32 Animal Origins and the Evolution of Body Plans

In 1822, nearly forty years before Darwin wrote *The Origin of Species*, a French naturalist, Étienne Geoffroy Saint-Hilaire, was examining a lobster. He noticed that when he turned the lobster upside down and viewed it with its ventral surface up, its central nervous system was located above its digestive tract, which in turn was located above its heart—the same relative positions these systems have in mammals when viewed *dorsally*. His observations led Geoffroy to conclude that the differences between arthropods (such as lobsters) and vertebrates (such as mammals) could be explained if the embryos of one of those groups were inverted during development.

Geoffroy's suggestion was regarded as preposterous at the time and was largely dismissed until recently. However, the discovery of two genes that influence a system of extracellular signals involved in development has lent new support to Geoffroy's seemingly outrageous hypothesis.

A vertebrate gene called *chordin* helps to establish cells on one side of the embryo as dorsal and on the other as ventral. A probably homologous gene in fruit flies, called *sog*, acts in a similar manner, but has the opposite effect. Fly cells where *sog* is active become ventral, whereas vertebrate cells where *chordin* is active become dorsal. However, when *sog* mRNA is injected into an embryo of the frog *Xenopus*, a vertebrate, it causes dorsal development. *Chordin* mRNA injected into fruit flies promotes ventral development. In both cases, injection of the mRNA promotes the development of the portion of the embryo that contains the central nervous system!

Chordin and *sog* are among many genes that regulate similar functions in very different organisms. Such genes are providing evolutionary biologists with information that can help them understand relationships among animal lineages that separated from one another in ancient times. As we saw in Chapter 25, new knowledge about gene functions and gene sequences is increasingly being used to infer evolutionary relationships.

In this chapter, we will apply the methods described in Chapter 25 to infer evolutionary relationships among the animals. First, we will review the defining characteristics of the animal way of life. Then we will describe several lineages of simple animals. Finally, we will describe the lophotro-

Genes that Control Development A human and a lobster carry similar genes that control the development of the body axis, but these genes position their body systems inversely. A lobster's nervous system runs up its ventral (belly) surface, whereas a vertebrate's runs down its dorsal (back) surface.

chozoans, one of the three great evolutionary lineages of animals. In the next two chapters, we will discuss the other two great animal lineages, the ecdysozoans and the deuterostomes.

Animals: Descendants of a Common Ancestor

Biologists have long debated whether animals arose once or several times from protist ancestors, but enough molecular and morphological evidence has now been assembled to indicate that, with the possible exception of sponges (Porifera), the Kingdom Animalia is a monophyletic group—that is, all animals are descendants of a single ancestral lineage. This conclusion is supported by the fact that all animals share several derived traits:

- Similarities in their small-subunit ribosomal RNAs (see Chapter 26)
- Similarities in their Hox genes (see Chapter 20)
- Special types of cell–cell junctions: tight junctions, desmosomes, and gap junctions (see Figure 5.6)
- A common set of extracellular matrix molecules, including collagen (see Figure 4.26)

Animals evolved from colonial flagellated protists as a result of division of labor among their aggregated cells. Within the ancestral colonies of cells—perhaps analogous to those still existing in the chlorophyte *Volvox* or some colonial choanoflagellates (see Figures 28.25*a* and 28.28)—some cells became specialized for movement, others became specialized for nutrition, and still others differentiated into gametes. Once this specialization by function had begun, working groups of cells continued to differentiate while improving their coordination with other groups of cells. Such coordinated groups of cells evolved into the larger and more complex organisms that we now call **animals**.

Animals are multicellular heterotrophs

What traits characterize the animals? In contrast to the Bacteria, Archaea, and most protists, all animals are *multicellular*. Unlike plants, animals must take in pre-formed organic molecules because they cannot synthesize them from inorganic chemicals. They acquire these organic molecules by ingesting other organisms or their products, either living or dead, and digesting them inside their bodies; thus animals are *heterotrophs*. Most animals have *circulatory systems* that take up O_2, get rid of CO_2, and carry nutrients from their guts to other body tissues.

To acquire food, animals must expend energy either to move through the environment and position themselves where food will pass close to them, or to move the environment and the food it contains to them. The foods animals ingest include most other members of the animal kingdom as well as members of all other kingdoms. Much of the diversity of animal sizes and shapes evolved as animals acquired the ability to capture and eat many different kinds of food and to avoid becoming food for other animals. The need to locate food has favored the evolution of sensory structures to provide animals with detailed information about their environment and nervous systems to receive and coordinate that information.

The accounts in this chapter and the following two chapters serve as an orientation to the major groups of animals, their similarities and differences, and the evolutionary pathways that resulted in the current richness of animal lineages and species. But how do biologists infer evolutionary relationships among animals?

Several traits show evolutionary relationships among animals

Biologists use a variety of traits in their efforts to infer animal phylogenies. Clues to these relationships are found in the fossil record, in patterns of embryonic development, in the comparative morphology and physiology of living and fossil animals, and in the structure of animal molecules, especially small subunit rRNAs and mitochondrial genes (see Chapters 25 and 26).

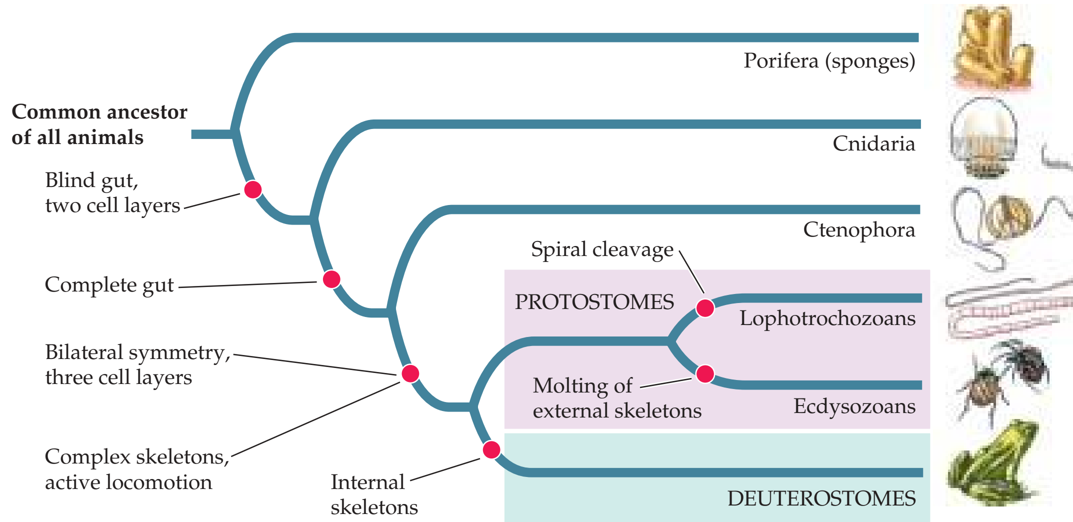
Using this wide variety of comparative data, zoologists concluded that sponges, cnidarians, and ctenophores separated from the remaining animal lineages early in evolutionary history. Biologists have divided the remaining animals into two major lineages: the protostomes and the deuterostomes. Figure 32.1 shows the postulated order of divergence of the major animal groups that we will use in these three chapters.

Several differences in patterns of embryonic development provide clues to animal phylogeny. During the development of an animal from a single-celled zygote to a multicellular adult, distinct layers of cells form. The embryos of **diploblastic** animals have only two of these cell layers: an outer *ectoderm* and an inner *endoderm*. The embryos of **triploblastic** animals have, in addition to ectoderm and endoderm, a third layer, the *mesoderm*, which lies between the ectoderm and the endoderm. The existence of three cell layers distinguishes the protostomes and deuterostomes from those groups of simple animals that diverged from them earlier.

During early development in many animals, a cavity forms in a spherical embryo. The opening of this cavity is called the *blastopore*. Among the **protostomes** (from the Greek, "mouth first"), the mouth arises from the blastopore; the anus forms later. Among the **deuterostomes** ("mouth second"), the blastopore becomes the anus; the mouth forms later.

In the common ancestor of the protostomes and deuterostomes, the pattern of early cleavage of the fertilized egg was

32.1 A Current Phylogeny of the Animals The phylogenetic tree used in this and the following two chapters assumes that the animals are monophyletic. The characters highlighted by red circles on the tree will be explained as we discuss the different phyla.



radial (see Figure 20.4). This cleavage pattern persisted during the evolution of the deuterostomes and in many protostomate lineages, but spiral cleavage evolved in one major protostomate lineage, as we will see.

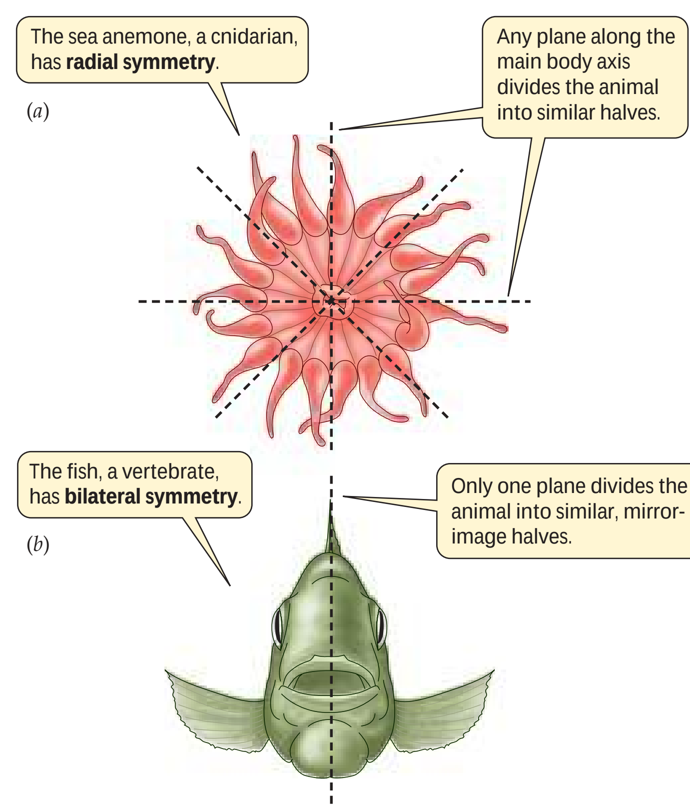
Body Plans: Basic Structural Designs

The general structure of an animal, its organ systems, and the integrated functioning of its parts are known as its **body plan**. A fundamental aspect of an animal's body plan is its overall shape, described in part by its **symmetry**. A symmetrical animal can be divided along at least one plane into similar halves. Animals that have no plane of symmetry are said to be **asymmetrical**. Many sponges are asymmetrical, but most animals have some kind of symmetry.

The simplest form of symmetry is **spherical symmetry**, in which body parts radiate out from a central point. An infinite number of planes passing through the central point can divide a spherically symmetrical organism into similar halves. Spherical symmetry is widespread among the protists, but most animals possess other forms of symmetry.

An organism with **radial symmetry** has one main axis around which its body parts are arranged. A perfectly radially symmetrical animal can be divided into similar halves by any plane that contains the main axis. Some simple sponges and a few other animals, such as sea anemones (Figure 32.2*a*), have radial symmetry. Most radially symmetrical animals are slightly modified so that fewer planes can divide them into identical halves. Two animal phyla—Cnidaria and Ctenophora—are composed primarily of radially symmetrical animals. These animals move slowly or not at all.

Bilateral symmetry is a common characteristic of animals that move rapidly through their environments. A bilaterally symmetrical animal can be divided into mirror images (left and right sides) by a single plane that passes through the dorsoventral midline of its body from the front (*anterior*) to the back (*posterior*) end (Figure 32.2*b*). A plane at right angles to the first one divides the body into two dissimilar sides; the back side of a bilaterally symmetrical animal is its *dorsal* surface; the belly side is its *ventral* surface.



32.2 Body Symmetry Most animals are either radially or bilaterally symmetrical.

Bilateral symmetry is strongly correlated with **cephalization**: the concentration of sensory organs and nervous tissues in a head at the anterior end of the animal. Cephalization is favored because the anterior end of a freely moving animal typically encounters new environments first.

Fluid-filled spaces, called **body cavities**, lie between the ectoderm and endoderm of most protostomes and deuterostomes. The type of body cavity an animal has strongly influences the way it moves.

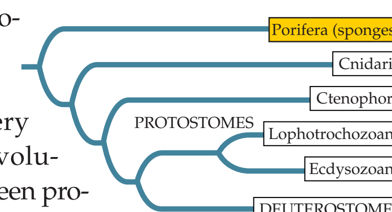
- Animals that lack an enclosed body cavity are called **acoelomates**. In these animals, the space between the gut and the body wall is filled with masses of cells called *mesenchyme* (Figure 32.3*a*).
- **Pseudocoelomate** animals have a body cavity called a *pseudocoel*, a liquid-filled space in which many of the internal organs are suspended. Their control over body shape is crude because the pseudocoel has muscles only on its outside; there is no inner layer of muscle surrounding the organs (Figure 32.3*b*).
- **Coelomate** animals have a *coelom*, a body cavity that develops within the mesoderm. It is lined with a special structure called the *peritoneum* and is enclosed on both the inside and the outside by muscles (Figure 32.3*c*).

The fluid-filled body cavities of simple animals function as **hydrostatic skeletons**. Because fluids are relatively incompressible, they move to another part of the cavity when the muscles surrounding them contract. If the body tissues around the cavity are flexible, fluids squeezed out of one region can cause some other region to expand. The moving fluids can thus move specific body parts. If a temporary attachment can be made to the substratum, the whole animals can move from one place to another.

In animals that have both circular muscles (encircling the body) and longitudinal muscles (running along the length of the body), the action of these antagonistic muscles on the fluid-filled body cavity gives the animal even greater control over its movement. A coelomate animal has better control over the movement of the fluids in its body cavity than does a pseudocoelomate animal, but its control is further improved if the coelom is separated into compartments or segments. Then muscles in each individual segment can change its shape independently of the other segments. Segmentation of the coelom evolved several different times among both protostomes and deuterostomes.

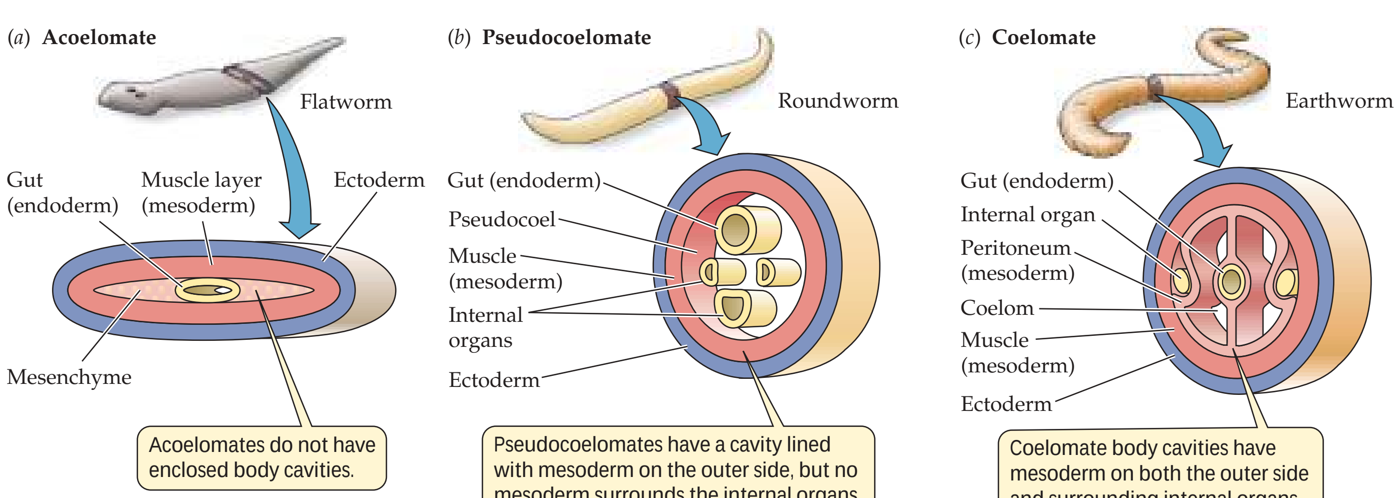
Other forms of skeletons developed in many animal lineages, either as substitutes for, or in combination with, hydrostatic skeletons. Some skeletons are internal (such as vertebrate bones); others are external (such as lobster shells). Some external skeletons consist of a single element (snail shells), others have two elements (clam shells), and still others have many elements (centipedes).

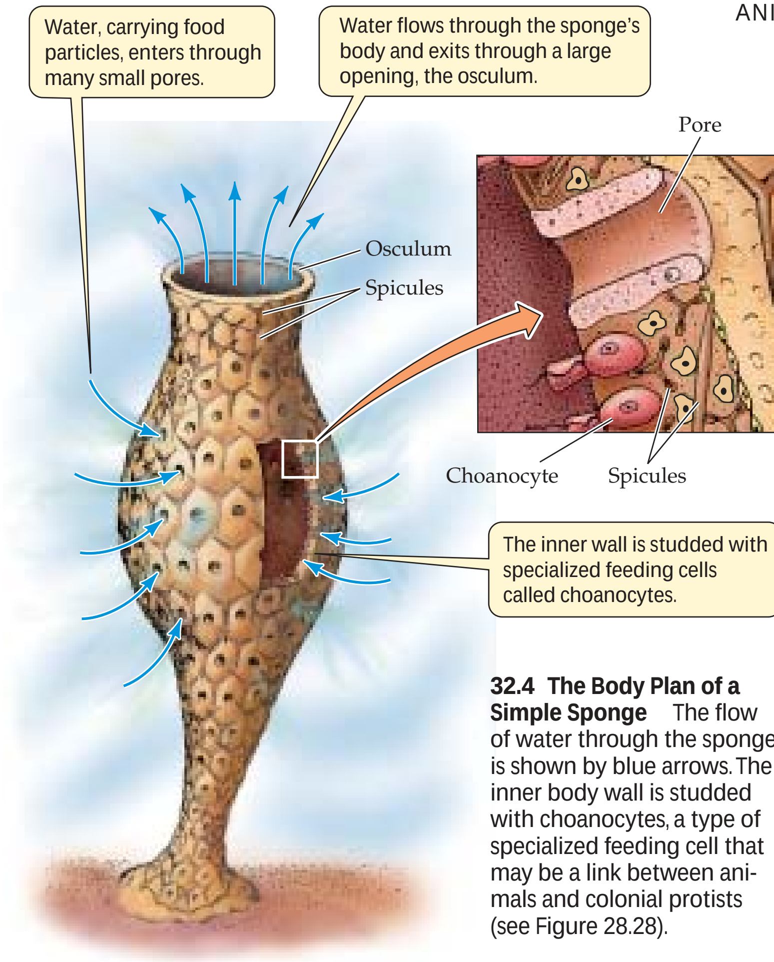
Sponges: Loosely Organized Animals



The lineage leading to modern sponges separated from the lineage leading to all other animals very early during animal evolution. The difference between protist colonies and simple multicellular animals is that the animal cells are differentiated and their activities are coordinated. However, sponge cells do not form true organs.

