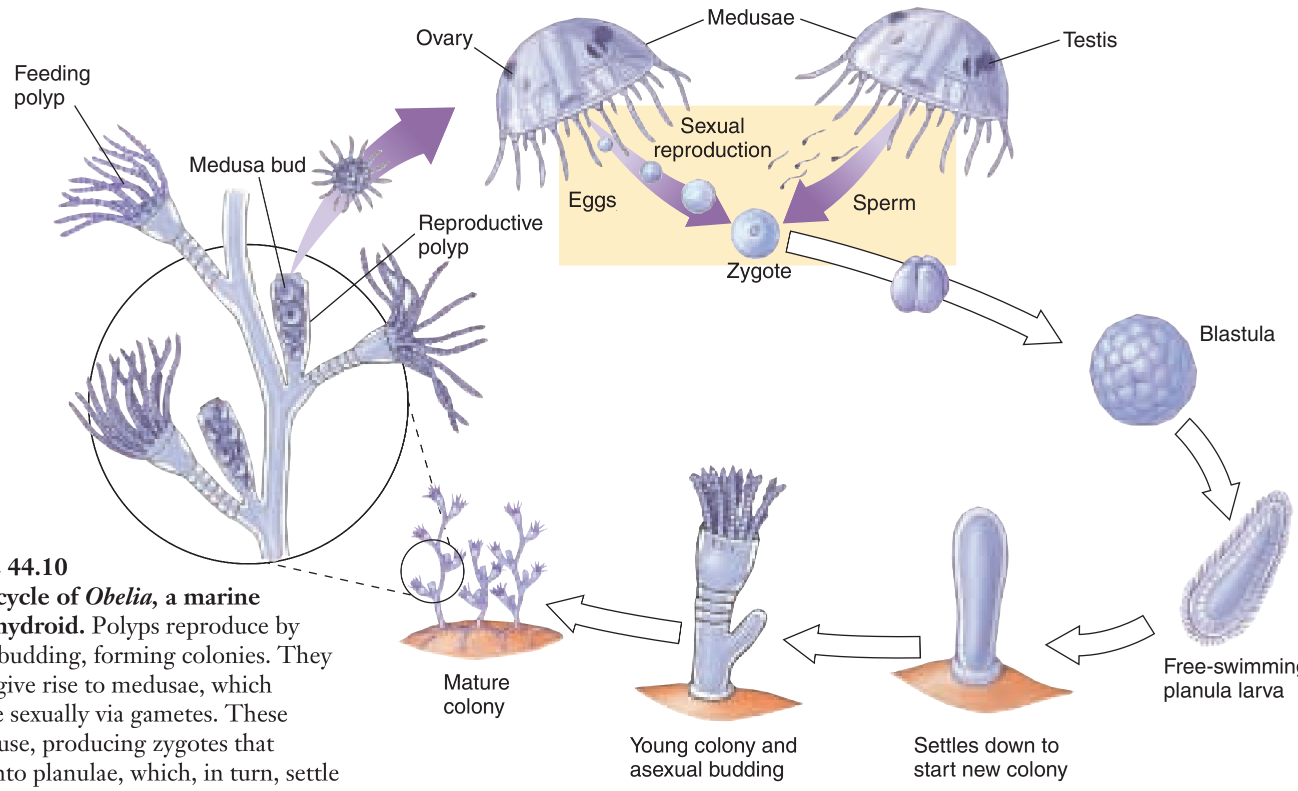


FIGURE 44.10
The life cycle of *Obelia*, a marine colonial hydroid. Polyps reproduce by asexually budding, forming colonies. They may also give rise to medusae, which reproduce sexually via gametes. These gametes fuse, producing zygotes that develop into planulae, which, in turn, settle down to produce polyps.

Classes of Cnidarians

There are four classes of cnidarians: Hydrozoa (hydroids), Scyphozoa (jellyfish), Cubozoa (box jellyfish), and Anthozoa (anemones and corals).

Class Hydrozoa: The Hydroids. Most of the approximately 2700 species of hydroids (class Hydrozoa) have both polyp and medusa stages in their life cycle (figure 44.10). Most of these animals are marine and colonial, such as Obelia and the already mentioned, very unusual Portuguese man-of-war. Some of the marine hydroids are bioluminescent.

A well-known hydroid is the abundant freshwater genus *Hydra*, which is exceptional in that it has no medusa stage and exists as a solitary polyp. Each polyp sits on a basal disk, which it can use to glide around, aided by mucous secretions. It can also move by somersaulting, bending over and attaching itself to the substrate by its tentacles, and then looping over to a new location. If the polyp detaches itself from the substrate, it can float to the surface.

Class Scyphozoa: The Jellyfish. The approximately 200 species of jellyfish (class Scyphozoa) are transparent or translucent marine organisms, some of a striking orange, blue, or pink color (figure 44.11). These animals spend most of their time floating near the surface of the sea. In all of them, the medusa stage is dominant—much larger and more complex than the polyps. The medusae are bell-shaped, with hanging tentacles around their margins. The polyp stage is small, inconspicuous, and simple in structure.

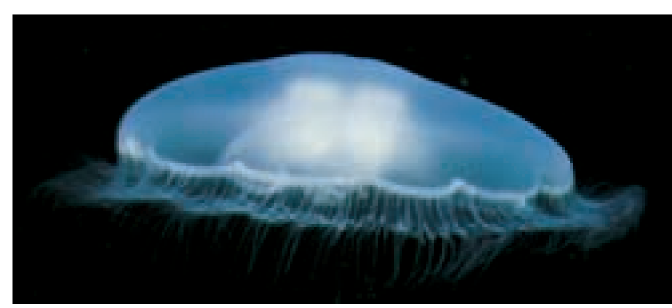


FIGURE 44.11
Class Scyphozoa. Jellyfish, *Aurelia aurita.*

The outer layer, or epithelium, of a jellyfish contains a number of specialized epitheliomuscular cells, each of which can contract individually. Together, the cells form a muscular ring around the margin of the bell that pulses rhythmically and propels the animal through the water. Jellyfish have separate male and female individuals. After fertilization, planulae form, which then attach and develop into polyps. The polyps can reproduce asexually as well as budding off medusae. In some jellyfish that live in the open ocean, the polyp stage is suppressed, and planulae develop directly into medusae.

Class Cubozoa: The Box Jellyfish. Until recently the cubozoa were considered an order of Scyphozoa. As their name implies, they are box-shaped medusa (the polyp stage is inconspicuous and in many cases not known). Most are only a few cm in height, although some are 25 cm tall. A tentacle or group of tentacles is found at each corner of the box (figure 44.12). Box jellies are strong swimmers and voracious predators of fish. Stings of some species can be fatal to humans.