32.3 Animal Body Cavities There are three major types of body cavities among the animals. (*a*) Acoelomates do not have enclosed body cavities. (*b*) Pseudocoelomates have only one layer of muscle, and it lies outside the body cavity. (*c*) Coelomates have a peritoneum surrounding the internal organs. The body cavities of some coelomates, such as this earthworm, are segmented.





32.4 The Body Plan of a Simple Sponge The flow of water through the sponge is shown by blue arrows. The inner body wall is studded with choanocytes, a type of specialized feeding cell that may be a link between animals and colonial protists (see Figure 28.28).

Sponges (phylum **Porifera**, from the Latin, "pore bearers"), the simplest of animals, are **sessile**: They live attached to the substratum and do not move about. The body plan of all sponges—even large ones, which may reach more than a meter in length—is an aggregation of cells built around a water canal system. Feeding cells called *choanocytes* line the inside of the internal chambers. These cells, with a collar of microscopic villi and a single flagellum, bear a striking resemblance to choanoflagellates (see Figure 28.28). By beating their flagella, choanocytes cause the surrounding water to flow through the animal. The water, along with any food particles it contains, enters by way of small pores and passes into the water canals, where food particles are captured by the choanocytes. Water then exits through one or more larger openings called *oscula* (Figure 32.4).

Between the thin epidermis and the choanocytes is another layer of cells, some of which are similar to amoebas and move about within the body. A supporting skeleton is also present, in the form of simple or branching spines, called *spicules*, and often an elastic, complex, network of fibers. A few species of sponges are carnivores that trap prey on hook-shaped spicules that protrude from the body surface. Sponges also have an extracellular matrix, composed of collagens, adhesive glycoproteins, and other molecules, that holds the cells together. This molecular adhesion system may also be involved in cell–cell signaling.

Thus, sponges are functionally more complex than a superficial look at their morphology might suggest. Nonetheless, sponges are loosely organized. Even if a sponge is completely disassociated by being strained through a filter, its cells can reassemble into a new sponge.

Most of the 5,500 species of sponges are marine animals; only about 50 species live in fresh water. Sponges come in a wide variety of sizes and shapes that are adapted to different movement patterns of water (Figure 32.5). Sponges living in intertidal or shallow subtidal environments, where they are subjected to strong wave action, hug the substratum. Many sponges that live in calm waters are simple, with a single large osculum on top of the body. Most sponges that live in slowly flowing water are flattened and are oriented at right

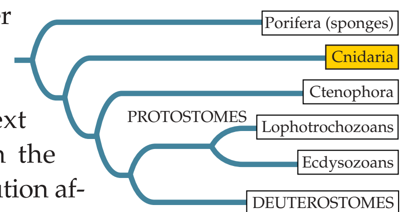
(*a*) *Euplectella aspergillum* (*b*) *Aplysina lacunosa* (*c*) *Asbestopluma* sp.

32.5 Sponges Differ in Size and Shape (*a*) Glass sponges are named after their glasslike spicules, which are formed of silicon. (*b*) The purple tube sponge is typical of many simple marine sponges. (*c*) This predatory sponge uses its hook-shaped spicules to capture small prey animals.

angles to the direction of current flow; they intercept water and the prey it contains as it flows past them.

Sponges reproduce both sexually and asexually. In most species, a single individual produces both eggs and sperm, but individuals do not self-fertilize. Water currents carry sperm from one individual to another. Asexual reproduction is by budding and fragmentation.

Cnidarians: Two Cell Layers and Blind Guts



Animals in all phyla other than Porifera have distinct cell layers and symmetrical bodies. The next lineage to diverge from the main line of animal evolution after the sponges led to a phylum of animals called the **cnidarians** (phylum **Cnidaria**). These animals are *diploblastic* (have two cell layers) and have a blind gut with only one entrance (the mouth/anus). Despite their relative structural simplicity, cnidarians have structural molecules (such as collagen, actin, and myosin) and homeobox genes.

Cnidarians are simple but specialized carnivores

Cnidarians appeared early in evolutionary history and radiated in the late Precambrian. About 11,000 cnidarian species—jellyfish, sea anemones, corals, and hydrozoans—live today (Figure 32.6), all but a few in the oceans. The smallest cnidarians can hardly be seen without a microscope; the largest known jellyfish is 2.5 meters in diameter. All cnidarians are carnivores; some gain additional nutrition from photosynthetic endosymbionts. The cnidarian body plan combines a low metabolic rate with the ability to capture large prey. These traits allow cnidarians to survive in environments where encounters with prey are infrequent.

All cnidarians possess tentacles covered with *cnidocytes*, specialized cells that contain stinging organelles called *nematocysts*, which can inject toxins into their prey (Figure 32.7). Cnidocytes allow cnidarians to capture large and complex prey, which are carried into the mouth by retracting the tentacles. Nematocysts are responsible for the stings that some jellyfish inflict on human swimmers.

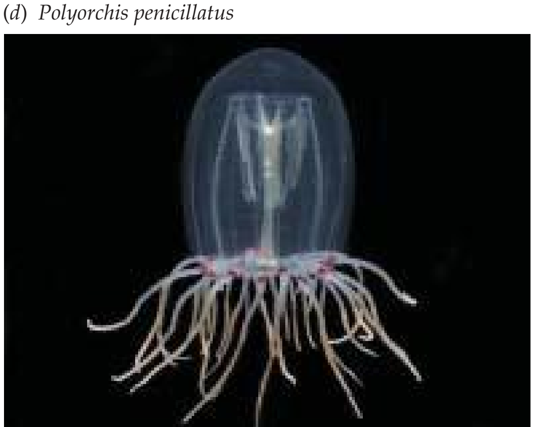
The cnidarian body is based on a "sac plan," in which the mouth is connected to a blind sac called the *gastrovascular cavity*. The sac functions in digestion, circulation, and gas exchange and acts as a hydrostatic skeleton. The single opening serves as both mouth and anus. Cnidarians also have epithelial cells with muscle fibers whose contractions enable the animals to move, as well as simple *nerve nets* that integrate their body activities.

(*a*) *Anthopleura elegantissima*

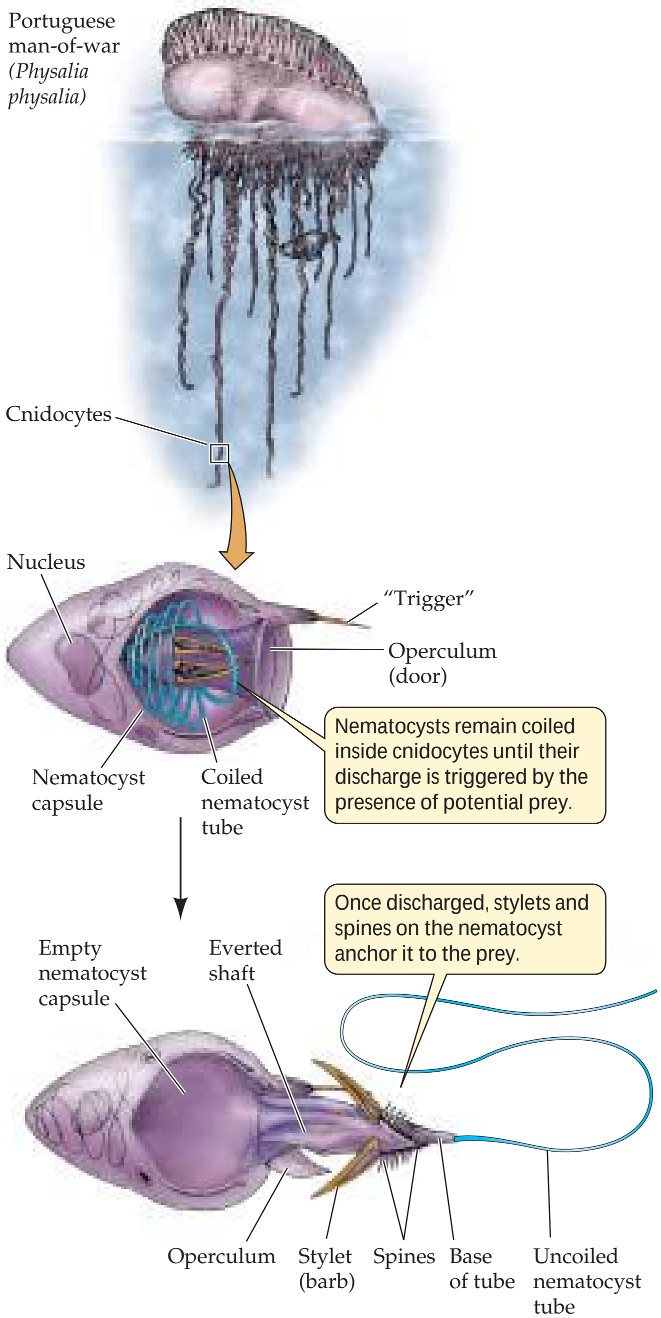
(*b*) *Ptilosarcus gurneyi*

(*c*) *Pelagia panopyra*

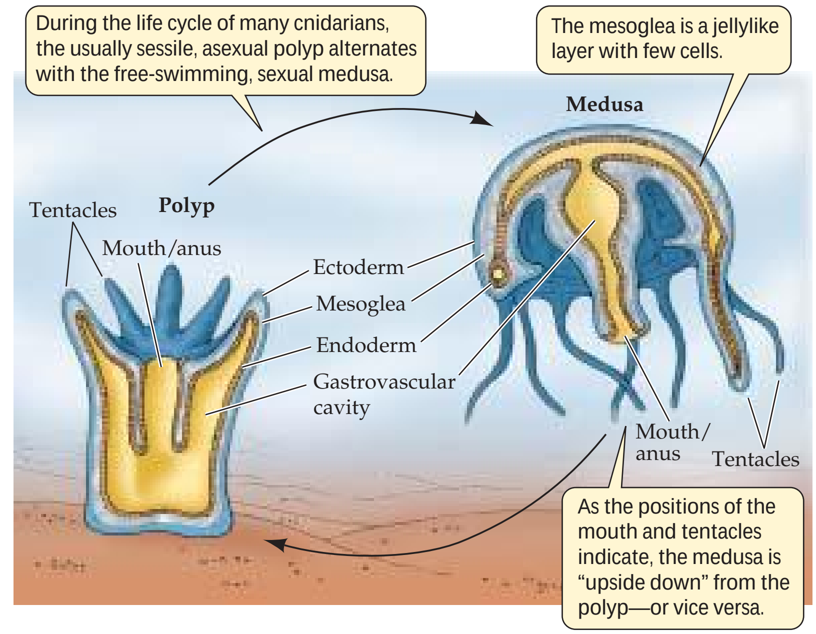
(*d*) *Polyorchis penicillatus*



32.6 Diversity among Cnidarians (*a*) The nematocyst-studded tentacles of this sea anemone from British Columbia are poised to capture large prey carried to the animal by water movement. (*b*) The orange sea pen is a colonial cnidarian that lives in soft bottom sediments and projects polyps above the substratum. (*c*) This purple jellyfish illustrates the complexity of a scyphozoan medusa. (*d*) The internal structure of the medusa of a North Atlantic colonial hydrozoan is visible here.



32.7 Nematocysts Are Potent Weapons Cnidarians such as the Portuguese man-of-war, which possesses a large number of nematocysts, can subdue and consume very large prey.



32.8 A Generalized Cnidarian Life Cycle Cnidarians typically have two body forms, one asexual (the polyp) and the other sexual (the medusa).

Cnidarian life cycles have two stages

The generalized cnidarian life cycle has two distinct stages (Figure 32.8), although many species lack one of these stages:

- The sessile **polyp** stage has a cylindrical stalk attached to the substratum. Tentacles surround a mouth/anus located at the end opposite from the stalk. Individual polyps may reproduce by budding, thereby forming a colony.
- The **medusa** (plural, medusae) is a free-swimming stage shaped like a bell or an umbrella. It typically floats with its mouth and tentacles facing downward. Medusae of many species produce eggs and sperm and release them into the water. When an egg is fertilized, it develops into a free-swimming, ciliated larva called a **planula**, which eventually settles to the bottom and develops into a polyp.

Although the polyp and medusa stages appear very different, they share a similar body plan. A medusa is essentially a polyp without a stalk. Most of the outward differences between polyps and medusae are due to the *mesoglea*, an internal mass of jellylike material that lies between the two cell layers. The mesoglea contains few cells and has a low metabolic rate. In polyps, the mesoglea is usually thin; in medusae it is very thick, constituting the bulk of the animal.

ANTHOZOANS. All 6,000 species of sea anemones and corals that constitute the **anthozoans** (class **Anthozoa**) are marine animals. Evidence from morphology, rRNA, and mitochondrial genes suggests that the anthozoans, which lack the medusa stage, are sister to the other classes of cnidarians, and that the medusa stage evolved after the anthozoa diverged from those other lineages. In the anthozoans, the polyp produces eggs and sperm, and the fertilized egg develops into a planula that develops directly into another polyp. Many species can also reproduce asexually by budding or fission. Sea anemones (see Figure 32.6*a*) are solitary. They are widespread in both warm and cold ocean waters. Many sea anemones are able to crawl slowly on the discs with which they attach themselves to the substratum. A few species can swim and some can burrow.

Sea pens (see Figure 32.6*b*), by contrast, are sessile and colonial. Each colony consists of at least two different kinds of polyps. The primary polyp has a lower portion anchored in the bottom sediment and a branched upper portion that projects above the substratum. Along the upper portion, the primary polyp produces smaller secondary polyps by budding. Some of these secondary polyps can differentiate into feeding polyps, while others circulate water through the colony.

Corals also are usually sessile and colonial. The polyps of most corals form a skeleton by secreting a matrix of organic molecules upon which they deposit calcium carbonate, which forms the eventual skeleton of the coral colony. The forms of coral skeletons are species-specific and highly diverse. The common names of coral groups—horn corals, brain corals, staghorn corals, and organ pipe corals, among others—describe their appearance (Figure 32.9*a*).

As a coral colony grows, old polyps die, but their calcareous skeletons remain. The living members form a layer on top of a growing bank of skeletal remains, eventually forming chains of islands and reefs (Figure 32.9*b*). The Great Barrier Reef along the northeastern coast of Australia is a system of coral formations more than 2,000 km long and as wide as 150 km. A reef hundreds of kilometers long in the Red Sea has been calculated to contain more material than all the buildings in the major cities of North America combined.

Corals flourish in nutrient-poor, clear, tropical waters. They can grow rapidly in such environments because the photosynthetic dinoflagellates that live symbiotically within their cells provide them with products of photosynthesis and contribute to calcium deposition. In turn, the corals provide the dinoflagellates with a place to live and nutrients. This symbiotic relationship explains why reef-forming corals are restricted to clear surface waters, where light levels are high enough to allow photosynthesis.

Coral reefs throughout the world are being threatened both by global warming, which is raising the temperatures of shallow tropical ocean waters, and by polluted runoff from development on adjacent shorelines. An overabundance of nitrogen in the runoff gives an advantage to algae, which overgrow and eventually smother the corals.

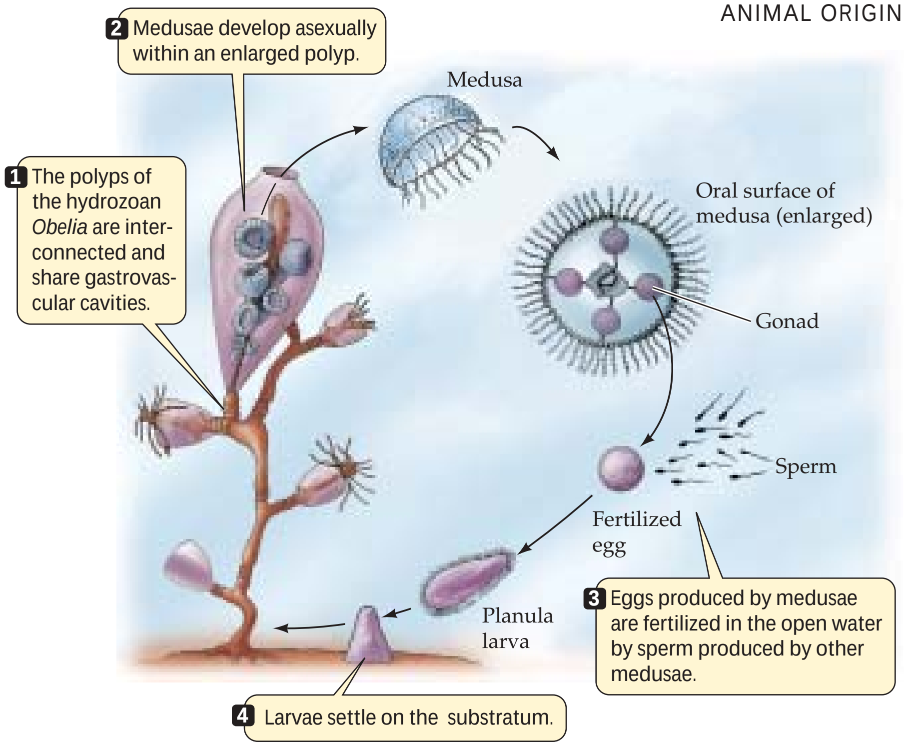
HYDROZOANS. Life cycles are diverse among the **hydrozoans** (class **Hydrozoa**). The polyp typically dominates the life cycle, but some species have only medusae and others only polyps. Most hydrozoans are colonial. A single planula eventually gives rise to a colony of many polyps, all interconnected and sharing a continuous gastrovascular cavity (Figure 32.10). Within such a colony (the man-of-war in Figure 32.7 is an example), some polyps have tentacles with many nematocysts; they capture prey for the colony. Others lack tentacles and are unable to feed, but are specialized for the production of medusae. Still others are fingerlike and defend the colony with their nematocysts.

SCYPHOZOANS. The several hundred species of **scyphozoans** (class **Scyphozoa**) are all marine. The mesoglea of their medusae is thick and firm, giving rise to their common names, jellyfish or sea jellies. The medusa, rather than the polyp, dominates the life cycle of scyphozoans. An indi-

32.9 Corals The South Pacific is home to many spectacular corals. (*a*) This unusually large formation of chalice coral was photographed off the coast of Fiji. (*b*) Many different species of corals and sponges grow together on this reef in Palau.

(*a*) *Montipora sp.*

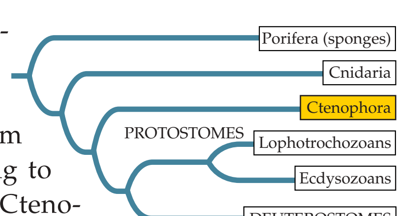
(*b*)



32.10 Hydrozoans Often Have Colonial Polyps The polyps within a hydrozoan colony may differentiate to perform specialized tasks. In the species whose life cycle is diagrammed here, the medusa is the sexual reproductive stage, producing eggs and sperm in organs called gonads.

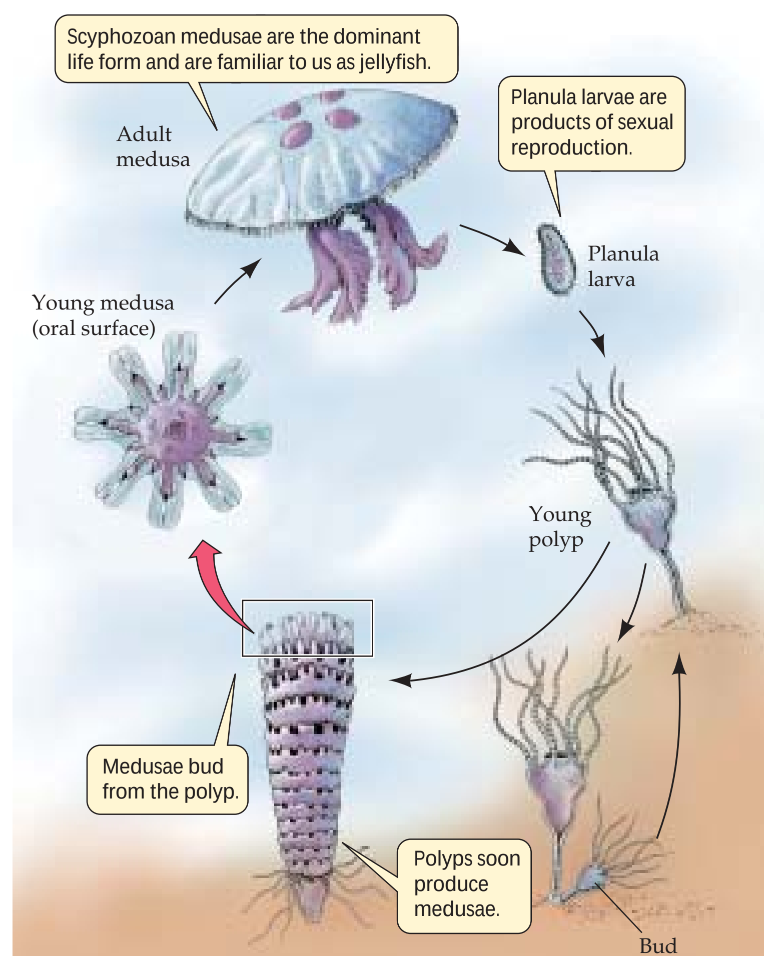
vidual medusa is male or female, releasing eggs or sperm into the open sea. The fertilized egg develops into a small planula that quickly settles on a substratum and develops into a small polyp. This polyp feeds and grows and may produce additional polyps by budding. After a period of growth, the polyp begins to bud off small medusae (Figure 32.11). These medusae feed, grow, and transform themselves into adult medusae, which are commonly seen during summer in harbors and bays.

Ctenophores: Complete Guts and Tentacles



Ctenophores (phylum **Ctenophora**) were the next lineage to diverge from the lineage leading to all other animals. Ctenophores, also known as comb jellies, have body plans that are superficially similar to those of cnidarians. Both have two cell layers separated by a thick, gelatinous mesoglea, and both have radial symmetry and feeding tentacles. Like cnidarians, ctenophores have low metabolic rates because they are composed primarily of inert mesoglea. Unlike cnidarians, however, ctenophores have a complete gut. Food enters through a mouth, and wastes are eliminated through two anal pores.

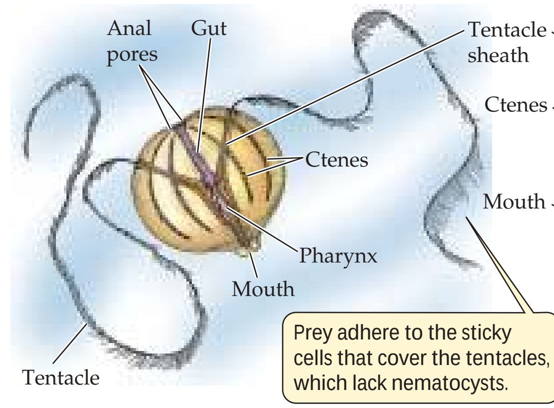
Ctenophores have eight comblike rows of fused plates of cilia, called *ctenes* (Figure 32.12). Ctenophores move by beating these cilia rather than by muscular contractions. Ctenophoran tentacles do not have nematocysts; rather, they are covered with cells that discharge adhesive material when they contact prey. After capturing its prey, a ctenophore retracts its tentacles to bring the food to its mouth. In some species, the entire surface of the body is coated with sticky mucus that captures prey. All of the 100 known species of ctenophores eat small animals. They are common in open seas.



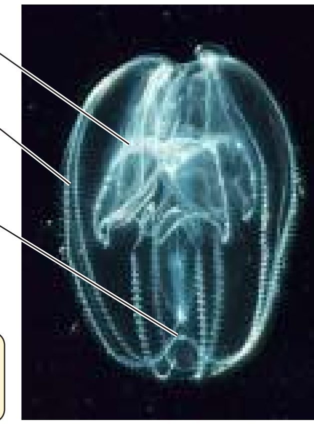
32.11 Medusae Dominate Scyphozoan Life Cycles Scyphozoan medusae are the familiar jellyfish of coastal waters. The small, sessile polyps quickly produce medusae (see Figure 32.6*c*).

32.12 Comb Jellies Feed with Tentacles (*a*) The body plan of a typical ctenophore. The long, sticky tentacles sweep through the water, efficiently harvesting small prey. (*b*) A comb jelly photographed in Sydney Harbour, Australia, has short tentacles.

(a)



(b) *Bolinopsis chuni*



Ctenophore life cycles are simple. Gametes are produced in structures called *gonads*, located on the walls of the gastrovascular cavity. The gametes are released into the cavity and then discharged through the mouth or the anal pores. Fertilization takes place in open seawater. In nearly all species, the fertilized egg develops directly into a miniature ctenophore that gradually grows into an adult.

The Evolution of Bilaterally Symmetrical Animals

The phylogenetic tree pictured in Figure 32.1 assumes that all bilaterally symmetrical animals share a common ancestor, but it does not tell us what that ancestor looked like. To infer the form of the earliest bilaterians, zoologists use evidence from the genes, development, and structure of existing animals. An important clue is provided by the fact that the development of all bilaterally symmetrical animals is controlled by homologous *Hox* and homeobox genes. Regulatory genes with similar functions are unlikely to have evolved independently in several different animal lineages.

Fossilized tracks from late Precambrian times provide additional clues to the nature of early bilaterians (Figure 32.13). The complexity of the movements recorded by these tracks suggests that early bilaterians had circulatory systems, systems of antagonistic muscles, and a tissue- or fluid-filled body cavity, structures that are also suggested by genetic data.

An early lineage split separated protostomes and deuterostomes

The next major split in the animal lineage after the divergence of the ctenophores occurred during the Cambrian period and separated two groups that have been evolving separately ever since. These two major lineages—the protostomes and the deuterostomes—dominate today's fauna. Members of both lineages are triploblastic (have three cell layers), bilaterally symmetrical, and cephalized. Because their skeletons and body cavities are more complex than those of the animals we have discussed so far, they are capable of more complex movements.

The most important shared, derived traits that unite the protostomes are

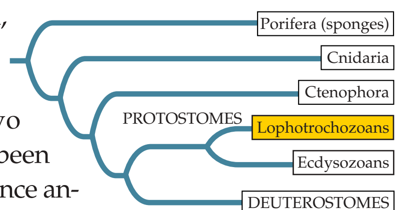
- An anterior brain that surrounds the entrance to the digestive tract
- A ventral nervous system consisting of paired or fused longitudinal nerve cords
- A free-floating larva with a food-collecting system consisting of compound cilia on multiciliate cells
- A blastopore that becomes the mouth
- Spiral cleavage (in some species)

32.13 The Trail of an Early Bilaterian These fossilized tracks indicate that their maker was able to crawl.

The major shared, derived traits that unite the deuterostomes are

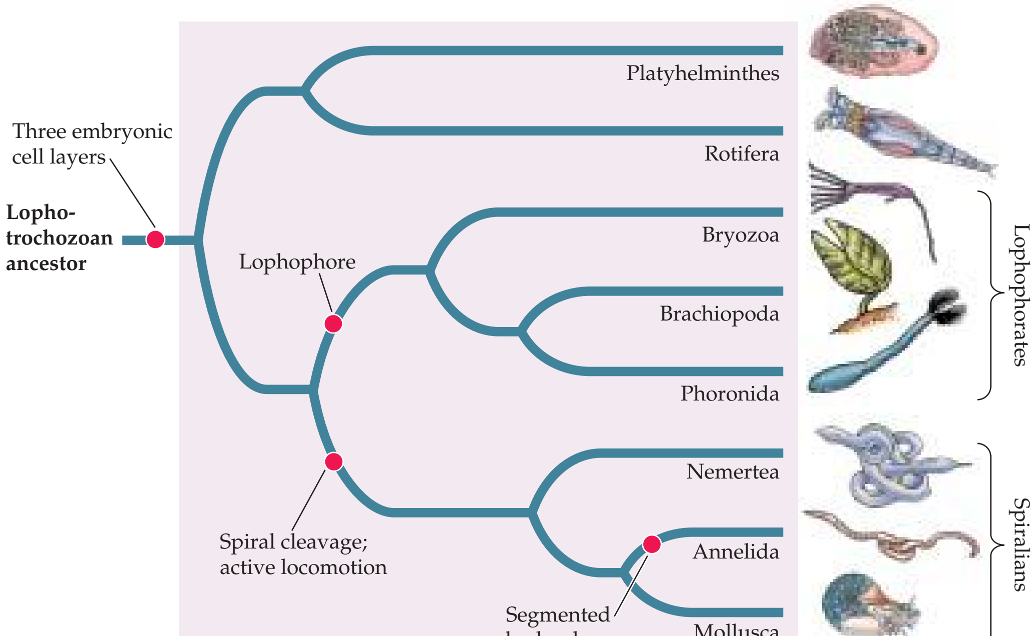
- A dorsal nervous system
- A larva, if present, that has a food-collecting system consisting of cells with a single cilium
- A blastopore that becomes the anus
- Radial cleavage

The protostomes split into two lineages



Developmental, structural, and molecular data all suggest that the protostomes soon split into two major lineages that have been evolving independently since ancient times: lophotrochozoans and ecdysozoans. **Lophotrochozoans**, the animals we will discuss in the remainder of this chapter, grow by adding to the size of their skeletal elements. Some of them use cilia for locomotion, and many lineages have a type of free-living larva known as a **trochophore** (see Figure 32.23) The phylogeny of lophotrochozoans we will use in this chapter is shown in Figure 32.14. In contrast, **ecdysozoans**, the animals we will discuss in the next chapter, increase in size by molting their external skeletons. They move by mechanisms other than ciliary action, and they all have a common set of homeobox genes.

32.14 A Current Phylogeny of Lophotrochozoans Three major lineages, including the lophophorate and spiralian phyla, dominate the tree. Some small phyla are not included here.



Simple Lophotrochozoans

The simplest lophotrochozoans—flatworms and rotifers—are small aquatic or parasitic animals. They move by rapidly beating cilia, and most have only simple organs.

Flatworms move by beating cilia

Members of the phylum **Platyhelminthes**, or **flatworms**, the simplest lophotrochozoans (Figure 32.15), are bilaterally symmetrical, unsegmented, acoelomate animals. They lack organs for transporting oxygen to internal tissues, and they have only simple cells for excreting metabolic wastes. Their lack of transport systems dictates that each cell must be near a body surface, a requirement met by their dorsoventrally flattened body form.

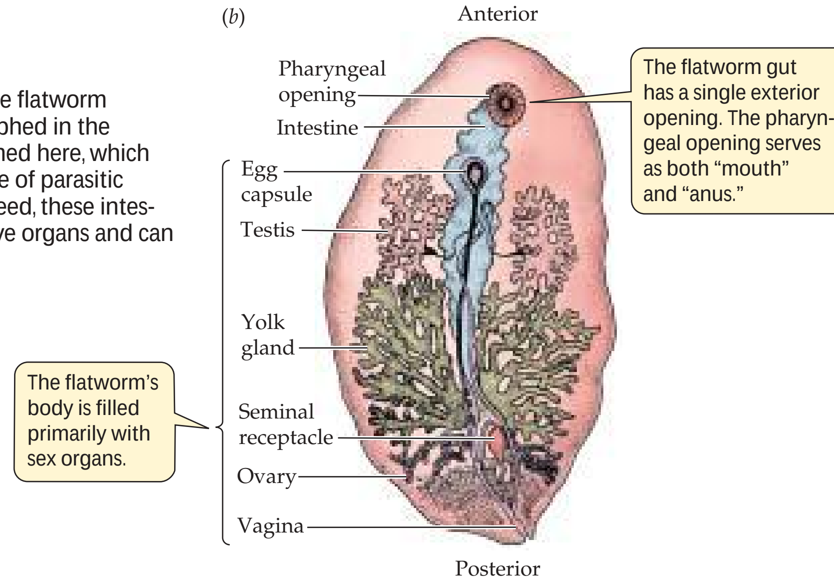
The digestive tract of a flatworm consists of a mouth opening into a blind sac. However, the sac is often highly branched, forming intricate patterns that increase the surface area available for the absorption of nutrients. Flatworms either feed on animal tissues (living or dead), or absorb nutients from a host's gut. Free-living flatworms glide over surfaces, powered by broad bands of cilia. This form of movement is very slow, but it is sufficient for small, scavenging animals.

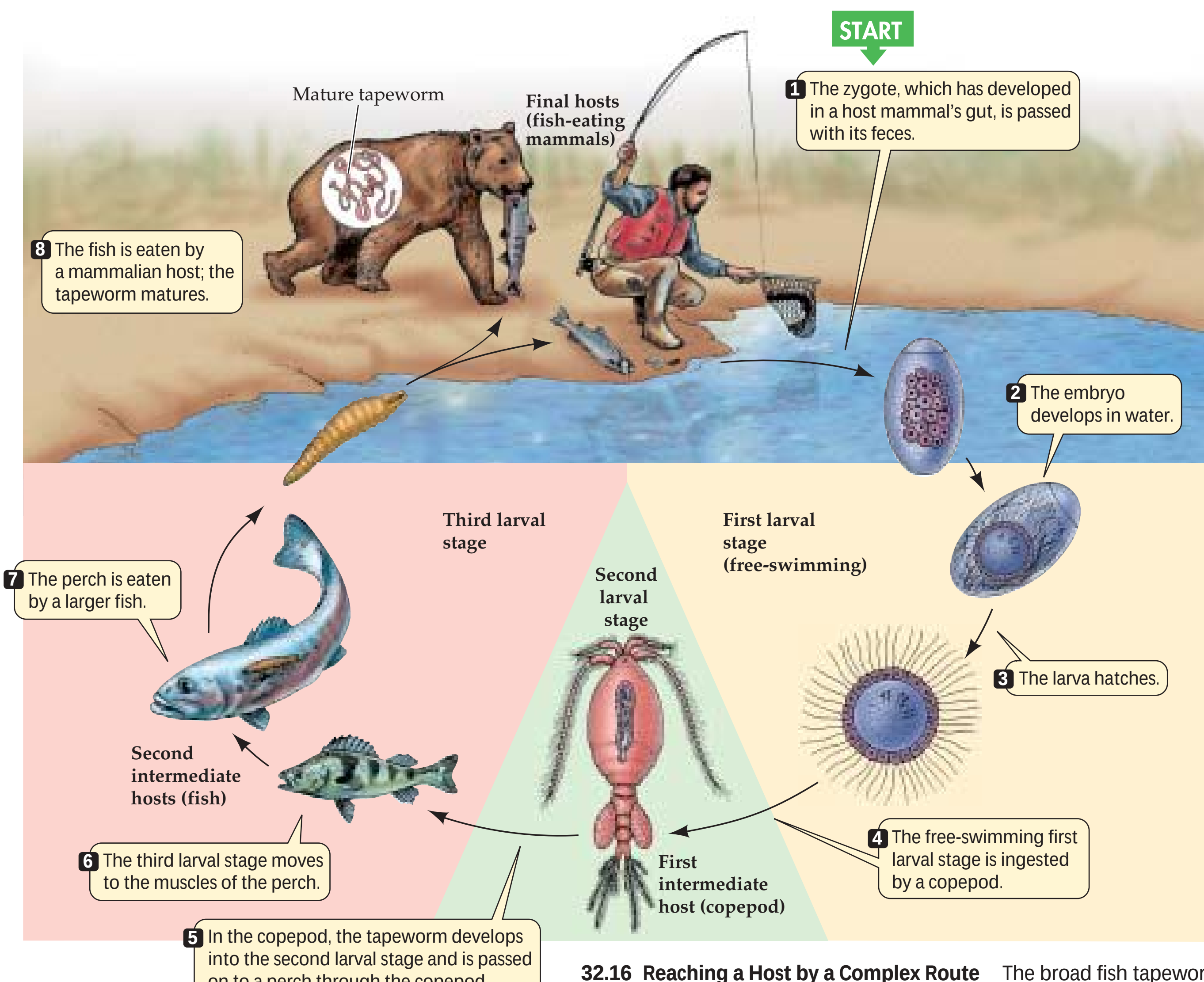
The flatworms that are probably most similar to the ancestral bilaterians are the turbellarians (class **Turbellaria**), which are small, free-living marine and freshwater animals (a few live in moist terrestrial habitats). At one end they have a head with chemoreceptor organs, two simple eyes, and a tiny brain composed of anterior thickenings of the longitudinal nerve cords.

Although the earliest flatworms were free-living (Figure 32.15*a*), many species evolved a parasitic existence. A likely evolutionary transition was from feeding on dead organisms to feeding on the body surfaces of dying hosts to invading and consuming parts of living, healthy hosts. Most of the 25,000 species of living flatworms—including the tapeworms (class **Cestoda**) and flukes (class **Trematoda**; Figure 32.15*b*)—are internal parasites. These flatworms absorb digested food from the digestive tracts of their hosts, so many of them lack digestive tracts. They inhabit the bodies of many vertebrates; some cause serious human diseases, such as schistoso-

32.15 Flatworms Live Freely and Parasitically (*a*) Some flatworm species are free-living, like this marine flatworm photographed in the oceans off Sulawesi, Indonesia. (*b*) The flatworm diagrammed here, which lives parasitically in the gut of sea urchins, is representative of parasitic flukes. Because their hosts provide all the nutrition they need, these intestinal parasites do not require elaborate feeding or digestive organs and can devote most of their bodies to reproduction.

(*a*) *Pseudoceros bifurcus*





32.16 Reaching a Host by a Complex Route The broad fish tapeworm, *Diphyllobothrium latum*, must pass through the bodies of a copepod (a type of crustacean) and a fish before it can reinfect its primary host, a mammal. Such complex life cycles assist the flatworm’s recolonization of hosts, but they also offer opportunities for humans to break the cycle with hygienic measures.

miasis. Monogeneans (class **Monogenea**) are external parasites of fishes and other aquatic vertebrates.

Parasites live in nutrient-rich environments where food is delivered to them, but they face other challenges. To complete their life cycle, parasites must overcome the defenses of their host. And because they die when their host dies, they must disperse their offspring to new hosts while their host is still living. The fertilized eggs of some parasitic flatworms are voided with the host's feces and later ingested directly by other host individuals. However, most parasitic species have complex life cycles involving one or more intermediate hosts and several larval stages (Figure 32.16). Such life cycles facilitate the transfer of individual parasites among hosts.