FIGURE 44.12
Class Cubozoa. Box jelly, *Chironex fleckeri.*

Class Anthozoa: The Sea Anemones and Corals. By far the largest class of cnidarians is Anthozoa, the "flower animals" (from the Greek *anthos*, meaning "flower"). The approximately 6200 species of this group are solitary or colonial marine animals. They include stonelike corals, soft-bodied sea anemones, and other groups known by such fanciful names as sea pens, sea pansies, sea fans, and sea whips (figure 44.13). All of these names reflect a plantlike body topped by a tuft or crown of hollow tentacles. Like other cnidarians, anthozoans use these tentacles in feeding. Nearly all members of this class that live in shallow waters harbor symbiotic algae, which supplement the nutrition of their hosts through photosynthesis. Fertilized eggs of anthozoans usually develop into planulae that settle and develop into polyps; no medusae are formed.

FIGURE 44.13
Class Anthozoa. The sessile soft-bodied sea anemone.

Sea anemones are a large group of soft-bodied anthozoans that live in coastal waters all over the world and are especially abundant in the tropics. When touched, most sea anemones retract their tentacles into their bodies and fold up. Sea anemones are highly muscular and relatively complex organisms, with greatly divided internal cavities. These animals range from a few millimeters to about 10 centimeters in diameter and are perhaps twice that high.

Corals are another major group of anthozoans. Many of them secrete tough outer skeletons, or exoskeletons, of calcium carbonate and are thus stony in texture. Others, including the gorgonians, or soft corals, do not secrete exoskeletons. Some of the hard corals help form coral reefs, which are shallow-water limestone ridges that occur in warm seas. Although the waters where coral reefs develop are often nutrient-poor, the coral animals are able to grow actively because of the abundant algae found within them.

The Ctenophorans (Comb Jellies)

The members of this small phylum range from spherical to ribbonlike and are known as comb jellies or sea walnuts. Traditionally, the roughly 90 marine species of ctenophores (phylum Ctenophora) were considered closely related to the cnidarians. However, ctenophores are structurally more complex than cnidarians. They have anal pores, so that water and other substances pass completely through the animal. Comb jellies, abundant in the open ocean, are transparent and usually only a few centimeters long. The members of one group have two long, retractable tentacles that they use to capture their prey.

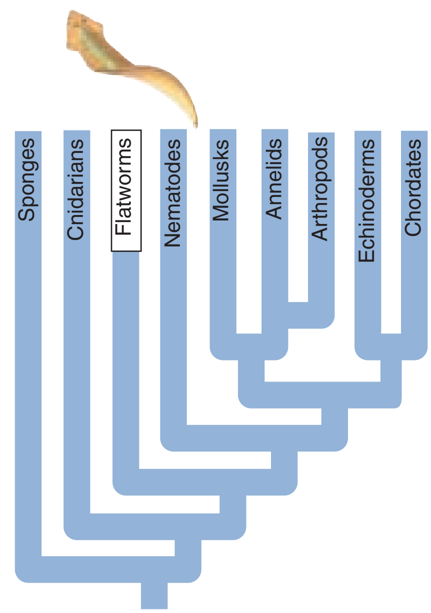
Ctenophores propel themselves through water with eight comblike plates of fused cilia that beat in a coordinated fashion (figure 44.14). They are the largest animals that use cilia for locomotion. Many ctenophores are bioluminescent, giving off bright flashes of light particularly evident in the open ocean at night.

Cnidarians and ctenophores have tissues and radial symmetry. Cnidarians have a specialized kind of cell called a cnidocyte. Ctenophores propel themselves through the water by means of eight comblike plates of fused cilia.

FIGURE 44.14
A comb jelly (phylum Ctenophora). Note the comblike plates along the ridges of the base.

44.3 Acoelomates are solid worms that lack a body cavity.

Eumetazoa: The Bilaterian Acoelomates



The Bilateria are characterized by the second key transition in the animal body plan, *bilateral symmetry*, which allowed animals to achieve high levels of specialization within parts of their bodies. The simplest bilaterians are the acoelomates; they lack any internal cavity other than the digestive tract. As discussed earlier, all bilaterians have three embryonic layers during development: ectoderm, endoderm, and mesoderm. We will focus our discussion of the acoelomates on the largest phylum of the group, the flatworms.

Phylum Platyhelminthes: The Flatworms

Phylum Platyhelminthes consists of some 20,000 species. These ribbon-shaped, soft-bodied animals are flattened dorsoventrally, from top to bottom. Flatworms are among the simplest of bilaterally symmetrical animals, but they do have a definite head at the anterior end and they do possess organs. Their bodies are solid: the only internal space consists of the digestive cavity (figure 44.15).

Flatworms range in size from a millimeter or less to many meters long, as in some tapeworms. Most species of flatworms are parasitic, occurring within the bodies of many other kinds of animals (figure 44.16). Other flatworms are free-living, occurring in a wide variety of marine and freshwater habitats, as well as moist places on land. Free-living flatworms are carnivores and scavengers; they eat various small animals and bits of organic debris. They move from place to place by means of ciliated epithelial cells, which are particularly concentrated on their ventral surfaces.

Those flatworms that have a digestive cavity have an incomplete gut, one with only one opening. As a result, they cannot feed, digest, and eliminate undigested particles of food simultaneously, and thus, flatworms cannot feed continuously, as more advanced animals can. Muscular contractions in the upper end of the gut cause a strong sucking force allowing flatworms to ingest their food and tear it into small bits. The gut is branched and extends throughout the body, functioning in both digestion and transport of food. Cells that line the gut engulf most of the food particles by phagocytosis and digest them; but, as in the cnidarians, some of these particles are partly digested extracellularly. Tapeworms, which are parasitic flatworms, lack digestive systems. They absorb their food directly through their body walls.