Rotifers are small but structurally complex

Rotifers (phylum **Rotifera**) are bilaterally symmetrical, unsegmented, pseudocoelomate lophotrochozoans. Most rotifers are tiny (50–500 μm long)—smaller than some ciliate protists—but they have highly developed internal organs (Figure 32.17). A complete gut passes from an anterior mouth to a posterior anus; the pseudocoel functions as a hydrostatic skeleton. Most rotifers propel themselves through the water by means of rapidly beating cilia rather than by muscular contraction. This type of movement is effective because rotifers are so small.

The most distinctive organs of rotifers are those they use to collect and process food. A conspicuous ciliated organ called the *corona* surmounts the head of many species. Coordinated beating of the cilia sweeps particles of organic matter from the water into the animal's mouth and down to a complicated structure called the *mastax*, in which food is ground into small pieces. By contracting the muscles around the pseudocoel, a few rotifer species that prey on protists and small animals can protrude the mastax through the mouth and seize small objects with it. Males and females are found in most species, but some species have only females that produce diploid eggs without being fertilized by a male.

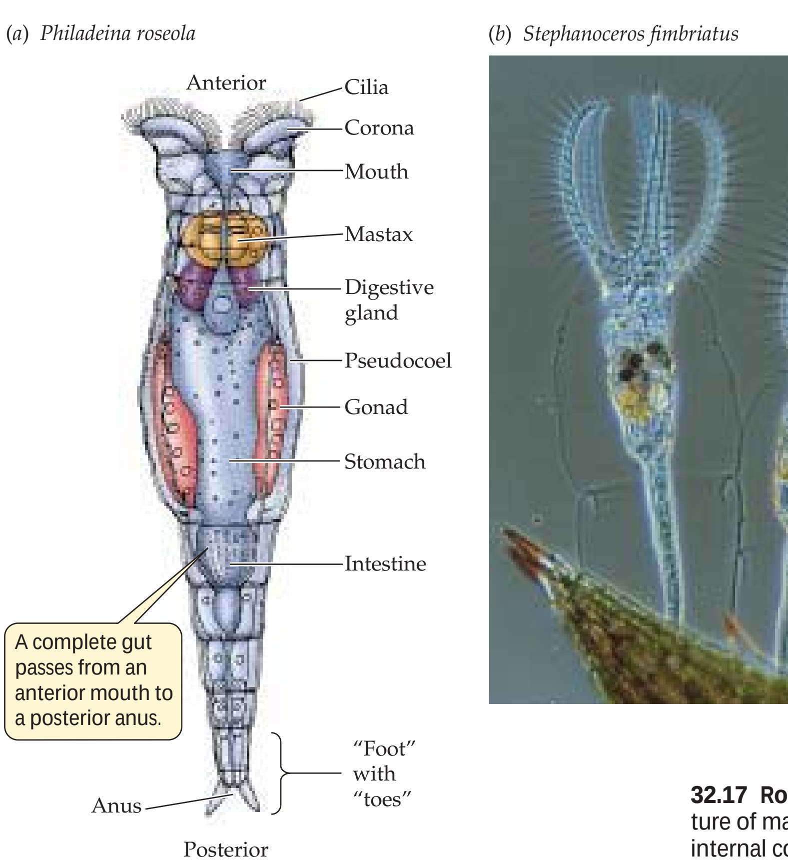
Some rotifers are marine, but most of the 1,800 known species live in fresh water. Members of a few species rest on the surface of mosses or lichens in a desiccated, inactive state until it rains. When rain falls, they absorb water and become mobile, feeding in the films of water that temporarily cover the plants. Most rotifers live no longer than 1 or 2 weeks.

Lophophorates: An Ancient Body Plan

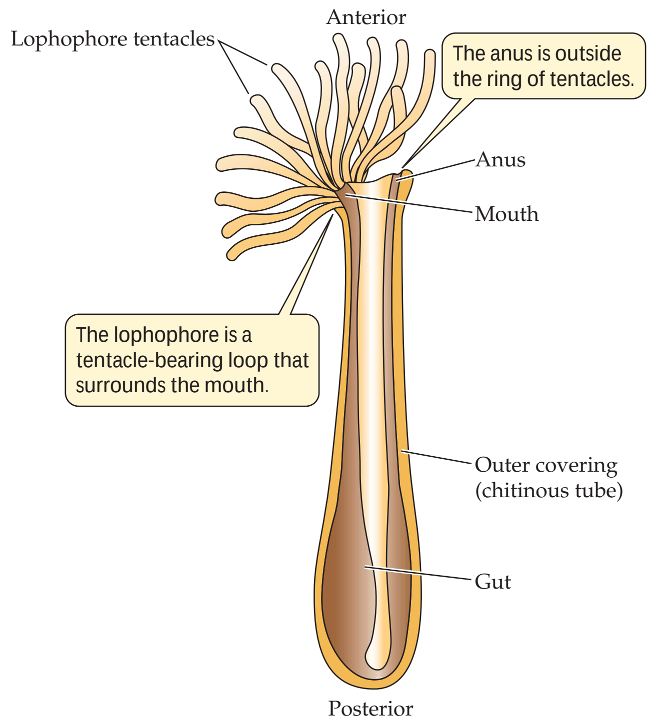
After the platyhelminthes and rotifers diverged from it, the lophotrochozoan lineage divided into two branches. The descendants of those branches became the modern **lophophorates**—the subject of this section—and the **spiralians**, which we will discuss in the following section.

About 4,850 living species of lophophorates are known, but many times that number of species existed during the Paleozoic and Mesozoic eras. Three lophophorate phyla survive today: Phoronida, Brachiopoda, and Ectoprocta. Nearly all members of these phyla are marine; only a few species of ectoprocts live in fresh water.

Lophophorate animals obtain food by filtering it from the surrounding water, a trait they share with many other protostomes. The most conspicuous feature of these animals is the **lophophore**, a circular or U-shaped ridge around the mouth that bears one or two rows of ciliated, hollow tentacles (Figure 32.18). This large and complex structure is an organ for both food collection and gas exchange. Nearly all adult lophophorate animals are sessile, and they use the tentacles and cilia of their lophophore to capture *plankton* (small floating organisms) from the water. Lophophorates also have a U-shaped gut; the anus is located close to the mouth, but outside the tentacles.



32.17 Rotifers (*a*) The rotifer diagrammed here reflects the general structure of many free-living species in the phylum. (*b*) A micrograph reveals the internal complexity of these living rotifers.



32.18 Lophophore Artistry The lophophore dominates the anatomy of this phoronid. The phoronid gut is U-shaped.

Phoronids are sedentary lophophorates

The 20 known species of **phoronids** (phylum **Phoronida**) are sedentary worms that live in muddy or sandy sediments or attached to a rocky substratum. Phoronids are found in marine waters ranging from intertidal zones to about 400 meters deep. They range in size from 5 to 25 cm in length. They secrete chitinous tubes, in which they live (Figure 32.18). The lophophore is the most conspicuous external feature of the phoronids. Cilia drive water into the top of the lophophore, and water exits through the narrow spaces between the tentacles. Suspended food particles are caught and transported to the mouth by ciliary action. In most species, eggs are released into the water, where they are fertilized, but some species produce large eggs that are fertilized internally, where they are brooded until they hatch.

Ectoprocts are colonial lophophorates

Ectoprocts (phylum **Ectoprocta**) are colonial lophophorates that live in a "house" made of material secreted by the external body wall. A colony consists of many small (1–2 mm) individuals connected by strands of tissue along which materials can be moved (Figure 32.19*a*). Most of the 4,500 species of ectoprocts are marine, but a few live in fresh water. They are able to oscillate and rotate the lophophore to increase contact with prey (Figure 32.19*b*) and can retract it into the tube.

A colony of ectoprocts is created by the asexual reproduction of its founding members. A single colony may contain as many as 2 million individuals. In some species, individual colony members are specialized for feeding, reproduction, defense, or support. Ectoprocts reproduce sexually by releasing sperm into the water, where they are collected by other individuals. Eggs are fertilized internally, and developing embryos are brooded before they exit as larvae to seek suitable sites for attachment to the substratum.

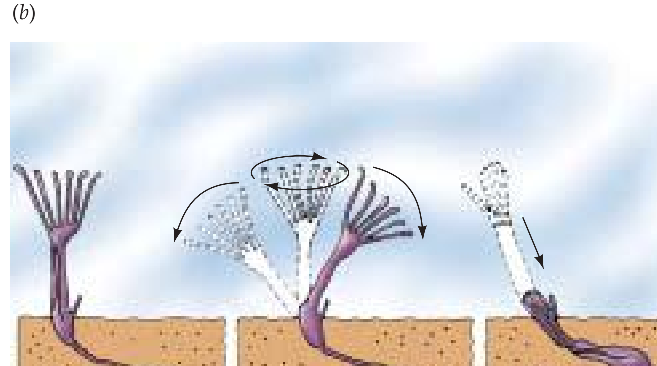
Brachiopods superficially resemble bivalve mollusks

Brachiopods (phylum **Brachiopoda**) are solitary marine lophophorate animals. Their shells are divided into two parts

(*a*) *Lophopus crystallinus*

32.19 Ectoprocts (*a*) Branching colonies of ectoprocts may appear plantlike. (*b*) Ectoprocts have greater control over the movement of their lophophores than members of other lophophorate phyla.

(*b*)



32.20 Brachiopods The lophophore of this North Pacific brachiopod can be seen between the valves of its shell.

that are connected by a ligament (Figure 32.20). The two halves can be pulled shut to protect the soft body. Brachiopods superficially resemble bivalve mollusks, but the brachiopod shell differs from that of mollusks in that the two halves are dorsal and ventral rather than lateral. The two-armed lophophore of a brachiopod is located within the shell. The beating of cilia on the lophophore draws water into the slightly opened shell. Food is trapped in the lophophore and directed to a ridge, along which it is transferred to the mouth. Most brachiopods are between 4 and 6 cm long, but some are as long as 9 cm.

Brachiopods live attached to a solid substratum or embedded in soft sediments. Most species are attached by means of a short, flexible stalk that holds the animal above the substratum. Gases are exchanged across body surfaces, especially the tentacles of the lophophore. Most brachiopods release their gametes into the water, where they are fertilized. The larvae remain among the plankton for only a few days before they settle and develop into adults.

Brachiopods reached their peak abundance and diversity in Paleozoic and Mesozoic times. More than 26,000 fossil species have been described. Only about 335 species survive, but they are common in some marine environments.

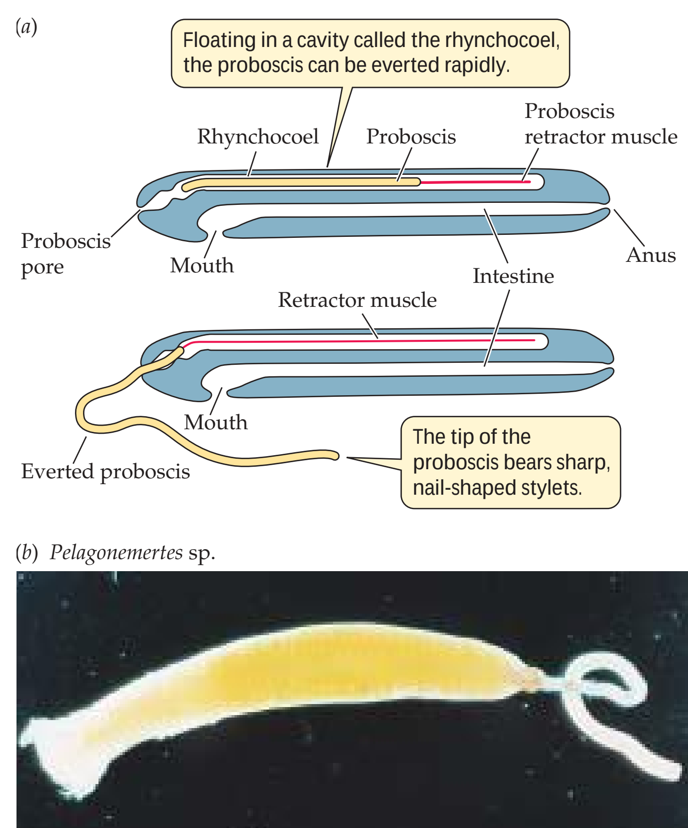
Spiralians: Spiral Cleavage and Wormlike Body Plans

The spiralian lineage, containing animals that typically have spiral cleavage patterns, gave rise to many phyla. Members of more than a dozen of these phyla are *wormlike*; that is, they are bilaterally symmetrical, legless, soft-bodied, and at least several times longer than they are wide. This body form enables animals to move efficiently through muddy and sandy marine sediments. Most of these phyla have no more than several hundred species. The most species-rich spiralian phylum, the mollusks, shows significant modifications of the wormlike body plan.

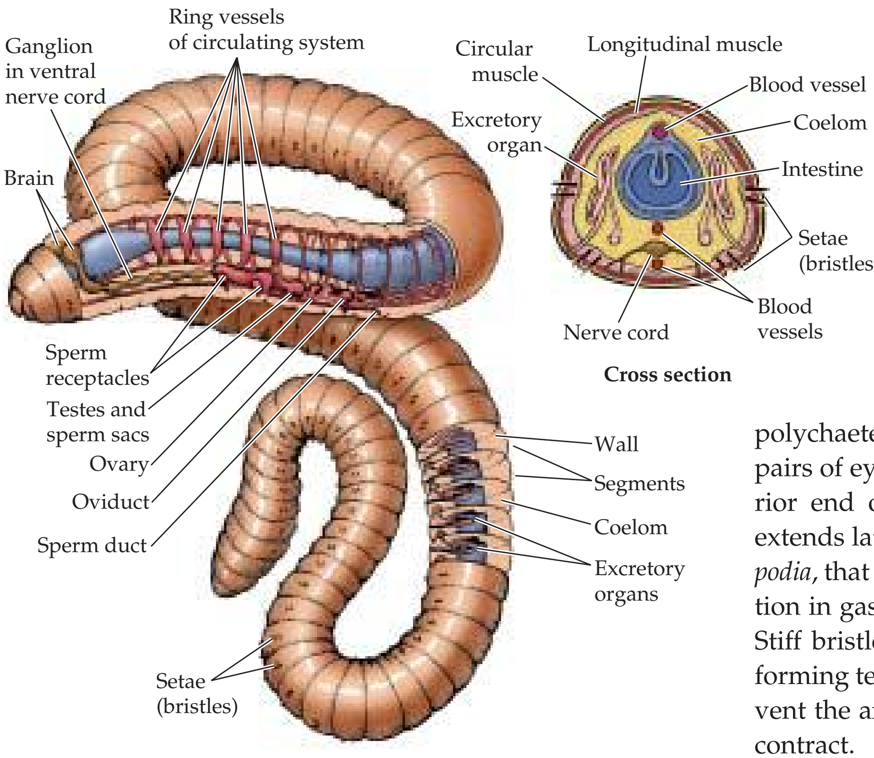
Ribbon worms are unsegmented

The carnivorous **ribbon worms** (phylum **Nemertea**) are dorsoventrally flattened. They have nervous and excretory systems similar to those of flatworms, but unlike flatworms, they have a complete digestive tract with a mouth at one end and an anus at the other. Food moves in one direction through the digestive tract and is acted on by a series of digestive enzymes. Small ribbon worms move by beating their cilia. Larger ones employ waves of muscle contraction to move over the surface of sediments or to burrow. Movement by both of these methods is slow.

Within the body of nearly all of the 900 species of ribbon worms is a fluid-filled cavity called the *rhynchocoel*, within which lies a hollow, muscular *proboscis*. The proboscis, which is the feeding organ, may extend much of the length of the worm. Contraction of the muscles surrounding the rhynchocoel causes the proboscis to be everted explosively through an anterior opening (Figure 32.21) without moving the rest of the animal. The proboscis of most ribbon worms



32.21 Ribbon Worms (*a*) The proboscis is the ribbon worm's feeding organ. (*b*) This deep-water nemertean displays an everted proboscis.



32.22 Annelids Have Many Body Segments The segmented structure of the annelids is apparent both externally and internally. Most organs of this earthworm are repeated serially.

is armed with a sharp stylet that pierces the prey. Paralysis-causing toxins produced by the proboscis are discharged into the wound. Reproduction and development in ribbon worms is highly varied.

Segmentation improved locomotion in the annelids

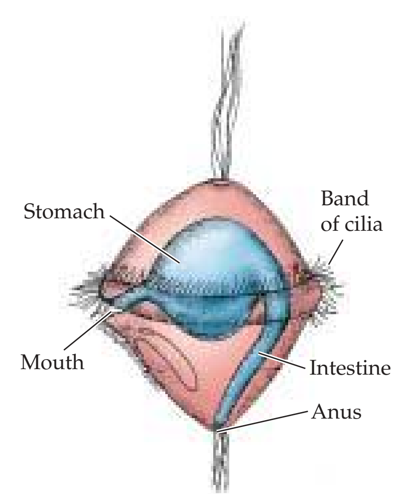
Segmentation allows an animal to alter the shape of its body in complex ways and to control its movements more precisely. Fossils of segmented worms are known from the middle Cambrian; the earliest forms are thought to have been burrowing marine animals. Segmentation evolved several times among spiralians; we will discuss only one of the phyla with segmented members: the annelids.

The **annelids** (phylum **Annelida**) are a diverse group of segmented spiralian worms (Figure 32.22). The coelom in each segment is isolated from those in other segments. A separate nerve center called a *ganglion* controls each segment, and the ganglia are connected by nerve cords that coordinate their functioning. Most annelids lack a rigid, external protective covering. The body wall serves as a general surface for gas exchange in most species, but this thin, permeable body surface restricts annelids to moist environments; they lose body water rapidly in dry air. The approximately 16,500 described species live in marine, freshwater, and terrestrial environments.

POLYCHAETES. More than half of all annelid species are members of the class **Polychaeta** ("many hairs"). Nearly all polychaetes are marine animals. Most have one or more pairs of eyes and one or more pairs of tentacles at the anterior end of the body. The body wall in most segments extends laterally as a series of thin outgrowths, called *parapodia*, that contain many blood vessels. The parapodia function in gas exchange, and some species use them to move. Stiff bristles called *setae* protrude from each parapodium, forming temporary attachments to the substratum that prevent the animal from slipping backward when its muscles contract.

Typically, males and female polychaetes release gametes into the water, where the eggs are fertilized and develop into trochophore larvae (Figure 32.23). The trochophore is a distinctive larval type found among polychaetes, mollusks, and several other marine lineages with spiral cleavage. The second half of the name "lophotrochozoans" is derived from this larva, which is believed by many researchers to represent an evolutionary link between the annelids and the mollusks.

As the polychaete trochophore develops, it forms body segments at its posterior end; eventually it becomes a small



32.23 The Trochophore Larva The trochophore ("wheel-bearer") is a distinctive larval form found in several animal lineages with spiral cleavage, most notably the marine polychaete worms and the mollusks.