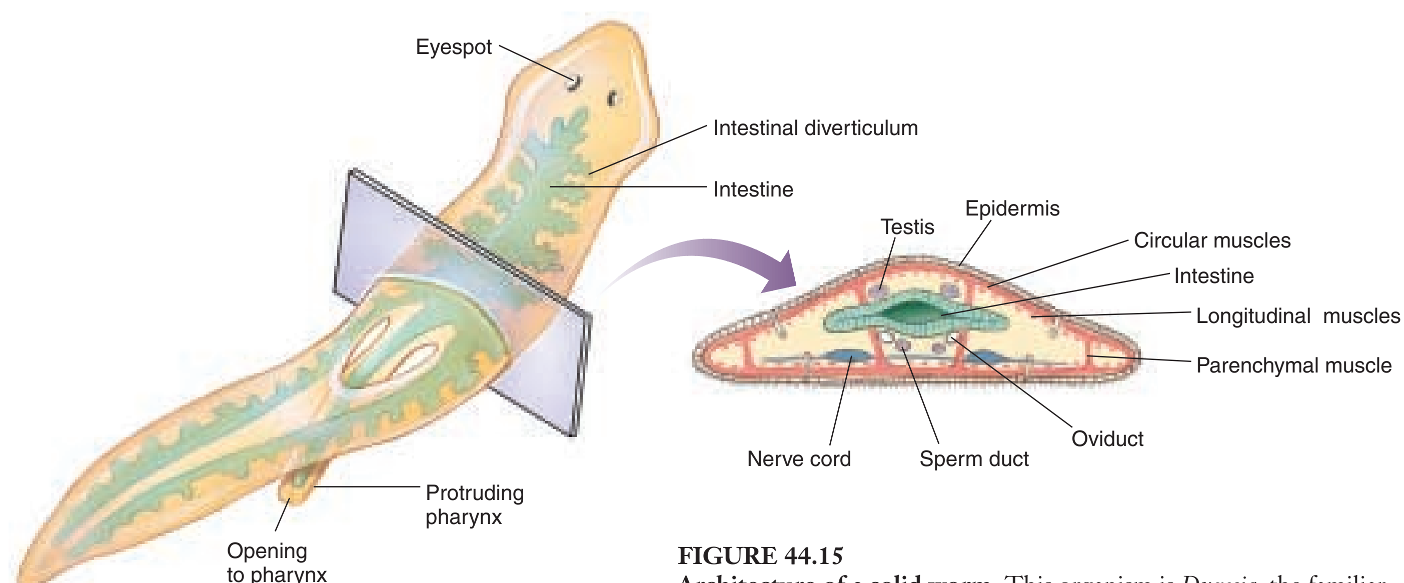


FIGURE 44.15
Architecture of a solid worm. This organism is *Dugesia*, the familiar freshwater "planaria" of many biology laboratories.

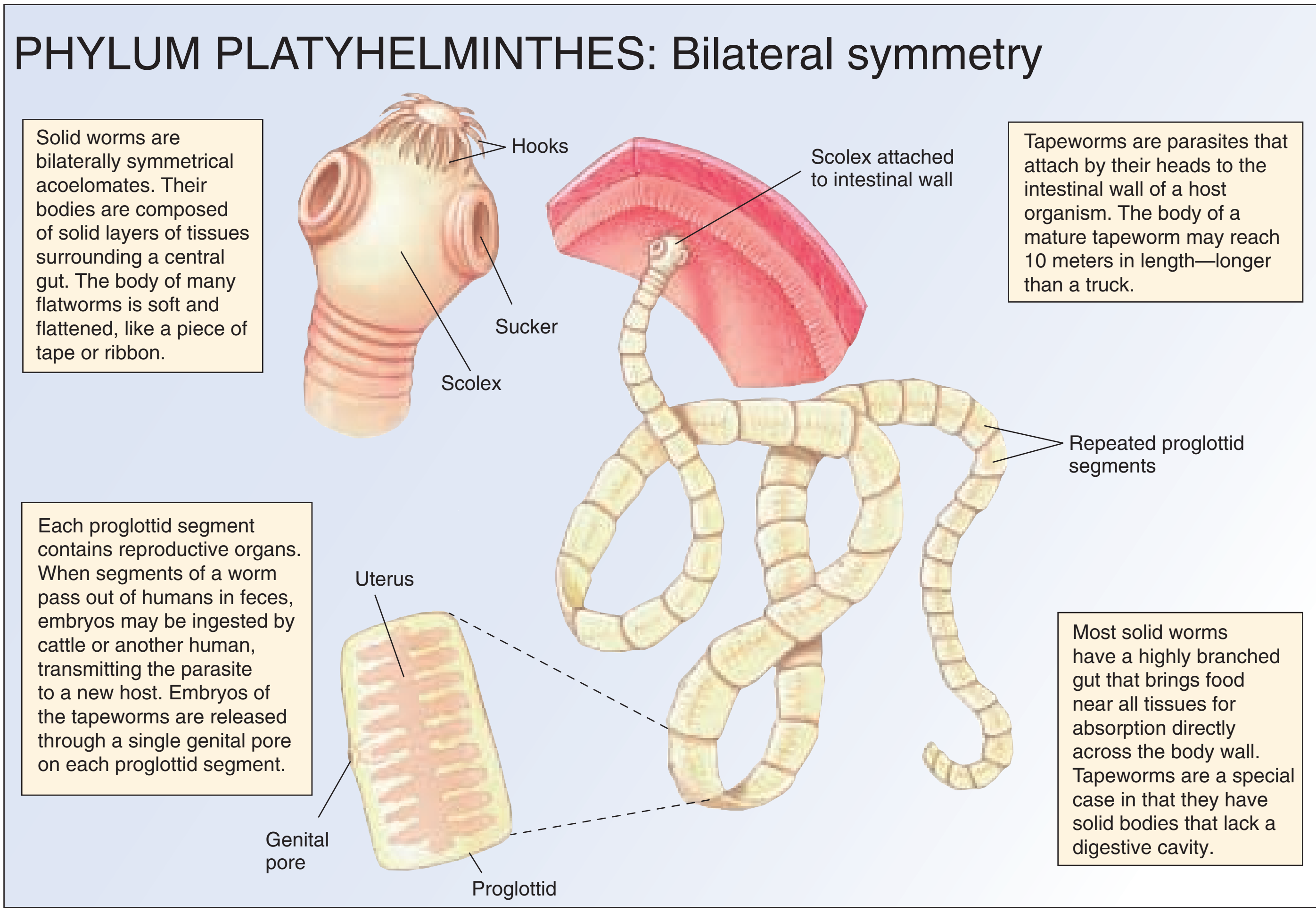


FIGURE 44.16
The evolution of bilateral symmetry. Acoelomate solid worms like this beef tapeworm, *Taenia saginata*, are bilaterally symmetrical. In addition, all bilaterians have three embryonic layers and exhibit cephalization.

Unlike cnidarians, flatworms have an excretory system, which consists of a network of fine tubules (little tubes) that runs throughout the body. Cilia line the hollow centers of bulblike **flame cells** located on the side branches of the tubules (see figure 58.9). Cilia in the flame cells move water and excretory substances into the tubules and then to exit pores located between the epidermal cells. Flame cells were named because of the flickering movements of the tuft of cilia within them. They primarily regulate the water balance of the organism. The excretory function of flame cells appears to be a secondary one. A large proportion of the metabolic wastes excreted by flatworms diffuses directly into the gut and is eliminated through the mouth.

Like sponges, cnidarians, and ctenophorans, flatworms lack circulatory systems for the transport of oxygen and food molecules. Consequently, all flatworm cells must be within diffusion distance of oxygen and food. Flatworms have thin bodies and highly branched digestive cavities that make such a relationship possible.

The nervous system of flatworms is very simple. Like cnidarians, some primitive flatworms have only a nerve net. However, most members of this phylum have longitudinal nerve cords that constitute a simple central nervous system.

Free-living members of this phylum have eyespots on their heads. These are inverted, pigmented cups containing light-sensitive cells connected to the nervous system. These eyespots enable the worms to distinguish light from dark; worms move away from strong light.

The reproductive systems of flatworms are complex. Most flatworms are **hermaphroditic,** with each individual containing both male and female sexual structures. In many of them, fertilization is internal. When they mate, each partner deposits sperm in the copulatory sac of the other. The sperm travel along special tubes to reach the eggs. In most free-living flatworms, fertilized eggs are laid in cocoons strung in ribbons and hatch into miniature adults. In some parasitic flatworms, there is a complex succession of distinct larval forms. Flatworms are also capable of asexual regeneration. In some genera, when a single individual is divided into two or more parts, each part can regenerate an entirely new flatworm.

Class Turbellaria: Turbellarians. Only one of the three classes of flatworms, the turbellarians (class Turbellaria) are free-living. One of the most familiar is the freshwater genus *Dugesia*, the common planaria used in biology laboratory exercises. Other members of this class are widespread and often abundant in lakes, ponds, and the sea. Some also occur in moist places on land.

Class Trematoda: The Flukes. Two classes of parasitic flatworms live within the bodies of other animals: flukes (class Trematoda) and tapeworms (class Cestoda). Both groups of worms have epithelial layers resistant to the digestive enzymes and immune defenses produced by their hosts—an important feature in their parasitic way of life. However, they lack certain features of the free-living flatworms, such as cilia in the adult stage, eyespots, and other sensory organs that lack adaptive significance for an organism that lives within the body of another animal.

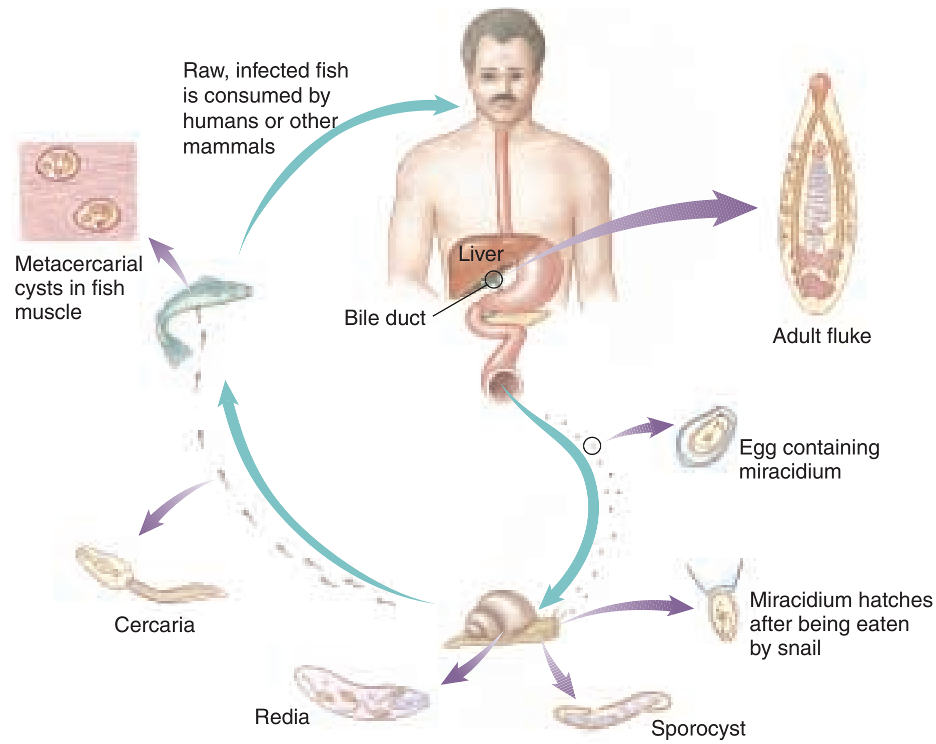


FIGURE 44.17
Life cycle of the human liver fluke, *Clonorchis sinensis*.

Flukes take in food through their mouth, just like their free-living relatives. There are more than 10,000 named species, ranging in length from less than 1 millimeter to more than 8 centimeters. Flukes attach themselves within the bodies of their hosts by means of suckers, anchors, or hooks. Some have a life cycle that involves only one host, usually a fish. Most have life cycles involving two or more hosts. Their larvae almost always occur in snails, and there may be other intermediate hosts. The final host of these flukes is almost always a vertebrate.

To human beings, one of the most important flatworms is the human liver fluke, *Clonorchis sinensis*. It lives in the bile passages of the liver of humans, cats, dogs, and pigs. It is especially common in Asia. The worms are 1 to 2 centimeters long and have a complex life cycle. Although they are hermaphroditic, cross-fertilization usually occurs between different individuals. Eggs, each containing a complete, ciliated first-stage larva, or **miracidium,** are passed in the feces (figure 44.17). If they reach water, they may be ingested by a snail. Within the snail an egg transforms into a *sporocyst*—a baglike structure with embryonic germ cells. Within the sporocysts are produced **rediae,** which are elongated, nonciliated larvae. These larvae continue growing within the snail, giving rise to several individuals of the tadpole-like next larval stage, **cercariae.**

Cercariae escape into the water, where they swim about freely. If they encounter a fish of the family Cyprinidae—the family that includes carp and goldfish—they bore into the muscles or under the scales, lose their tails, and transform into **metacercariae** within cysts in the muscle tissue. If a human being or other mammal eats raw infected fish, the cysts dissolve in the intestine, and the young flukes migrate to the bile duct, where they mature. An individual fluke may live for 15 to 30 years in the liver. In humans, a heavy infestation of liver flukes may cause cirrhosis of the liver and death.

Other very important flukes are the blood flukes of genus *Schistosoma*. They afflict about 1 in 20 of the world's population, more than 200 million people throughout tropical Asia, Africa, Latin America, and the Middle East. Three species of *Schistosoma* cause the disease called schistosomiasis, or bilharzia. Some 800,000 people die each year from this disease.

Recently, there has been a great deal of effort to control schistosomiasis. The worms protect themselves in part from the body's immune system by coating themselves with a variety of the host's own antigens that effectively render the worm immunologically invisible (see chapter 57). Despite this difficulty, the search is on for a vaccine that would cause the host to develop antibodies to one of the antigens of the young worms before they protect themselves with host antigens. This vaccine would prevent humans from infection. The disease can be cured with drugs after infection.

Class Cestoda: The Tapeworms. Class Cestoda is the third class of flatworms; like flukes, they live as parasites within the bodies of other animals. In contrast to flukes, tapeworms simply hang on to the inner walls of their hosts by means of specialized terminal attachment organs and absorb food through their skins. Tapeworms lack digestive cavities as well as digestive enzymes. They are extremely specialized in relation to their parasitic way of life. Most species of tapeworms occur in the intestines of vertebrates, about a dozen of them regularly in humans.