(*a*) *Spirobranchus* sp.

(*b*) *Lumbricus* sp.

(*c*) *Microbdella* sp.

(*d*) *Riftia* sp.

32.24 Diversity among the Annelids
(*a*) The feather duster worm is a marine polychaete with striking feeding tentacles. (*b*) Earthworms are hermaphroditic (each individual is simultaneously both male and female). When they copulate, each individual donates and receives sperm. (*c*) This Australian tiger leech is attached to a leaf by its posterior sucker as it waits for a mammalian host. (*d*) Vestimentiferans live around hydrothermal vents deep in the ocean. Their skin secretes chitin and other substances, forming tubes.

adult worm. Many polychaete species live in burrows in soft sediments and filter prey from the surrounding water with elaborate, feathery tentacles (Figure 32.24*a*).

OLIGOCHAETES. More than 90 percent of the approximately 3,000 described species of **oligochaetes** (class **Oligochaeta**) live in freshwater or terrestrial habitats. Oligochaetes ("few hairs") have no parapodia, eyes, or anterior tentacles, and they have relatively few setae. Earthworms—the most familiar oligochaetes (see Figure 32.22)—are scavengers and ingesters of soil, from which they extract food particles.

Unlike polychaetes, all oligochaetes are *hermaphroditic:* that is, each individual is both male and female. Sperm are exchanged simultaneously between two copulating individuals (Figure 32.24*b*). Eggs are laid in a cocoon outside the adult's body. The cocoon is shed, and when development is complete, miniature worms emerge and begin independent life.

LEECHES. **Leeches** (class **Hirudinea**) probably evolved from oligochaete ancestors. Most species live in freshwater or terrestrial habitats and, like oligochaetes, lack parapodia and tentacles. Like oligochaetes, leeches are hermaphroditic. The coelom of leeches is not divided into compartments; the coelomic space is largely filled with undifferentiated tissue. Groups of segments at each end of the body are modified to form suckers, which serve as temporary anchors that aid the leech in movement (Figure 32.24*c*). With its posterior sucker attached to a substratum, the leech extends its body by contracting its circular muscles. The anterior sucker is then attached, the posterior one detached, and the leech shortens itself by contracting its longitudinal muscles.

Many leeches are external parasites of other animals, but some species also eat snails and other invertebrates. A leech makes an incision in its host, from which blood flows. It can ingest so much blood in a single feeding that its body may enlarge several times. An anticoagulant secreted by the leech into the wound keeps the host's blood flowing. For hundreds of years leeches were widely employed in medicine. Even today they are used to reduce fluid pressure and prevent blood clotting in damaged tissues and to eliminate pools of coagulated blood.

VESTIMENTIFERANS. Members of one lineage of annelids, the **vestimentiferans** (class **Pogonophora**), evolved burrowing forms with a crown of tentacles through which gases are exchanged; they entirely lost their digestive systems (Figure 32.24*d*). Vestimentiferans secrete chitin and other substances to form the tubes in which they live.

A vestimentiferan's coelom consists of an anterior compartment into which the tentacles can be withdrawn, and a long, subdivided cavity that extends much of the length of its body. The posterior end of the body is segmented. Experiments using radioactively labeled molecules have shown that vestimentiferans take up dissolved organic matter at high rates from either the sediments in which they live or the surrounding water.

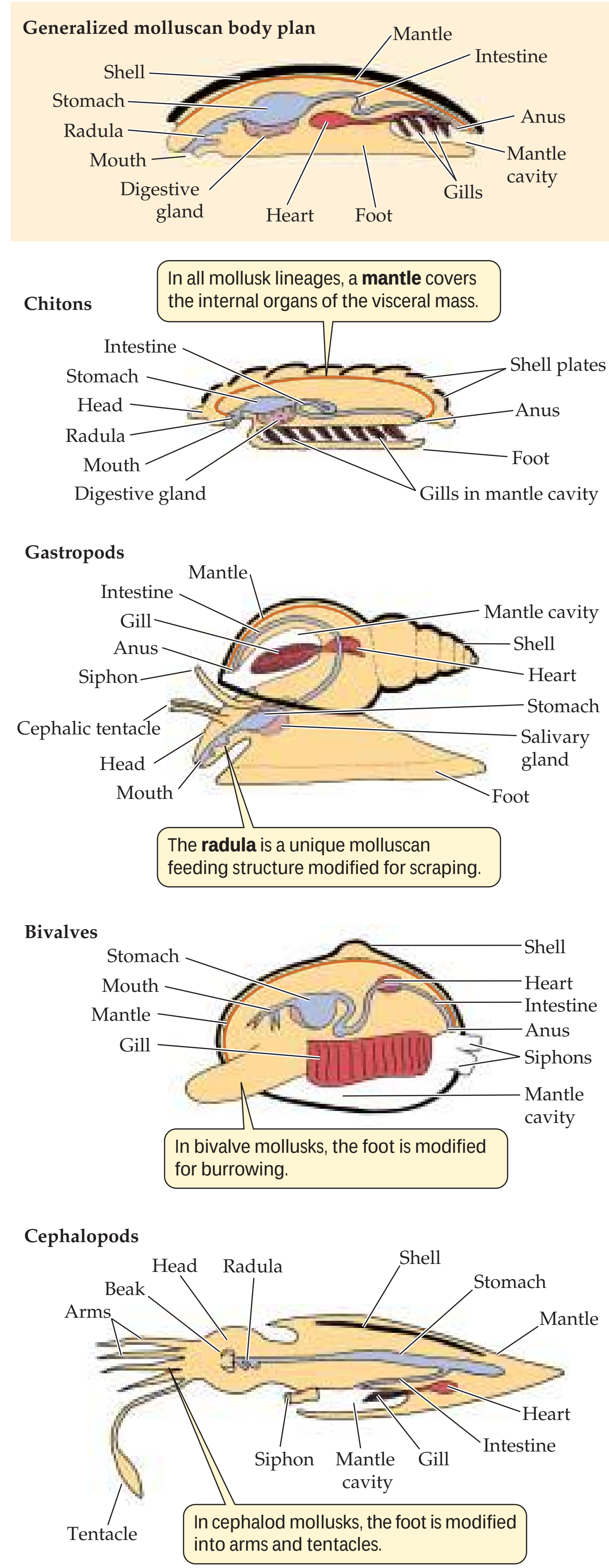
Vestimentiferans were not discovered until the twentieth century, when deep-sea exploration revealed them living many thousands of meters below the ocean surface. In these deep oceanic sediments, they are abundant, reaching densities of many thousands per square meter. About 145 species have been described. The largest and most remarkable vestimentiferans, which grow to 2 meters in length, live near deep-sea hydrothermal vents—volcanic openings in the sea floor through which hot, sulfide-rich water pours. The tissues of these species harbor endosymbiotic bacteria that fix carbon using energy obtained from oxidation of hydrogen sulfide (H_2S).

Mollusks evolved shells

Mollusks (phylum **Mollusca**) range in size from snails only a millimeter high to giant squids more than 18 meters long—the largest known invertebrates. Mollusks underwent one of the most dramatic of animal evolutionary radiations, based on a unique body plan with three major structural components: a foot, a mantle, and a visceral mass. Animals that appear very different, such as snails, clams, and squids, are all built from these components (Figure 32.25).

The molluscan *foot* is a large, muscular structure that originally was both an organ of locomotion and a support for the internal organs. In the lineage leading to squids and octopuses, the foot was modified to form arms and tentacles borne on a head with complex sense organs. In other groups, such as clams, the foot was transformed into a burrowing organ. In some lineages the foot is greatly reduced.

The *mantle* is a fold of tissue that covers the *visceral mass* of internal organs. In many mollusks, the mantle extends beyond the visceral mass to form a *mantle cavity*. The mantle secretes the hard, calcarous skeleton typical of most mollusks. The *gills*, which are used for gas exchange and, in some



32.25 Molluscan Body Plans The diverse modern mollusks are all variations on a general body plan that includes a foot, a mantle, and a visceral mass of internal organs.

species, for feeding, lie in this cavity. When the cilia on the gills beat, they create a flow of water over the gills. The tissue of the gills, which is highly *vascularized* (contains many blood vessels), takes up O_2 from the water and releases CO_2.

Mollusks have an *open circulatory system* that empties into large fluid-filled cavities, through which fluids move around the animal and deliver O_2 to internal organs. Mollusks also developed a rasping feeding structure known as the *radula*. The radula was originally an organ for scraping algae from rocks, a function it retains in many living mollusks. However, in some mollusks, it has been modified into a drill or poison dart. In others, such as clams, it is absent.

Although individual components have been lost in some lineages, these three unique, shared derived characteristics—the foot, the mantle, and the visceral mass—lead zoologists to believe that all 95,000 species of mollusks have a common ancestor. A small sample of these species is shown in Figure 32.26.

MONOPLACOPHORANS. **Monoplacophorans** (class **Monoplacophora**) were the most abundant mollusks during the Cambrian period, 550 million years ago, but today there are only a few surviving species. Unlike all other living mollusks, the surviving monoplacophorans have respiratory organs, muscles, and excretory pores that are repeated over the length of the body. The respiratory organs are located in a large cavity under the shell, through which oxygen-bearing water circulates.

CHITONS. **Chitons** (class **Polyplacophora**) have multiple gills and shell plates, but the body is not truly segmented (Figure 32.26*a*). The chiton body is bilaterally symmetrical, and its internal organs, particularly the digestive and nervous systems, are relatively simple. The larvae of chitons are almost indistinguishable from those of annelids. Most chitons are marine herbivores that scrape algae from rocks with their sharp radulae. An adult chiton spends most of its life clinging tightly to rock surfaces with its large, muscular, mucus-covered foot. It moves slowly by means of rippling waves of muscular contraction in the foot. Fertilization in most chitons takes place in the water, but in a few species fertilization is internal and embryos are brooded within the body.

BIVALVES. One lineage of early mollusks developed a hinged, two-part shell that extended over the sides of the body as well as the top, giving rise to the **bivalves** (class **Bivalvia**), which include the familiar clams, oysters, scallops, and mussels (Figure 32.26*b*). Bivalves are largely sedentary and have greatly reduced heads. The foot is compressed, and in many clams, it is used for burrowing into mud and sand. Bivalves feed by taking in water through an opening called an *incurrent siphon* and extracting food from the water with their large gills, which are also the main sites of gas exchange. Water and gametes exit through the *excurrent siphon*. Fertilization takes place in open water in most species.

GASTROPODS. Another lineage of early mollusks gave rise to the **gastropods** (class **Gastropoda**), which include snails, whelks, limpets, slugs, abalones, and the often brilliantly ornamented nudibranchs. Gastropods, unlike bivalves, have one-piece shells. Most gastropods are motile, using the large foot to move slowly across the substratum or to burrow through it. Gastropods are the most species-rich and widely distributed of the molluscan classes (Figure 32.26*c*,*d*). Most species move by gliding on the muscular foot, but in a few species—the sea butterflies and heteropods—the foot is modified into a swimming organ with which the animal moves through open ocean waters. The only mollusks that live in terrestrial environments—land snails and slugs—are gastropods. In these terrestrial species, the mantle tissue is modified into a highly vascularized lung. Fertilization is internal in most species.

CEPHALOPODS. In one lineage of mollusks, the cephalopods (class **Cephalopoda**), the excurrent siphon became modified to allow the animal to control the water content of the mantle cavity. Ultimately, the modification of the mantle into a device for forcibly ejecting water from the cavity enabled these animals to move rapidly through the water. Furthermore, many early cephalopods had chambered shells into which gas could be secreted to adjust buoyancy. Together, these adaptations allow cephalopods to live in open water.

The cephalopods include the squids, octopuses, and nautiluses (Figure 32.26*e*, *f*). They first appeared about 600 million years ago, near the beginning of the Cambrian period. By the Ordovician period a wide variety of types were present. With their greatly enhanced mobility, some cephalopods, such as squids, became the major predators in the open waters of the Devonian oceans.They remain important marine predators today. Cephalopods capture and subdue their prey with their tentacles; octopuses also use their tentacles to move over the substratum. As is typical of active predators, cephalopods have a head with complex sensory organs, most notably eyes that are comparable to those of vertebrates in their ability to resolve images. The head is closely associated with a large, branched foot that bears the tentacles and a siphon. The large muscular mantle provides a solid external supporting structure. The gills hang in the mantle cavity. As is typical of behaviorally complex animals, many cephalopods have elaborate courtship behavior, which may involve striking color changes.

(*a*) *Mopalia* sp.

(*b*) *Tridacna gigas*

(*c*) *Phidiana hiltoni*

(*d*) *Helminthoglypta walkeriana*

(*e*) *Octopus bimaculoides*

(*f*) *Nautilus pompilius*

32.26 Diversity among the Mollusks (*a*) Chitons are common in the intertidal zones of the temperate zone coasts. (*b*) The giant clam of Indonesia is among the largest of the bivalve mollusks. (*c*) Slugs are gastropods that have lost their shells; this shell-less sea slug is very conspicuously colored. (*d*) Land snails are shelled, terrestrial gastropods. (*e*) Cephalopods such as the octopus are active predators. (*f*) The boundaries of its chambers are clearly visible on the outer surface of this shelled *Nautilus*, another cephalopod.

The earliest cephalopod shells were divided by partitions penetrated by tubes through which liquids could be moved. Nautiloids (genus *Nautilus*) are the only cephalopods with external chambered shells that survive today (Figure 32.26*f*).

Mollusks and brachiopods are among the lophotrochozoans that evolved hard shells that help to protect them from predators and the physical environment. A sturdy outer covering is the main feature of the second protostomate lineage, the ecdysozoans—the subject of the next chapter.

Chapter Summary

Animals: Descendants of a Common Ancestor

- All members of the kingdom Animalia are believed to have a common ancestor, which was a colonial flagellated protist.
- The specialization of cells by function made possible the complex, multicellular body plan of animals.
- Animals are multicellular heterotrophs. They take in complex organic molecules, expending energy to do so.
- Morphological, developmental, and molecular data all support similar animal phylogenies.
- The two major animal lineages—protostomes and deuterostomes—are believed to have diverged early in animal evolution; they differ in several components of their early development. **Review Figure 32.1**

Body Plans Are Basic Structural Designs

- Most animals have either radial or bilateral symmetry. Radially symmetrical animals move slowly or not at all. Bilateral symmetry is strongly correlated with more rapid movement and the concentration of sense organs at the anterior end of the animal. **Review Figure 32.2**
- The body cavity of an animal is strongly correlated with its ability to move. On the basis of their body cavities, animals are classified as acoelomates, pseudocoelomates, or coelomates. **Review Figure 32.3**

Sponges: Loosely Organized Animals

- Sponges (phylum Porifera) are simple animals that lack cell layers and true organs, but have several different cell types.
- Sponges feed by means of choanocytes, feeding cells that draw water through the sponge body and filter out food particles. **Review Figure 32.4**
- Sponges come in a variety of sizes and shapes that are adapted to different movement patterns of water.

Cnidarians: Two Cell Layers and Blind Guts

- Cnidarians (phylum Cnidaria) are radially symmetrical and diploblastic, but with their nematocyst-studded tentacles, they can capture prey larger and more complex than themselves. **Review Figure 32.7**
- Most cnidarian life cycles have a sessile polyp stage and a free-swimming, sexual, medusa stage, but some species lack one of the stages. **Review Figures 32.8, 32.10, 32.11**

See Web/CD Tutorial 32.1

Ctenophores: Complete Guts and Tentacles

- Ctenophores (phylum Ctenophora) are diploblastic marine carnivores with a complete gut and simple life cycles. **Review Figure 32.12**

The Evolution of Bilaterally Symmetrical Animals

- All bilaterally symmetrical animals probably share a common ancestor.
- Protostomes and deuterostomes are each monophyletic lineages that have been evolving separately since the Cambrian period. Their members are structurally more complex than cnidarians and ctenophores.
- Protostomes have a ventral nervous system, paired nerve cords, and larvae with compound cilia.
- Deuterostomes have a dorsal nervous system and larvae with a single cilium per cell.
- The protostomes split into two major groups: lophotrochozoans and ecdysozoans. **Review Figure 32.14**

Simple Lophotrochozoans

- Flatworms (phylum Platyhelminthes) are acoelomate, lack organs for oxygen transport, have only one entrance to the gut, and move by beating their cilia. Many species are parasitic. **Review Figures 32.15, 32.16**
- Although they are no larger than many ciliated protists, rotifers (phylum Rotifera) have highly developed internal organs. **Review Figure 32.17**

Lophophorates: An Ancient Body Plan

- The lophotrochozoan lineage split into two branches, whose descendants became the modern lophophorates and the spiralians.
- The lophophore dominates the anatomy of many lophophorate animals. **Review Figure 32.18**
- Ectoprocts are colonial lophophorates that can move their lophophores. **Review Figure 32.19**
- Brachiopods, which superficially resemble bivalve mollusks, were much more abundant in the past than they are today.

Spiralians: Spiral Cleavage and Wormlike Body Plans

- The spiralian lineage gave rise to many phyla, most of whose members are wormlike.
- Ribbon worms (phylum Nemertea) have a complete digestive tract and capture prey with an eversible proboscis. **Review Figure 32.21**
- Annelids (phylum Annelida) are a diverse group of segmented worms that live in marine, freshwater, and terrestrial environments. **Review Figures 32.22**
- Mollusks (phylum Mollusca) have a body plan with three basic components: foot, mantle, and visceral mass. **Review Figure 32.25**
- The molluscan body plan has been modified to yield a diverse array of animals that superficially appear very different from one another.

See Web/CD Activities 32.1 and 32.3 for a concept review of this chapter

Self-Quiz

1. The body plan of an animal is
   a. its general structure.
   b. the integrated functioning of its parts.
   c. its general structure and the integrated functioning of its parts.
   d. its general structure and its evolutionary history.
   e. the integrated functioning of its parts and its evolutionary history.