The long, flat bodies of tapeworms are divided into three zones: the **scolex,** or attachment organ; the unsegmented **neck;** and a series of repetitive segments, the **proglottids** (see figure 44.16). The scolex usually bears several suckers and may also have hooks. Each proglottid is a complete hermaphroditic unit, containing both male and female reproductive organs. Proglottids are formed continuously in an actively growing zone at the base of the neck, with maturing ones moving farther back as new ones are formed in front of them. Ultimately the proglottids near the end of the body form mature eggs. As these eggs are fertilized, the zygotes in the very last segments begin to differentiate, and these segments fill with embryos, break off, and leave their host with the host's feces. Embryos, each surrounded by a shell, emerge from the proglottid through a pore or the ruptured body wall. They are deposited on leaves, in water, or in other places where they may be picked up by another animal.

The beef tapeworm *Taenia saginata* occurs as a juvenile in the intermuscular tissue of cattle but as an adult in the intestines of human beings. A mature adult beef tapeworm may reach a length of 10 meters or more. These worms attach themselves to the intestinal wall of their host by a scolex with four suckers. The segments that are shed from the end of the worm pass from the human in the feces and may crawl onto vegetation. The segments ultimately rupture and scatter the embryos. Embryos may remain viable for up to five months. If they are ingested by cattle, they burrow through the wall of the intestine and ultimately reach muscle tissues through the blood or lymph vessels. About 1% of the cattle in the United States are infected, and some 20% of the beef consumed is not federally inspected. When infected beef is eaten rare, infection of humans by these tapeworms is likely. As a result, the beef tapeworm is a frequent parasite of humans.

Phylum Nemertea: The Ribbon Worms

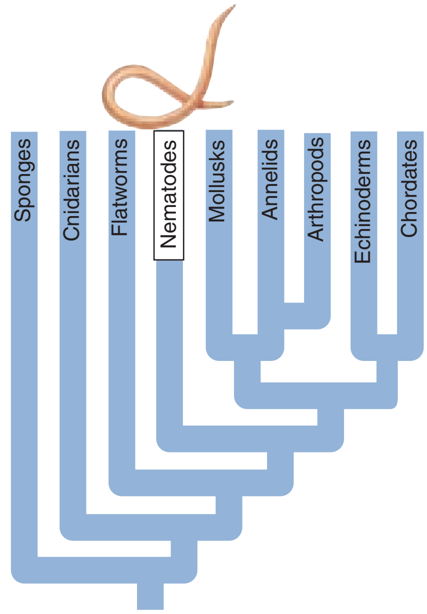
The phylogenetic relationship of phylum Nemertea (figure 44.18) to other free-living flatworms is unclear. Nemerteans are often called ribbon worms or proboscis worms. These aquatic worms have the body plan of a flatworm, but also possess a fluid-filled sac that may be a primitive coelom. This sac serves as a hydraulic power source for their proboscis, a long muscular tube that can be thrust out quickly from a sheath to capture prey. Shaped like a thread or a ribbon, ribbon worms are mostly marine and consist of about 900 species. Ribbon worms are large, often 10 to 20 centimeters and sometimes many meters in length. They are the simplest animals that possess a **complete digestive system,** one that has two separate openings, a mouth and an anus. Ribbon worms also exhibit a circulatory system in which blood flows in vessels. Many important evolutionary trends that become fully developed in more advanced animals make their first appearance in the Nemertea.

The acoelomates, typified by flatworms, are the most primitive bilaterally symmetrical animals and the simplest animals in which organs occur.

FIGURE 44.18
A ribbon worm, *Lineus* *(phylum Nemertea)*. This is the simplest animal with a complete digestive system.

44.4 Pseudocoelomates have a simple body cavity.

The Pseudocoelomates



All bilaterians except solid worms possess an internal *body cavity*, the third key transition in the animal body plan. Seven phyla are characterized by their possession of a pseudocoel (see figure 44.4). Their evolutionary relationships remain unclear, with the possibility that the pseudocoelomate condition arose independently many times. The pseudocoel serves as a hydrostatic skeleton—one that gains its rigidity from being filled with fluid under pressure. The animals' muscles can work against this "skeleton," thus making the movement of pseudocoelomates far more efficient than that of the acoelomates.

Pseudocoelomates lack a defined circulatory system; this role is performed by the fluids that move within the pseudocoel. Most pseudocoelomates have a complete, one-way digestive tract that acts like an assembly line. Food is first broken down, then absorbed, and then treated and stored.

Phylum Nematoda: The Roundworms

Nematodes, eelworms, and other roundworms constitute a large phylum, Nematoda, with some 12,000 recognized species. Scientists estimate that the actual number might approach 100 times that many. Members of this phylum are found everywhere. Nematodes are abundant and diverse in marine and freshwater habitats, and many members of this phylum are parasites of animals (figure 44.19) and plants. Many nematodes are microscopic and live in soil. It has been estimated that a spadeful of fertile soil may contain, on the average, a million nematodes.

Nematodes are bilaterally symmetrical, unsegmented worms. They are covered by a flexible, thick cuticle, which is molted as they grow. Their muscles constitute a layer beneath the epidermis and extend along the length of the worm, rather than encircling its body. These longitudinal muscles pull both against the cuticle and the pseudocoel, which forms a hydrostatic skeleton. When nematodes move, their bodies whip about from side to side.

Near the mouth of a nematode, at its anterior end, are usually 16 raised, hairlike, sensory organs. The mouth is often equipped with piercing organs called **stylets.** Food passes through the mouth as a result of the sucking action of a muscular chamber called the **pharynx.** After passing through a short corridor into the pharynx, food continues through the other portions of the digestive tract, where it is broken down and then digested. Some of the water with which the food has been mixed is reabsorbed near the end of the digestive tract, and material that has not been digested is eliminated through the anus (figure 44.20).

Nematodes completely lack flagella or cilia, even on sperm cells. Reproduction in nematodes is sexual, with sexes usually separate. Their development is simple, and the adults consist of very few cells. For this reason, nematodes have become extremely important subjects for genetic and developmental studies (see chapter 17). The 1-millimeter-long *Caenorhabditis elegans* matures in only three days, its body is transparent, and it has only 959 cells. It is the only animal whose complete developmental cellular anatomy is known.

FIGURE 44.19
***Trichinella* nematode encysted in pork.** The serious disease trichinosis can result from eating undercooked pork or bear meat containing such cysts.

About 50 species of nematodes, including several that are rather common in the United States, regularly parasitize human beings. The most serious common nematode-caused disease in temperate regions is trichinosis, caused by worms of the genus *Trichinella.* These worms live in the small intestine of pigs, where fertilized female worms burrow into the intestinal wall. Once it has penetrated these tissues, each female produces about 1500 live young. The young enter the lymph channels and travel to muscle tissue throughout the body, where they mature and form highly resistant, calcified cysts. Infection in human beings or other animals arises from eating undercooked or raw pork in which the cysts of *Trichinella* are present. If the worms are abundant, a fatal infection can result, but such infections are rare; only about 20 deaths in the United States have been attributed to trichinosis during the past decade.

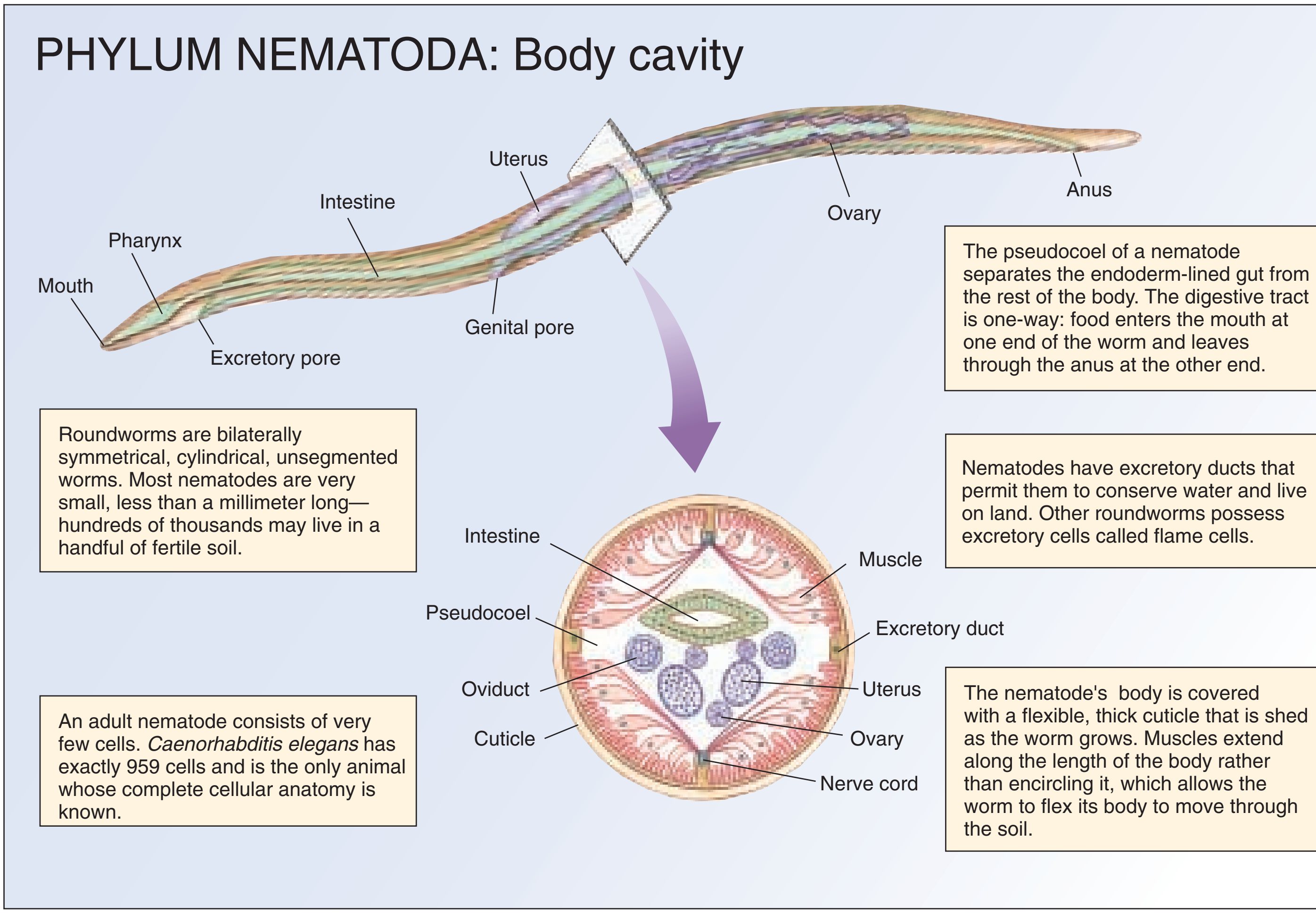


FIGURE 44.20
The evolution of a simple body cavity. The major innovation in body design in roundworms (phylum Nematoda) is a body cavity between the gut and the body wall. This cavity is the pseudocoel. It allows chemicals to circulate throughout the body and prevents organs from being deformed by muscle movements.

Phylum Rotifera: Rotifers

Phylum Rotifera includes common, small, bilaterally symmetrical, basically aquatic animals that have a crown of cilia at their heads. Rotifers are pseudocoelomates but are very unlike nematodes. They have several features that suggest their ancestors may have resembled flatworms. There are about 2000 species of this phylum. While a few rotifers live in soil or in the capillary water in cushions of mosses, most occur in fresh water, and they are common everywhere. Very few rotifers are marine. Most rotifers are between 50 and 500 micrometers in length, smaller than many protists.

Rotifers have a well-developed food-processing apparatus. A conspicuous organ on the tip of the head called the corona gathers food. It is composed of a circle of cilia which sweeps their food into their mouths, as well as being used for locomotion. Rotifers are often called "wheel animals" because the cilia, when they are beating together, resemble the movement of spokes radiating from a wheel.

A Relatively New Phylum: Cycliophora

In December 1995, two Danish biologists reported the discovery of a strange new kind of creature, smaller than a period on a printed page. The tiny organism had a striking circular mouth surrounded by a ring of fine, hairlike cilia and has so unusual a life cycle that they assigned it to an entirely new phylum, Cycliophora (Greek for "carrying a small wheel"). There are only about 35 known animal phyla, so finding a new one is extremely rare! When the lobster to which it is attached starts to molt, the tiny symbiont begins a bizarre form of sexual reproduction. Dwarf males emerge, with nothing but brains and reproductive organs. Each dwarf male seeks out another female symbiont on the molting lobster and fertilizes its eggs, generating free-swimming individuals that can seek out another lobster and renew the life cycle.

The pseudocoelomates, including nematodes and rotifers, all have fluid-filled pseudocoels.

44.5 The coming revolution in animal taxonomy will likely alter traditional phylogenies.

Reevaluating How the Animal Body Plan Evolved

The great diversity see in the body plan of animals is difficult to fit into any one taxonomic scheme. Biologists have traditionally inferred the general relationships among the 35 animal phyla by examining what seemed to be fundamental characters—segmentation, possession of a coelom, and so on. The general idea has been that such characters are most likely to be conserved during a group's evolution. Animal phyla that share a fundamental character are more likely to be closely related to each other than to other phyla that do not exhibit the character. The phylogeny presented in figure 44.2 is a good example of the sort of taxonomy this approach has generated.