2. A bilaterally symmetrical animal can be divided into mirror images by
   a. any plane through the midline of its body.
   b. any plane from its anterior to its posterior end.
   c. any plane from its dorsal to its ventral surface.
   d. any plane through the midline of its body from its anterior to its posterior end.
   e. a single plane through the midline of its body from its dorsal to its ventral surface.
3. Among protostomes, cleavage of the fertilized egg is
   a. delayed while the egg continues to mature.
   b. always radial.
   c. spiral in some species and radial in others.
   d. triploblastic.
   e. diploblastic.
4. The sponge body plan is characterized by
   a. a mouth and digestive cavity but no muscles or nerves.
   b. muscles and nerves but no mouth or digestive cavity.
   c. a mouth, digestive cavity, and spicules.
   d. muscles and spicules but no digestive cavity or nerves.
   e. no mouth, digestive cavity, muscles, or nerves.
5. Which are phyla of diploblastic animals?
   a. Porifera and Cnidaria
   b. Cnidaria and Ctenophora
   c. Cnidaria and Platyhelminthes
   d. Ctenophora and Platyhelminthes
   e. Porifera and Ctenophora
6. Cnidarians have the ability to
   a. live in both salt and fresh water.
   b. move rapidly in the water column.
   c. capture and consume large numbers of small prey.
   d. survive where food is scarce, because of their low metabolic rate.
   e. capture large prey and to move rapidly.
7. Many parasites evolved complex life cycles because
   a. they are too simple to disperse readily.
   b. they are poor at recognizing new hosts.
   c. they were driven to it by host defenses
   d. complex life cycles increase the probability of a parasite's transfer to a new host.
   e. their ancestors had complex life cycles and they simply retained them.
8. Members of which phyla have lophophores?
   a. Phoronida, Brachiopoda, and Nemertea
   b. Phoronida, Brachiopoda, and Ectoprocta
   c. Brachiopoda, Ectoprocta, and Platyhelminthes
   d. Phoronida, Rotifera, and Ectoprocta
   e. Rotifera, Ectoprocta, and Brachiopoda
9. Which of the following is not part of the molluscan body plan?
   a. Mantle
   b. Foot
   c. Radula
   d. Visceral mass
   e. Jointed skeleton
10. Cephalopods control their buoyancy by
    a. adjusting salt concentrations in their blood.
    b. forcibly expelling water from the mantle.
    c. pumping water in and out of internal chambers.
    d. using the complex sense organs in their heads.
    e. swimming rapidly.

For Discussion

1. Differentiate among the members of each of the following sets of related terms:
   a. radial symmetry/bilateral symmetry
   b. protostome/deuterostome
   c. diploblastic/triploblastic
   d. coelomate/pseudocoelomate/acoelomate
2. In this chapter we listed some of the traits shared by all animals that convince most biologists that all animals are descendants of a single common ancestral lineage. In your opinion, which of these traits provides the most compelling evidence that animals are monophyletic?
3. Describe some features that allow animals to capture prey that are larger and more complex than they themselves are.
4. Why is bilateral symmetry strongly associated with cephalization, the concentration of sense organs in an anterior head?
5. Why might mollusks not have evolved segmentation, given that a segmented body enables improved control over locomotion?

33 Ecdysozoans: The Molting Animals

Early in animal evolution, the protostomate lineage split into two branches—the lophotrochozoans and the ecdysozoans—as we saw in the previous chapter. The distinguishing feature of the ecdysozoans is an **exoskeleton**, a nonliving covering that provides an animal with both protection and support. Once formed, however, an exoskeleton cannot grow. How, then, can ecdysozoans increase in size? Their solution is to shed, or **molt**, the exoskeleton and replace it with a new, larger one.

Before the animal molts, a new exoskeleton is already forming underneath the old one. When the old exoskeleton is shed, the new one expands and hardens. But until it has hardened, the animal is very vulnerable to its enemies both because its outer surface is easy to penetrate and because it can move only slowly.

The exoskeleton presented new challenges in other areas besides growth. Ecdysozoans cannot use cilia for locomotion, and most exdysozoans have hard exoskeletons that impede the passage of oxygen into the animal. To cope with these challenges, ecdysozoans evolved new mechanisms of locomotion and respiration.

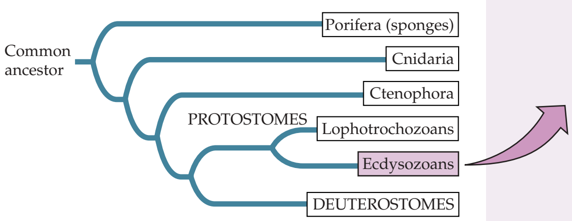
Despite these constraints, the ecdysozoans—the molting animals—have more species than all other animal lineages combined. An increasingly rich array of molecular and genetic evidence, including a set of homeobox genes shared by all ecdysozoans, suggests that molting may have evolved only once during animal evolution.

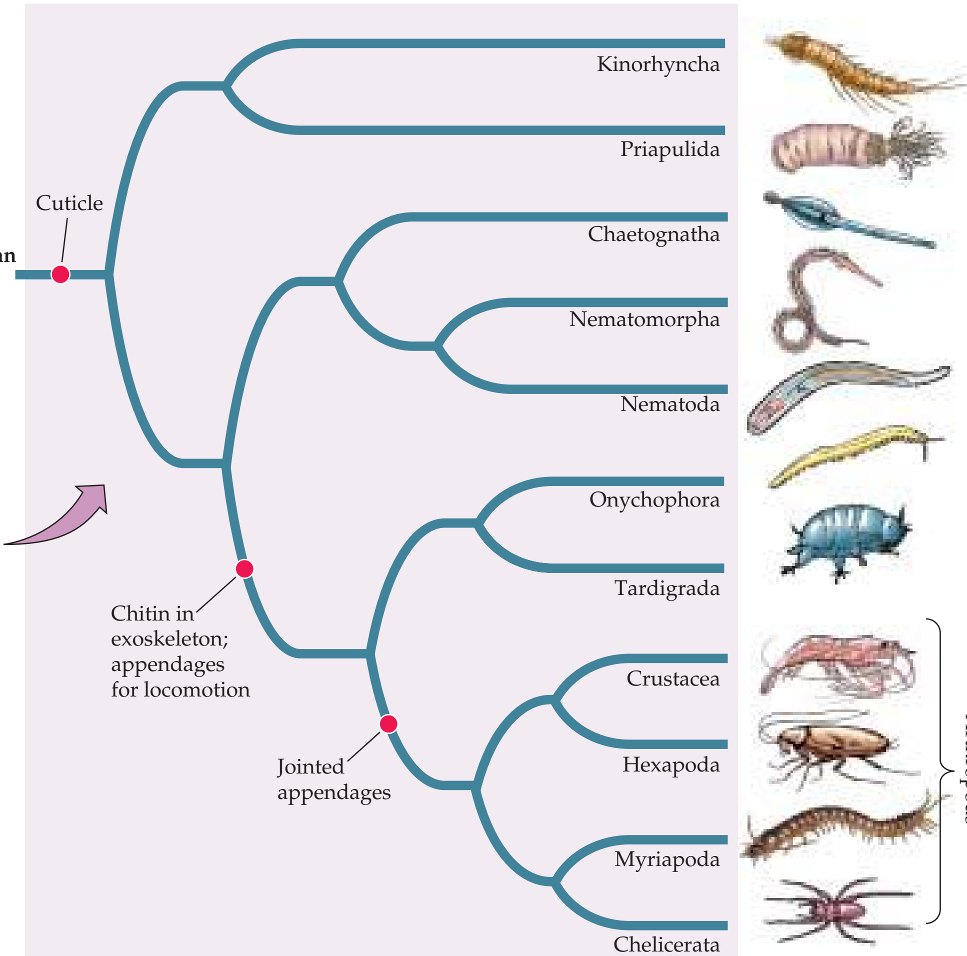
In this chapter, we will review the diversity of the ecdysozoans. We will look at the characteristics of animals in the various ecdysozoan phyla and see how having an exoskeleton has influenced their evolution. The phylogeny we will follow is presented in Figure 33.1. In the first part of the chapter, we will look at several small phyla of wormlike ecdysozoans. Then we will detail the characteristics of the arthropods, an incredibly species-rich group of ecdysozoan phyla with hardened exoskeletons. We will close the chapter with an overview of evolutionary themes found in the evolution of the protostomate phyla, including both the lophotrochozoan and ecdysozoan lineages.

Shedding the Exoskeleton This dragonfly has just gone through a molt, a shedding of the outer exoskeleton. Such molts are necessary in order for the insect to grow larger or to change its form.

Cuticles: Flexible, Unsegmented Exoskeletons

Some ecdysozoans have wormlike bodies covered by exoskeletons that are relatively thin and flexible. Such an exoskeleton, called a **cuticle**, offers the animal some protection, but does not provide body support. The action of circular and longitudinal muscles on fluids in



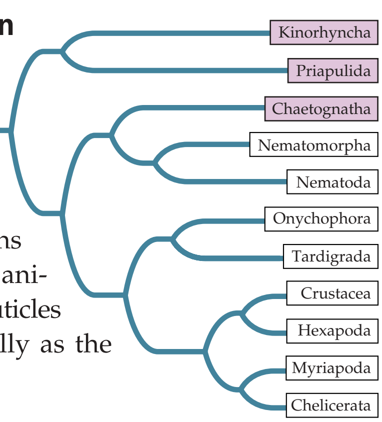


33.1 A Current Phylogeny of the Ecdysozoans Those ecdysozoan phyla with jointed appendages are often placed in a single phylum, Arthropoda. Arthropods are the most numerous animals on the planet.

the body cavity provides a hydrostatic skeleton for many of these animals, which can move only slowly. A cuticle allows the exchange of gases, minerals, and water across the body surface, but restricts the animal to moist habitats.

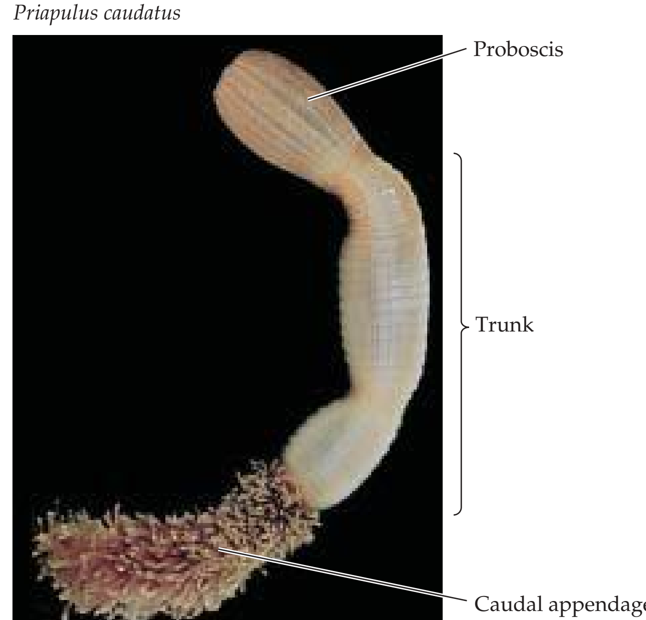
Some marine ecdysozoan phyla have few species

Several phyla of marine wormlike animals branched off early within the ecdysozoan lineage. Each of these phyla contains only a few species. These animals have relatively thin cuticles that are molted periodically as the animals grow to full size.

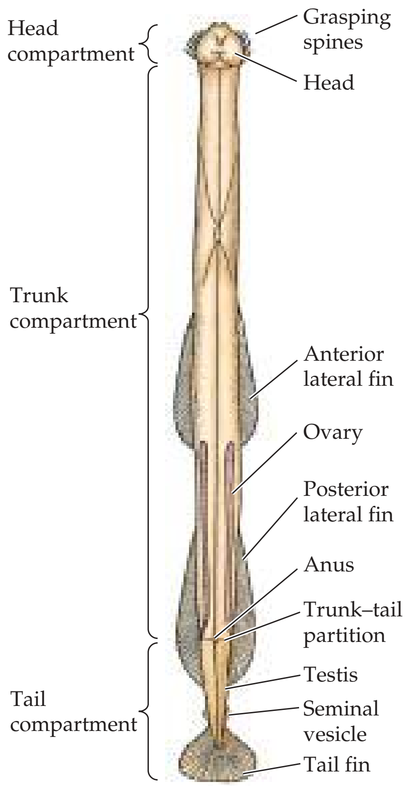


PRIAPULIDS AND KINORHYNCHS. The 16 species of **priapulids** (phylum **Priapulida**) are cylindrical, unsegmented, wormlike animals that range in size from half a millimeter to 20 centimeters in length (Figure 33.2). They burrow in fine marine sediments and prey on soft-bodied invertebrates, such as polychaete worms. They capture prey with a toothed pharynx, a muscular organ that is everted through the mouth and then withdrawn into the body together with the grasped prey. Fertilization is external, and most species have a larval form that lives in the mud.

Priapulus caudatus



33.2 A Priapulid Priapulids are marine worms that live, usually as burrowers, on the ocean floor. They capture prey with a toothed pharynx that everts through the proboscis. They take their name from Priapus, the Greek god of procreation, who was typically portrayed with an oversize penis.



33.3 An Arrow Worm Arrow worms have a three-part body plan. Their fins and grasping spines are adaptations for a predatory lifestyle.

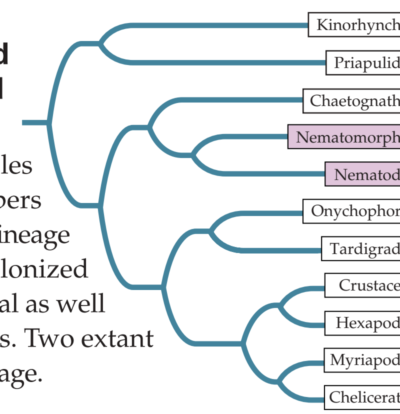
About 150 species of **kinorhynchs** (phylum **Kinorhyncha**) have been described. They are all less than 1 millimeter in length and live in marine sands and muds. Their bodies are divided into 13 segments, each with a separate cuticular plate. These plates are periodically molted during growth. Kinorhynchs feed by ingesting sediments and digesting the organic material found within them, which may include living algae as well as dead matter. Kinorhynchs have no distinct larval stage; fertilized eggs develop directly into juveniles, which emerge from their egg cases with 11 of the 13 body segments already formed.

ARROW WORMS. The phylogeny of the **arrow worms** (phylum **Chaetognatha**) is uncertain. Recent evidence indicates that these animals may in fact belong among the deuterostomes; however, this placement is still in question, and we continue to include them among the ecdysozoans.

The arrow worms body plan is based on a coelom divided into head, trunk, and tail compartments (Figure 33.3). Most arrow worms swim in the open sea, but a few live on the sea floor. Their abundance as fossils indicates that they were common more than 500 million years ago. The 100 or so living species of arrow worms are small enough—less than 12 cm long—that their gas exchange and excretion requirements are met by diffusion through the body surface, and they lack a circulatory system. Wastes and nutrients are moved around the body in the coelomic fluid, which is propelled by cilia that line the coelom. There is no distinct larval stage. Miniature adults hatch directly from eggs that are fertilized internally following elaborate courtship.

Arrow worms are stabilized in the water by means of one or two pairs of lateral fins and a tail fin. They are major predators of small organisms in the open oceans, ranging in size from small protists to young fish as large as the arrow worms themselves. An arrow worm typically lies motionless in the water until water movement signals the approach of prey. The arrow worm then darts forward and grasps the prey with the stiff spines adjacent to its mouth.

Tough cuticles evolved in some unsegmented worms



Tough external cuticles evolved in some members of another ecdysozoan lineage whose descendants colonized freshwater and terrestrial as well as marine environments. Two extant phyla represent this lineage.

HORSEHAIR WORMS. About 320 species of horsehair worms (phylum **Nematomorpha**) have been described. As their name implies, horsehair worms are extremely thin, and they range from a few millimeters up to a meter in length (Figure 33.4). Most adult horsehair worms live in fresh water among leaf litter and algal mats near the edges of streams and ponds. The larvae of horsehair worms are internal par-

Paragordius sp.

33.4 Horsehair Worms These worms get their name from their hair- or threadlike shape. They can grow to be up to a meter long.

asites of terrestrial and aquatic insects and freshwater crayfish. The horsehair worm's gut is greatly reduced, has no mouth opening, and is probably nonfunctional. These worms may feed only as larvae, absorbing nutrients from their hosts across the body wall, but many continue to grow after they have left their hosts, suggesting that adult worms may also absorb nutrients from their environment.

ROUNDWORMS. Roundworms (phylum **Nematoda**) have a thick, multilayered cuticle secreted by the underlying epidermis that gives their body its shape (Figure 33.5*a*). As a roundworm grows, it sheds its cuticle four times.

Roundworms exchange oxygen and nutrients with their environment through both the cuticle and the intestine, which is only one cell layer thick. Materials are moved through the gut by rhythmic contraction of a highly muscular organ, the *pharynx*, at the worm's anterior end. Roundworms move by contracting their longitudinal muscles.

Roundworms are one of the most abundant and universally distributed of all animal groups. About 25,000 species have been described, but the actual number of living species may be more than a million. Countless roundworms live as scavengers in the upper layers of the soil, on the bottoms of lakes and streams, in marine sediments (Figure 33.5*c*), and as parasites in the bodies of most kinds of plants and animals. The topsoil of rich farmland contains up to 3 billion nematodes per acre.

Many roundworms are predators, preying on protists and other small animals (including other roundworms). Many roundworms live parasitically within their hosts. The largest known roundworm, which reaches a length of 9 meters, is a parasite in the placentas of female sperm whales. The roundworms that are parasites of humans (causing serious tropical diseases such as trichinosis, filariasis, and elephantiasis), domestic animals, and economically important plants have been studied intensively in an effort to find ways of controlling them. One soil-inhabiting nematode, *Caenorhabitis elegans*, is a "model organism" in the laboratories of geneticists and developmental biologists.

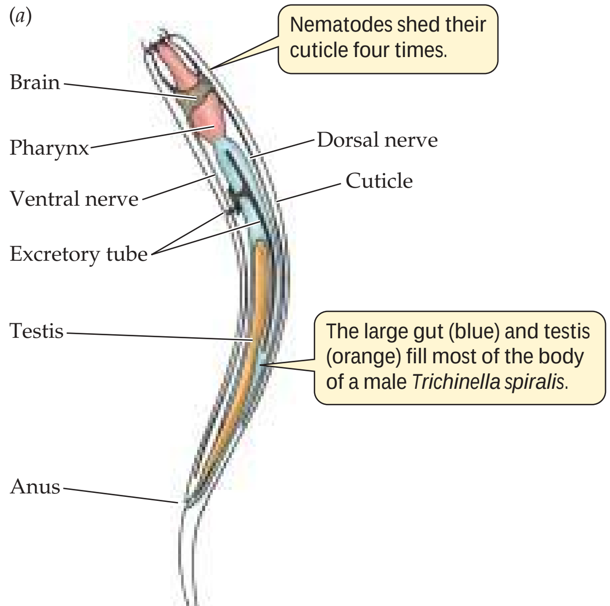
The structure of parasitic roundworms is similar to that of free-living species, but the life cycles of many parasitic species have special stages that facilitate the transfer of individuals among hosts. *Trichinella spiralis*, the species that causes the human disease trichinosis, has a relatively simple life cycle. A person may become infected by eating the flesh of an animal (usually a pig) containing larvae of *Trichinella* encysted in its muscles. The larvae are activated in the digestive tract, emerge from their cysts, and attach to the person's intestinal wall, where they feed. Later, they bore through the intestinal wall and are carried in the bloodstream to muscles, where they form new cysts (Figure 33.5*b*). If present in great numbers, these cysts cause severe pain or death.

Arthropods and Their Relatives: Segmented External Skeletons

In Precambrian times, the cuticle of some wormlike ecdysozoan lineages became thickened by the incorporation of layers of protein and a strong, flexible, waterproof polysaccharide called **chitin**. This rigid body covering may originally have had a protective function, but eventually it acquired both support and locomotory functions as well.