However, not every animal can be easily accommodated by this approach. Take, for example, the myzostomids (figure 44.21), an enigmatic and anatomically bizarre group of marine animals that are parasites or symbionts of echinoderms. Myzostomid fossils are found associated with echinoderms since the Ordovician, so the myzostomid-echinoderm relationship is a very ancient one. Their long history of obligate association has led to the loss or simplification of many myzostomid body elements, leaving them, for example, with no body cavity (they are acoelomates) and only incomplete segmentation.

This character loss has led to considerable disagreement among taxonomists. However, while taxonomists have disagreed about the details, all have generally allied myzostomids is some fashion with the annelids, sometimes within the polychaetes, sometimes as a separate phylum closely allied to the annelids.

Recently, this view has been challenged. New taxonomical comparisons using molecular data have come to very different conclusions. Researchers examined two components of the protein synthesis machinery, the small ribosomal subunit rRNA gene, and an elongation factor gene (called 1 alpha). The phylogeny they obtain does not place the myzostomids in with the annelids. Indeed, they find that the myzostomids have no close links to the annelids at all. Instead, surprisingly, they are more closely allied with the flatworms!

This result hints strongly that the key morphological characters that biologists have traditionally used to construct animal phylogenies—segmentation, coeloms, jointed appendages, and the like—are not the conservative characters we had supposed. Among the myzostomids these features appear to have been gained and lost again during the course of their evolution. If this unconservative evolutionary pattern should prove general, our view of the evolution of the animal body plan, and how the various animal phyla relate to one another, will soon be in need of major revision.

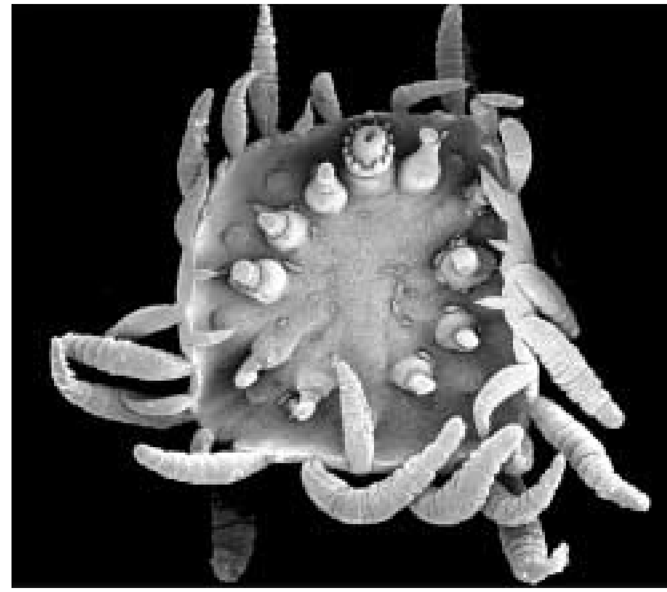


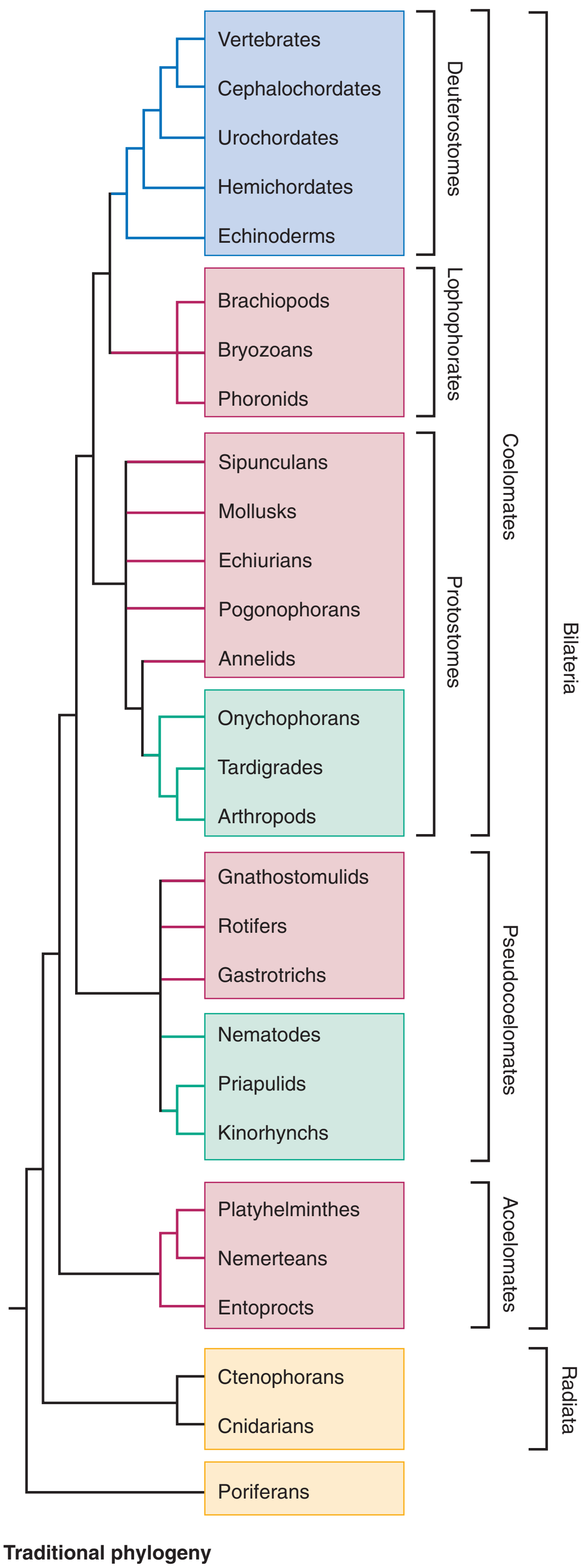
FIGURE 44.21
A taxonomic puzzle. *Myzostoma martenseni* has no body cavity and incomplete segmentation. Animals such as this present a classification challenge, causing taxonomists to reconsider traditional animal phylogenies based on fundamental characters.

Molecular Phylogenies

The last decade has seen a wealth of new molecular sequence data on the various animal groups. The animal phylogenies that these data suggest are often significantly at odds with the traditional phylogeny used in this text and presented in figure 44.2. One such phylogeny, developed from ribosomal RNA studies, is presented in figure 44.22. It is only a rough outline; in the future more data should allow us to resolve relationships within groupings. Still, it is clear that major groups are related in very different ways in the molecular phylogeny than in the more traditional one.

At present, molecular phylogenetic analysis of the animal kingdom is in its infancy. Molecular phylogenies developed from different molecules often tend to suggest different evolutionary relationships. However, the childhood of this approach is likely to be short. Over the next few years, a mountain of additional molecular data can be anticipated. As more data are brought to bear, we can hope that the confusion will lessen, and that a consensus phylogeny will emerge. When and if this happens, it is likely to be very different from the traditional view.

The use of molecular data to construct phylogenies is likely to significantly alter our understanding of relationships among the animal phyla.



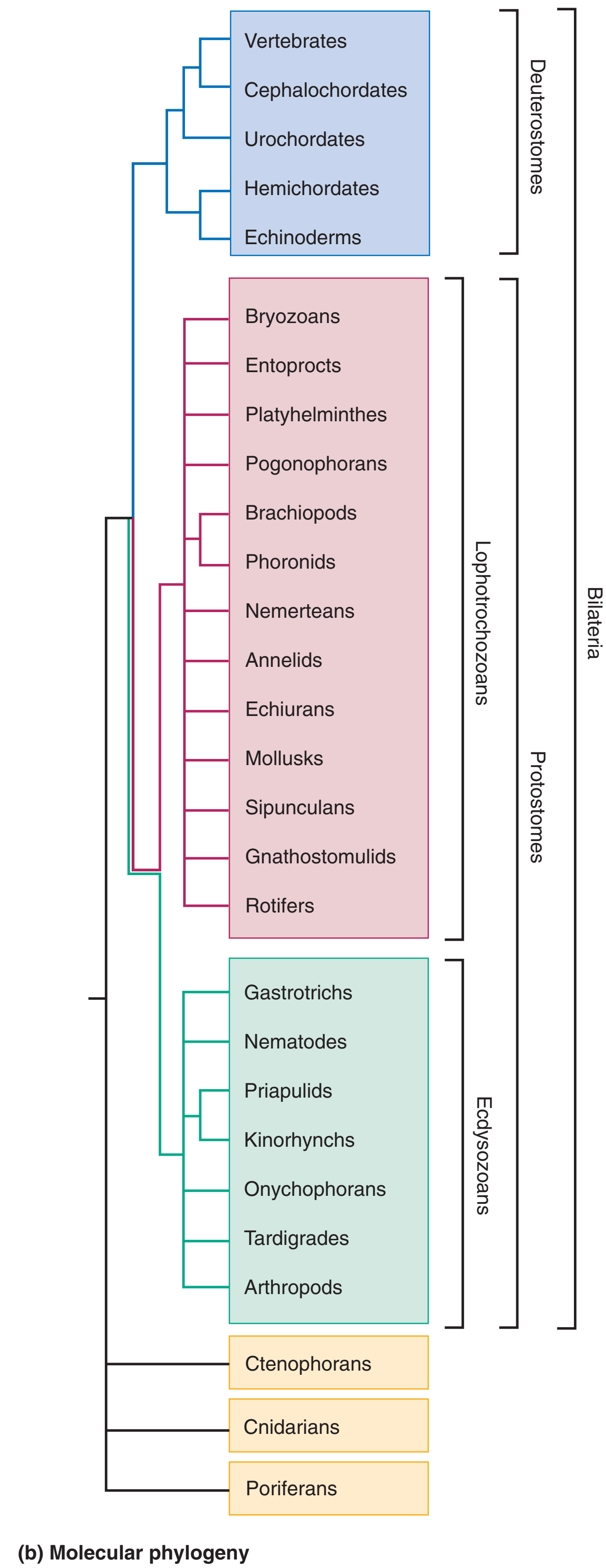


FIGURE 44.22
Traditional versus molecular animal phylogenies. (*a*) Traditional phylogenies are based on fundamental morphological characters. (After L. H. Hyman, *The Invertebrates*, 1940.) (*b*) More recent phylogenies are often based on molecular analyses, this one on comparisons of rRNA sequence differences among the animal phyla. (After Adoutte, et al., *Proc. Nat. Acad. Sci* 97: p. 4454, 2000.)

Chapter 44

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Summary | Questions | Media Resources

44.1 Animals are multicellular heterotrophs without cell walls.

- Animals are heterotrophic, multicellular, and usually have the ability to move. Almost all animals reproduce sexually. Animal cells lack rigid cell walls and digest their food internally.
- The kingdom Animalia is divided into two subkingdoms: Parazoa, which includes only the asymmetrical phylum Porifera, and Eumetazoa, characterized by body symmetry.

1. What are the characteristics that distinguish animals from other living organisms?

2. What are the two subkingdoms of animals? How do they differ in terms of symmetry and body organization?

- Activity: Invertebrates
- Characteristics of Invertebrates
- Body Organization

- Symmetry in Nature
- Posterior to Anterior
- Sagittal Plane
- Frontal to Coronal Plane
- Transvere/Cross-sectional Planes

44.2 The simplest animals are not bilaterally symmetrical.

- The sponges (phylum Porifera) are characterized by specialized, flagellated cells called choanocytes. They do not possess tissues or organs, and most species lack symmetry in their body organization.
- Cnidarians (phylum Cnidaria) are predominantly marine animals with unique stinging cells called cnidocytes, each of which contains a specialized harpoonlike apparatus, or nematocyst.

3. From what kind of ancestor did sponges probably evolve?

4. What are the specialized cells used by a sponge to capture food?

5. What are the two ways sponges reproduce? What do larval sponges look like?

6. What is a planula?

- Sponges
- Radical Phyla

44.3 Acoelomates are solid worms that lack a body cavity.

- Acoelomates lack an internal cavity, except for the digestive system, and are the simplest animals that have organs.
- The most prominent phylum of acoelomates, Platyhelminthes, includes the free-living flatworms and the parasitic flukes and tapeworms.
- Ribbon worms (phylum Nemertea) are similar to free-living flatworms, but have a complete digestive system and a circulatory system in which the blood flows in vessels.

7. What body plan do members of the phylum Platyhelminthes possess? Are these animals parasitic or free-living? How do they move from place to place?

8. How are tapeworms different from flukes? How do tapeworms reproduce?

- Bilateral Acoelomates

- Student Research: Parasitic Flatworms

44.4 Pseudocoelomates have a simple body cavity.

- Pseudocoelomates, exemplified by the nematodes (phylum Nematoda), have a body cavity that develops between the mesoderm and the endoderm.
- Rotifers (phylum Rotifera), or wheel animals, are very small freshwater pseudocoelomates.

9. Why are nematodes structurally unique in the animal world?

10. How do rotifers capture food?

- Pseudocoelomates

44.5 The coming revolution in animal taxonomy will likely alter traditional phylogenies.

- Molecular data are suggesting animal phylogenies that are in considerable disagreement with traditional phylogenies.

11. With what group are myzostomids most closely allied?

- Student Research: Molecular Phylogeny of Gastropods