A rigid body covering precludes wormlike movement. To move, the animal requires extensions of the body that can be

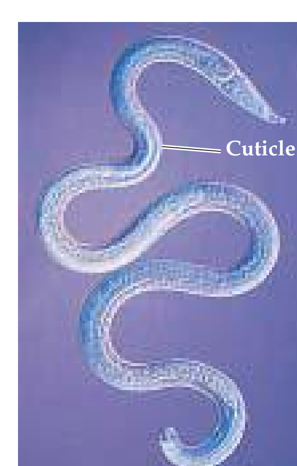
(*a*)



33.5 Roundworms (*a*) The body plan of *Trichinella spiralis*, a roundworm that causes trichinosis. (*b*) A cyst of *Trichinella spiralis* in the muscle tissue of a host. (*c*) This free-living roundworm moves through marine sediments.

(*b*)

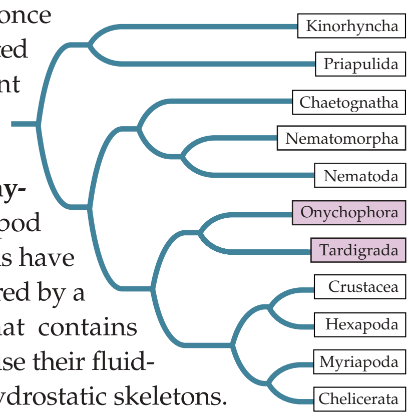
(*c*)



manipulated by muscles. Such **appendages** evolved several times in the late Precambrian, leading to the lineages collectively called the **arthropods** ("jointed foot"). Divisions among the arthropod lineages are ancient and have been the subject of much research in the past decade. These phylogenetic relationships are being examined daily in the light of a wealth of new information, much of it concerning gene expression. There is currently no consensus on an exact phylogeny, but most researchers agree that these important animal groups are monophyletic, and some taxonomists consider them as members of a single phylum: **Arthropoda**.

Before presenting one current view of arthropod phylogeny, let's look at some arthropod relatives that have segmented bodies but unjointed legs, and at an early arthropod lineage that disappeared but left an important fossil record.

Some relatives of the arthropods have unjointed legs



Although they were once thought to be closely related to annelid worms, recent molecular evidence links the 110 species of **onychophorans** (phylum **Onychophora**) to the arthropod lineages. Onychophorans have soft bodies that are covered by a thin, flexible cuticle that contains chitin. Onychophorans use their fluid-filled body cavities as hydrostatic skeletons. Their soft, fleshy, unjointed, claw-bearing legs are formed by outgrowths of the body (Figure 33.6*a*). These animals are probably similar in appearance to ancestral arthropods. Fertilization is internal, and the large, yolky eggs are brooded with the body of the female.

Like the onychophorans, **water bears** (phylum **Tardigrada**) have fleshy, unjointed legs and use their fluid-filled body cavities as hydrostatic skeletons (Figure 33.6*b*). Water bears are extremely small (0.1–0.5 mm in length), and they lack circulatory systems and gas exchange organs. The 600 extant species of water bears live in marine sands and on temporary water films on plants. When these films dry out, the water bears also lose water and shrink to small, barrel-shaped objects that can survive for at least a decade in a dormant state. They have been found at densities as high as 2 million per square meter of moss.

Jointed legs appeared in the trilobites

The **trilobites** (phylum **Trilobita**) were among the earliest arthropods. They flourished in Cambrian and Ordovician seas, but disappeared in the great Permian extinction at the close of the Paleozoic era (245 mya). Because their heavy exoskeletons provided ideal material for fossilization, they left behind an abundant record of their existence (Figure 33.7).

Trilobites were heavily armored, and their body segmentation and appendages followed a relatively simple, repetitive plan. But their appendages were jointed, and some of them were modified for different functions. This specialization of appendage function became a theme as the evolution of the arthropod lineage continued.

Modern arthropods dominate Earth's fauna

Arthropod appendages have evolved an amazing variety of forms, and they serve many functions, including walking and swimming, gas exchange, food capture and manipulation, copulation, and sensory perception. The pattern of segmentation is similar among most arthropods because their development is governed by a common cascade of regula-

(*a*) *Peripatus* sp.

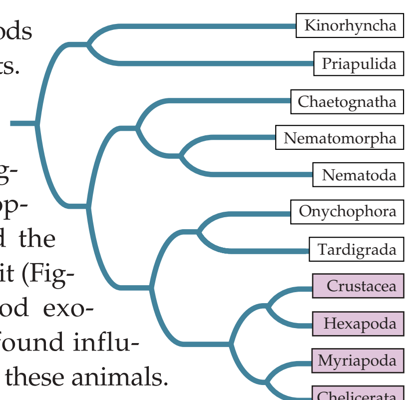
(*b*) *Echiniscus springer*

33.6 Unjointed Legs (*a*) Onychophorans, also called "velvet worms," have unjointed legs and use the body cavity as a hydrostatic skeleton. (*b*) The appendages and general anatomy of water bears superficially resemble those of onychophorans.

Odontochile rugosa

33.7 A Trilobite The relatively simple, repetitive segments of the now-extinct trilobites are illustrated by a fossil trilobite from the shallow seas of the Devonian period, some 400 million years ago.

tory genes (see Figure 19.15), including homeotic genes that determine the kinds of appendages that are borne on each segment.



The bodies of arthropods are divided into segments. Their muscles are attached to the inside of the exoskeleton. Each segment has muscles that operate that segment and the appendages attached to it (Figure 33.8). The arthropod exoskeleton has had a profound influence on the evolution of these animals. Encasement within a rigid body covering provides support for walking on dry land, and the waterproofing provided by chitin keeps the animal from dehydrating in dry air. Aquatic arthropods were, in short, excellent candidates to invade terrestrial environments. As we will see, they did so several times.

There are four major arthropod phyla living today: the crustaceans, hexapods (insects), myriapods, and chelicerates. Collectively, the arthropods (including both terrestrial and marine species) are the dominant animals on Earth, both in numbers of species (about 1.5 million described) and number of individuals (estimated at some 10^{18} individuals, or a billion billion).

Crustaceans: Diverse and Abundant

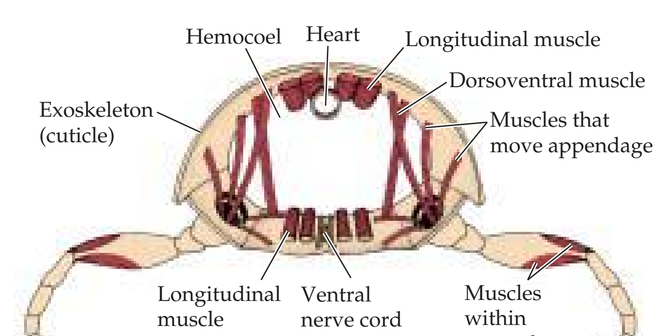
Crustaceans (phylum **Crustacea**) are the dominant marine arthropods today. The most familiar crustaceans belong to the class Malacostraca, which includes shrimp, lobsters, crayfish, and crabs (decapods; Figure 33.9*a*); and sow bugs (isopods; Figure 33.9*b*). Also included among the crustaceans are a variety of small species, many of which superficially resemble shrimp. The individuals of one group alone, the copepods (class Copepoda; Figure 33.9*c*), are so numerous that they may be the most abundant of all animals.

Barnacles (class Cirripedia) are unusual crustaceans that are sessile as adults (Figure 33.9*d*). With their calcareous shells, they superficially resemble mollusks but, as the zoologist Louis Agassiz remarked more than a century ago, a barnacle is "nothing more than a little shrimp-like animal, standing on its head in a limestone house and kicking food into its mouth."

Most of the 40,000 described species of crustaceans have a body that is divided into three regions: *head*, *thorax*, and *abdomen*. The segments of the head are fused together, and the head bears five pairs of appendages. Each of the multiple thoracic and abdominal segments usually bears one pair of appendages. In some cases, the appendages are branched, with different branches serving different functions. In many species, a fold of the exoskeleton, the *carapace*, extends dorsally and laterally back from the head to cover and protect some of the other segments (Figure 33.10*a*).

The fertilized eggs of most crustacean species are attached to the outside of the female's body, where they remain during their early development. At hatching, the young of some species are released as larvae; those of other species are released as juveniles that are similar in form to the adults. Still other species release eggs into the water or attach them to an object in the environment. The typical crustacean larva, called a **nauplius**, has three pairs of appendages and one central eye (Figure 33.10*b*). In many crustaceans, the nauplius larva develops within the egg before it hatches.

There is a growing recognition among researchers that a crustacean lineage may have been ancestral to all present-day arthropods. Therefore, the phylum Crustacea, as we recognize it here, may be paraphyletic (see Chapter 25). Molecular evidence points especially to a link between the crustaceans and another important lineage, the hexapods.



33.8 Arthropod Exoskeletons Are Rigid and Jointed This cross section through a thoracic segment of a generalized arthropod illustrates the arthropod body plan, which is characterized by a rigid exoskeleton with jointed appendages.

(*a*) *Opisthopus transversus*

(*b*) *Ligia occidentalis*

(*c*) *Cyclops* sp.

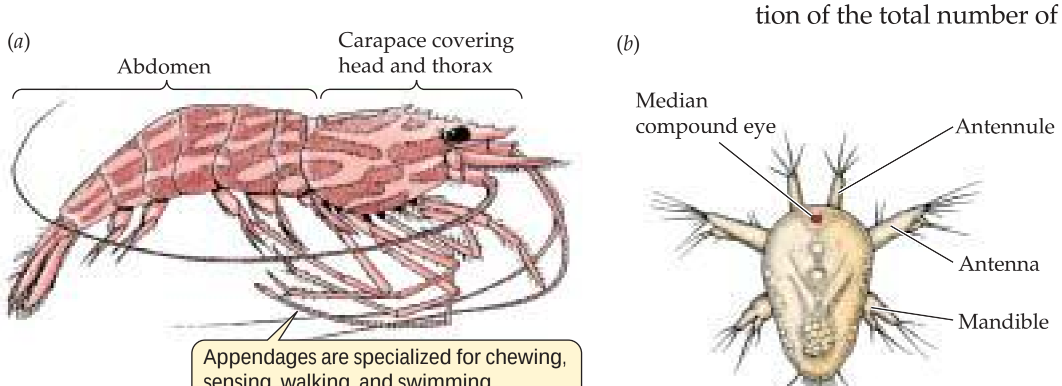
(*d*) *Lepas pectinata*

33.9 Crustacean Diversity (*a*) This mottled pea crab is a decapod crustacean. Its pigmentation depends on the food it ingests. (*b*) This isopod is found on the beaches of the California coast. (*c*) This microscopic freshwater copepod is only about 30 μm long. (*d*) Gooseneck barnacles attach to a substratum and feed by protruding and retracting feeding appendages from their shells.

Insects: Terrestrial Descendants of Marine Crustaceans

During the Devonian, more than 400 million years ago, arthropods made the leap from the marine environment onto land. Of the several groups who successfully colonized the terrestrial habitat, none is more prominent today than the six-legged individuals of the phylum **Hexapoda**—the insects.

Insects are found in most terrestrial and freshwater habitats, and they utilize nearly all species of plants and many species of animals as food. Some are internal parasites of plants and animals; others suck their host's blood or consume surface body tissues. The 1.4 million species of insects that have been described are believed to be only a small fraction of the total number of species living today.



33.10 Crustacean Structure (*a*) The bodies of crustaceans are divided into three regions, each of which bears appendages. (*b*) A nauplius larva has one compound eye and three pairs of appendages.

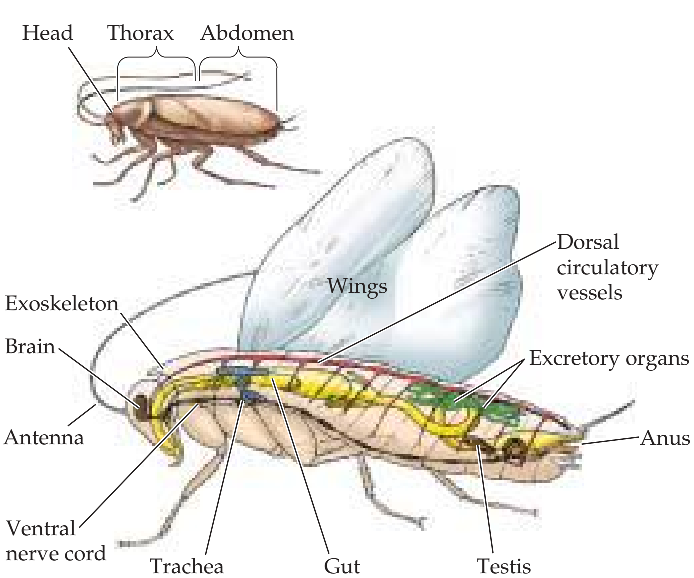
Very few insect species live in the ocean. In freshwater environments, on the other hand, they are sometimes the dominant animals, burrowing through the substratum, extracting suspended prey from the water, and actively pursuing other animals. Insects were the first animals to achieve the ability to fly, and they are important pollinators of flowering plants.

Insects, like crustaceans, have three basic body regions: head, thorax, and abdomen. They have a single pair of antennae on the head and three pairs of legs attached to the thorax (Figure 33.11). Unlike the other arthropods, insects have no appendages growing from their abdominal segments (see Figure 21.5).

An insect exchanges gases by means of air sacs and tubular channels called *tracheae* (singular, trachea) that extend from external openings inward to tissues throughout the body. The adults of most flying insects have two pairs of stiff, membranous wings attached to the thorax. However, flies have only one pair of wings, and in beetles the forewings form heavy, hardened wing covers.

Wingless insects include springtails and silverfish (Figure 33.12). Of the modern insects, they are probably the most similar in form to insect ancestors. Apterygote insects have a simple life cycle, hatching from eggs as miniature adults.

Development in the winged insects (Figure 33.13) is complex. The hatchlings do not look like adults, and they undergo substantial changes at each molt. The immature stages of insects between molts are called **instars**. A substantial change that occurs between one developmental stage and another is called **metamorphosis**. If the changes between its instars are gradual, an insect is said to have **incomplete metamorphosis**.



33.11 Structure of an Insect This diagram of a generalized insect illustrates its three-part body plan. The middle region, the thorax, bears three pairs of legs and, in most groups, two pairs of wings.

Hydropodura aquatica

33.12 Wingless Insects The wingless insects have a simple life cycle. They hatch looking like miniature adults, then grow by successive moltings of the cuticles as these springtails are doing.

In some insect groups, the larval and adult forms appear to be completely different animals. The most familiar example of such **complete metamorphosis** occurs in members of the order Lepidoptera, in which the larval caterpillar transforms itself into the adult butterfly (see Figure 1.1). During complete metamorphosis, the wormlike larva transforms itself during a specialized phase, called the **pupa**, in which many larval tissues are broken down and the adult form develops. In many of these groups, the different life stages are specialized for living in different environments and using different food sources. In many species, the larvae are adapted for feeding and growing, and the adults are specialized for reproduction and dispersal.

Entomologists divide the winged insects into about 29 different orders. We can make sense of this bewildering variety by recognizing three major lineages:

- Winged insects that cannot fold their wings against the body
- Winged insects that can fold their wings and that undergo incomplete metamorphosis
- Winged insects that can fold their wings and that undergo complete metamorphosis

Because they can fold their wings over their backs, flying insects belonging to the second and third lineages can tuck their wings out of the way upon landing and crawl into crevices and other tight places.

33.13 The Diversity of Insects (*a*) Unlike most flying insects, this dragonfly cannot fold its wings over its back. (*b*) The Mexican bush katydid represents the order Orthoptera. (c) Harlequin bugs are "true" bugs (order Hemiptera); (*d*) These mating mantophasmatodeans represent a recently discovered Hemipteran lineage found only in the Cape region of South Africa. (*e*) A predatory diving beetle (order Coleoptera). (*f*) The California dogface butterfly is a member of the Lepidoptera. (*g*) The flies, including this Mediterranean fruit fly, comprise the order Diptera. (*h*) Many genera in the order Hymenoptera, such as honeybees, are social insects. ▶

(*a*) *Anax imperator*

(*b*) *Scudderia mexicana*

(*c*) *Murgantia histrionica*

(*d*) *Timema* sp.

(*e*) *Dytiscus marginalis*

(*f*) *Colias eurydice*

(*g*) *Ceratitis capitata*

(*h*) *Apis mellifera*

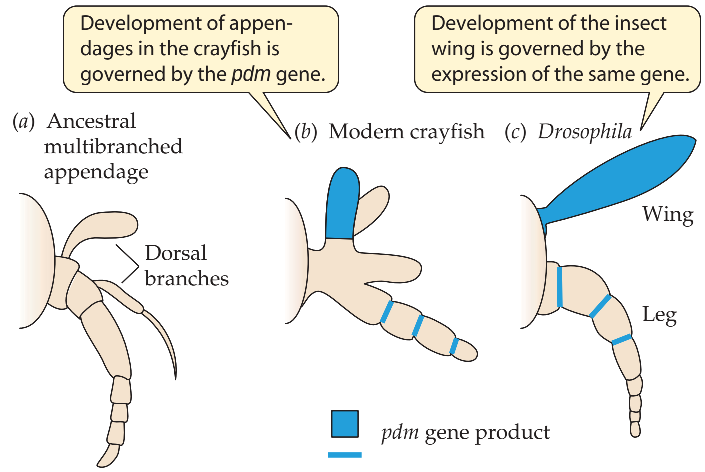
The only surviving members of the lineage whose members cannot fold their wings against the body are the orders Odonata (dragonflies and damselflies, Figure 33.13*a*) and Ephemeroptera (mayflies). All members of these two orders have aquatic larvae that transform themselves into flying adults after they crawl out of the water. Although many of these insects are excellent flyers, they require a great deal of open space in which to maneuver. Dragonflies and damselflies are active predators as adults, but adult mayflies lack functional digestive tracts and live only long enough to mate and lay eggs.

The second lineage, whose members can fold their wings and have incomplete metamorphosis, includes the orders Orthoptera (grasshoppers, crickets, roaches, mantids, and walking sticks; Figure 33.13*b*), Isoptera (termites), Plecoptera (stone flies), Dermaptera (earwigs), Thysanoptera (thrips), Hemiptera (true bugs; Figure 33.13*c*), and Homoptera (aphids, cicadas, and leafhoppers). In these groups, hatchlings are sufficiently similar in form to adults to be recognizable. They acquire adult organ systems, such as wings and compound eyes, gradually through several juvenile instars. Remarkably, a new insect order in this lineage, the Mantophasmatodea, was first described in 2002 (Figure 33.13*d*). These small insects are common in the Cape Region of southern Africa, an area of exceptional species richness and endemism for many animal and plant groups.

Insects belonging to the third lineage undergo complete metamorphosis. About 85 percent of all species of winged insects belong to this lineage. Familiar examples are the orders Neuroptera (lacewings and their relatives), Coleoptera (beetles; Figure 33.13*e*), Trichoptera (caddisflies), Lepidoptera (butterflies and moths; Figure 33.13*f*), Diptera (flies; Figure 33.13*g*), and Hymenoptera (sawflies, bees, wasps, and ants; Figure 33.13*h*).

Members of several orders of winged insects, including the Phthiraptera (lice) and Siphonaptera (fleas), are parasitic. Although descended from flying ancestors, these insects have lost the ability to fly.

Molecular data suggest that the lineage leading to the insects separated from the lineage leading to modern crustaceans about 450 million years ago, about the time of the appearance of the first land plants. These ancestral forms penetrated a terrestrial environment that was ecologically empty, which in part accounts for their remarkable success. But this success of the insects is also due to their wings, which arose only once early during insect evolution. Homologous genes control the development of insect wings and crustacean appendages, suggesting that that the insect wing evolved from a dorsal branch of a crustacean limb (Figure 33.14). The dorsal limb branch of crustaceans is used for respiration and osmoregulation. This finding suggests that the insect wing evolved from a gill-like structure that had a respiratory function.



33.14 Origin of Insect Wings The insect wing may have evolved from an ancestral appendage similar to that of modern crustaceans. (*a*) A diagram of the ancestral, multibranched arthropod limb. (*b, c*) The *pdm* gene, a Hox gene, is expressed throughout the dorsal limb branch and walking leg of the thoracic limb of a crayfish (*a*) and in the wings and legs of *Drosophila* (*b*).

Arthropods with Two Body Regions

Insects and most crustaceans have tripartite body plans, with a head, thorax, and abdomen. In two other arthropod lineages, evolution resulted in a body plan with two regions—a head and a trunk.

Myriapods have many legs

Centipedes, millipedes, and the two other groups of animals comprise the phylum **Myriapoda**. Centipedes and millipedes have a well-formed head and a long, flexible, segmented trunk that bears many pairs of legs (Figure 33.15). Centipedes, which have one pair of legs per segment, prey on insects and other small animals. Millipedes, which have two pairs of legs per segment, scavenge and eat plants. More than 3,000 species of centipedes and 10,000 species of millipedes have been described; many more species probably remain unknown. Although most myriapods are less than a few centimeters long, some tropical species are ten times that size.

Most chelicerates have four pairs of walking legs

In the body plan of **chelicerates** (phylum **Chelicerata**), the anterior region (head) bears two pairs of appendages modified to form mouthparts. In addition, many chelicerates have four pairs of walking legs. The 63,000 described chelicerate species are usually placed in three classes: Pycnogonida, Merostomata, and Arachnida; most of them belong to Arachnida.

The **pycnogonids** (class **Pycnogonida**), or sea spiders, are a poorly known group of about 1,000 marine species (Figure 33.16*a*). Most are small, with leg spans less than 1 cm, but some deep-sea species have leg spans up to 60 cm. A few py-

(*a*) *Scolopendra heros*

(*b*) *Harpaphe haydeniana*

33.15 Myriapods
(*a*) Centipedes have powerful jaws for capturing active prey. (*b*) Millipedes, which are scavengers and plant eaters, have smaller jaws and legs. They have two pairs of legs per segment, in contrast to the one pair on each segment of centipedes.

cnogonids feed on algae, but most are carnivorous, feeding on a variety of small invertebrates.

The class **Merostomata** contains the horseshoe crabs (order Xiphosura), with five living species, and the extinct giant water scorpions (order Eurypterida). Horseshoe crabs, which have changed very little during their long fossil history, have a large horseshoe-shaped covering over most of the body. They are common in shallow waters along the eastern coasts of North America and Southeast Asia, where they scavenge and prey on bottom-dwelling invertebrates. Periodically they crawl into the intertidal zone in large numbers to mate and lay eggs (Figure 33.16*b*).

Arachnids (class **Arachnida**) are abundant in terrestrial environments. Most arachnids have a simple life cycle in which miniature adults hatch from internally fertilized eggs and begin independent lives almost immediately. Some arachnids retain their eggs during development and give birth to live young.

The most species-rich and abundant arachnids are the spiders, scorpions, harvestmen, mites, and ticks (Figure 33.17). The 30,000 described species of mites and ticks live in soil, leaf litter, mosses, and lichens, under bark, and as parasites of plants, invertebrates, and vertebrates. They are vectors for wheat and rye mosaic viruses, and they cause mange in domestic animals and skin irritation in humans.

Spiders are important terrestrial predators. Some have excellent vision that enables them to chase and seize their prey. Others spin elaborate webs made of protein threads in which they snare prey. The threads are produced by modified abdominal appendages connected to internal glands that secrete the proteins, which dry on contact with air. The webs of different groups of spiders are strikingly varied, and this variation enables the spiders to position their snares in many different environments. Spiders also use protein threads to construct safety lines during climbing and as homes, mating

(*a*) *Decalopoda sp.*

(*b*) *Limulus polyphemus*

33.16 Minor Chelicerate Phyla (*a*) Although they are not spiders, it is easy to see why sea spiders were given their common name. (*b*) This spawning aggregation of horseshoe crabs was photographed on a sandy beach in Delaware.

(*a*) *Phidippus formosus*

(*b*) *Pseudouroctonus minimus*

(*c*) *Hadrobunus maculosus*

(*d*) *Brevipalpus phoenicis*

33.17 Arachnid Diversity (*a*) The black jumping spider's bite produces an inflammatory reaction on mammalian skin. (*b*) Scorpions are nocturnal predators. (*c*) Harvestmen, also called daddy longlegs, are scavengers. (*d*) Mites are blood-sucking, external parasites on vertebrates.

structures, protection for developing young, and means of dispersal.

Themes in the Evolution of Protostomes

We end this chapter by reviewing some of the evolutionary trends we have seen in the animal groups we have discussed so far. Most of protostomate evolution took place in the oceans. Early protostomes used their fluid-filled body cavities as hydrostatic skeletons. Segmentation permitted different parts of the body to be moved independently of one another. Thus species in some protostomate lineages gradually evolved the ability to change their shape in complex ways and to move rapidly over and through the substratum or through the water.

During much of animal evolution, the only food in the water consisted of dissolved organic matter and very small organisms. Consequently, many different lineages of animals, including lophophorates, mollusks, tunicates, and some crustaceans, evolved feeding structures designed to filter small prey from water, as well as structures for moving water through or over their prey-collecting devices. Animals that feed in this manner are abundant and widespread in marine waters today.

Because water flows readily, bringing food with it, sessile lifestyles also evolved repeatedly during lophotrochozoan and ecdysozoan evolution. Most phyla today have at least some sessile members. Being sessile presents certain challenges. For example, sessile animals cannot come together to mate. Some species eject both eggs and sperm into the water; others retain their eggs within their bodies and extrude only their sperm, which are carried by the water to other individuals. Species whose adults are sessile often have motile larvae, many of which have complicated mechanisms for locating suitable sites on which to settle.

A sessile animal gains access to local resources, but forfeits access to more distant resources. Many colonial sessile pro-

33.1 Anatomical Characteristics of the Major Protostomate Phyla

PHYLUM	BODY CAVITY	DIGESTIVE TRACT	CIRCULATORY SYSTEM
Lophotrochozoans			
Platyhelminthes	None	Dead-end sac	None
Rotifera	Pseudocoelom	Complete	None
Bryozoa	Coelom	Complete	None
Brachiopoda	Coelom	Complete in most	Open
Phoronida	Coelom	Complete	Closed
Nemertea	Coelom	Complete	Closed
Annelida	Coelom	Complete	Closed or open
Mollusca	Reduced coelom	Complete	Open except in cephalopods
Ecdysozoans			
Chaetognatha	Coelom	Complete	None
Nematomorpha	Pseudocoelom	Greatly reduced	None
Nematoda	Pseudoceolom	Complete	None
Crustacea	Hemocoel	Complete	Open
Hexapoda	Hemocoel	Complete	Open
Myriapoda	Hemocoel	Complete	Open
Chelicerata	Hemocoel	Complete	Open

Note: All protostomes have bilateral symmetry.

tostomes, however, are able to grow in the direction of better resources or into sites offering better protection. Individual members of colonies, if they are directly connected, can share resources. The ability to share resources enables some individuals to specialize for particular functions, such as reproduction, defense, or feeding. The nonfeeding individuals derive their nutrition from their feeding associates.

Predation may have been the major selective pressure for the development of hard, external body coverings. Such coverings evolved independently in many lophotrochozoan and ecdysozoan lineages. In addition to providing protection, they became key elements in the development of new systems of locomotion. Locomotory abilities permitted prey to escape more readily from predators, but also allowed predators to pursue their prey more effectively. Thus, the evolution of animals has been, and continues to be, a complex "arms race" among predators and prey.

Although we have concentrated on the evolution of greater complexity in animal lineages, many lineages whose members have remained simple have been very successful. Cnidarians are common in the oceans; roundworms are abundant in most aquatic and terrestrial environments. Parasites have lost complex body plans but have evolved complex life cycles.

The characteristics of the major existing phyla of protostomate animals are summarized in Table 33.1. Many major evolutionary trends were shared by protostomes and deuterostomes, the lineage that includes the chordates, the group to which humans belong. We will consider the evolution of diversity among the deuterostomes in the next chapter.

Chapter Summary

- The ecdysozoan lineage is characterized by a nonliving external covering—an exoskeleton, or cuticle. **Review Figure 33.1**
- An animal with an exoskeleton grows by periodically shedding its exoskeleton and replacing it with a larger one, a process called molting.

Cuticles: Flexible, Unsegmented Exoskeletons

- Members of several phyla of marine worms with thin cuticles are descendants of an early split in the ecdysozoan lineage. **Review Figure 33.3**
- Tough cuticles are found in members of two phyla, the horsehair worms and the roundworms.
- Roundworms (phylum Nematoda) are one of the most abundant and universally distributed of all animal groups. Many are parasites. **Review Figure 33.5**

Arthropods and Their Relatives: Segmented External Skeletons

- Animals with rigid exoskeletons lack cilia for locomotion. To move, they have appendages that can be manipulated by muscles. **Review Figure 33.8**
- Although there is currently no consensus on an exact phylogeny, most researchers agree that the arthropod groups are monophyletic.
- Onychophorans and tardigrades have soft, unjointed legs. They are probably similar to ancestral arthropods.
- Trilobites flourished in Cambrian and Ordovician seas, but they became extinct at the close of the Paleozoic era.

Crustaceans: Species-Rich and Abundant

- The segments of the crustacean body are divided among three regions: head, thorax, and abdomen. **Review Figure 33.10**
- The most familiar crustaceans are shrimp, lobsters, crayfish, crabs, sow bugs, and sand fleas. Copepod crustaceans may be the most abundant animals on the planet.
- Recent molecular evidence indicates that the crustacean lineage may be ancestral to all the arthropods.

Insects: Terrestrial Descendants of Marine Crustaceans

- About 1.4 million species of insects (phylum Hexapoda) have been described, but that number is a small fraction of the total number of existing species. Although few species are found in marine environments, they are among the dominant animals in virtually all terrestrial and many freshwater habitats.
- Like crustaceans, insects have three body regions (head, thorax, abdomen). They bear a single pair of antennae on the head and three pairs of legs attached to the thorax. No appendages grow from their abdominal segments. **Review Figure 33.11**
- Wingless insects look like miniature adults when they hatch. Hatchlings of some winged insects resemble adults, but others undergo substantial changes at each molt.

- The winged insects can be divided into three major subgroups. Members of one subgroup cannot fold their wings back against the body. Members of the other two subgroups can.
- The wings of insects probably evolved from the dorsal branches of multibranched ancestral appendages. **Review Figure 33.14**

Arthropods with Two Body Regions

- Individuals of the remaining arthropod phyla generally have segmented bodies with two distinct regions, head and trunk.
- Myriapods (centipedes and millipedes) have many segments and many pairs of legs.
- Most chelicerates (phylum Chelicerata) have four pairs of legs.
- Arachnids—scorpions, harvestmen, spiders, mites, and ticks—are abundant in terrestrial environments.

Themes in the Evolution of Protostomes

- Most evolution of protostomes took place in the oceans.
- Early animals used fluid-filled body cavities as hydrostatic skeletons. Subdivision of the body cavity into segments allowed better control of movement.
- During much of animal evolution, the only food in the water consisted of dissolved organic matter and very small organisms.
- Flowing water brings food with it, allowing many aquatic animals to obtain food while being sessile.
- Predation may have been the major selective pressure for the development of hard, external body coverings.

See Web/CD Activities 33.1 and 33.2 for a concept review of this chapter.

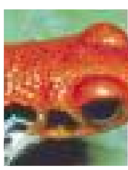
Self-Quiz

1. The outer covering of ecdysozoans
   a. is always hard and rigid.
   b. is always thin and flexible.
   c. is present at some stage in the life cycle but not always among adults.
   d. ranges from very thin to hard and rigid.
   e. prevents the animals from changing their shapes.
2. The primary support for members of several small phyla of marine worms is
   a. their exoskeletons.
   b. their internal skeletons.
   c. their hydrostatic skeletons.
   d. the surrounding sediments.
   e. the bodes of other animals within which they live.
3. Roundworms are abundant and diverse because
   a. they are both parasitic and free-living and eat a wide variety of foods.
   b. they are able to molt their exoskeletons.
   c. their thick cuticle enables them to move in complex ways.
   d. their body cavity is a pseudocoelom.
   e. their segmented bodies enable them to live in many different places.
4. The arthropod exoskeleton is composed of a
   a. mixture of several kinds of polysaccharides.
   b. mixture of several kinds of proteins.
   c. single complex polysaccharide called chitin.
   d. single complex protein called arthropodin.
   e. mixture of layers of proteins and a polysaccharide called chitin.
5. Which phyla are arthropod relatives with unjointed legs?
   a. Trilobita and Onychophora
   b. Onychophora and Tardigrada
   c. Trilobita and Tardigrada
   d. Onychophora and Chelicerata
   e. Tardigrada and Chelicerata
6. The members of which crustacean group are probably the most abundant of all animals?
   a. Decapoda
   b. Amphipoda
   c. Copepoda
   d. Cirripedia
   e. Isopoda
7. The body plan of insects is composed of which of the three following regions?
   a. Head, abdomen, and trachea
   b. Head, abdomen, and cephalothorax
   c. Cephalothorax, abdomen, and trachea
   d. Head, thorax, and abdomen
   e. Abdomen, trachea, and mantle
8. Insects that hatch from eggs into juveniles that resemble miniature adults are said to have
   a. instars.
   b. neopterous development.
   c. accelerated development.
   d. incomplete metamorphosis.
   e. complete metamorphosis.
9. Which of the following groups of insects cannot fold their wings back against the body?
   a. Beetles
   b. True bugs
   c. Earwigs
   d. Stone flies
   e. Mayflies
10. Factors that may have contributed to the remarkable evolutionary diversification of insects include
    a. the terrestrial environments penetrated by insects lacked any other similar organisms.
    b. insects evolved the ability to fly.
    c. some lineages of insects evolved complete metamorphosis.
    d. insects evolved effective means of delivering oxygen to their internal tissues.
    e. All of the above

For Discussion

1. Segmentation has arisen several times during animal evolution. What advantages does segmentation provide? Given these advantages, why do so many unsegmented animals survive?
2. The British biologist J. B. S. Haldane is reputed to have quipped that "God was unusually fond of beetles." Beetles are, indeed, the most species-rich lineage of organisms. What features of beetles have contributed to the evolution and survival of so many species?
3. In Part Four of this book, we pointed out that major structural novelties have arisen infrequently during the course of evolution. Which of the features of protostomes do you think are major evolutionary novelties? What criteria do you use to judge whether a feature is a major as opposed to a minor novelty?
4. There are more described and named species of insects than of all other animal lineages combined. However, only a very few species of insects live in marine environments, and those species are restricted to the intertidal zone or the ocean surface. What factors may have contributed to the inability of insects to be successful in the oceans?

34 Deuterostomate Animals



Complex social systems, in which individuals associate with one another to breed and care for their offspring, characterize many species of fish, birds, and mammals—the most conspicuous and familiar deuterostomate animals. We tend to think of these social systems as having evolved relatively recently, but some amphibians, members of an ancient deuterostomate group, also have elaborate courtship and parental care behavior. For example, the male of the European midwife toad gathers eggs around his hind legs as the female lays them. He then carries the eggs until they are ready to hatch.

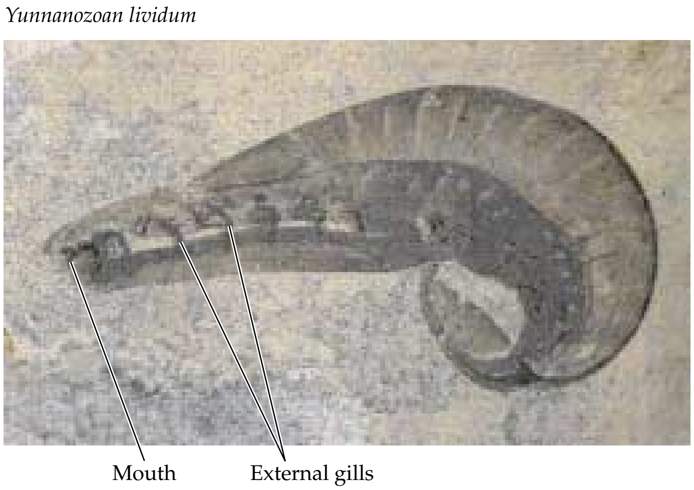
In the Surinam toad, mating and parental care are exquisitely coordinated, as an elaborate mating "dance" results in the female depositing eggs on the male's belly. The male fertilizes the eggs and, as the ritual ends, he presses them against the female's back, where they are carried until they hatch. The female poison dart frog lays clutches of eggs on a leaf or on the ground, which both parents then work to keep moist and protected. When the tadpoles hatch, they wiggle onto the back of one of their parents, who then carries the tadpoles to water.

There are fewer major lineages and many fewer species of deuterostomes than of protostomes (Table 34.1 on page 658), but we have a special interest in the deuterostomes because we are members of that lineage. In this chapter, we will describe and discuss the deuterostomate phyla: Echinodermata, Hemichordata, and Chordata. We close with a brief overview of some major themes in the evolution of animals.

Some Amphibian Parents Nurture Their Young Poison dart frogs (*Dendrobates reticulatus*) of the Amazon basin lay their eggs on land. Both parents protect and nurture the eggs until they hatch, at which time a parent carries the tadpoles to water on its back.

Deuterostome Ancestors

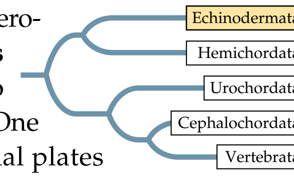
A group of extinct animals known as the yunnanozoans are the likely ancestors of all deuterostomes. Many fossils of these animals have been discovered in China's Yunnan province. These well-preserved fossils show that the animals had a large mouth, six pairs of external gills, and a lightly cuticularized, segmented posterior body section (Figure 34.1). Later in deuterostome evolution, gills became internal and were connected to the exterior via slits in the body wall. These gill slits subsequently were lost in the lineage leading to the modern echinoderms.



34.1 The Ancestral Deuterostomes Had External Gills The extinct Yunnanozoan lineage is probably ancestral to all deuterostomes. This fossil, which dates from the Cambrian, shows the six pairs of external gills and segmented posterior body that characterized these animals.

Modern deuterostomes fall into two major clades (Figure 34.2). One clade, composed of echinoderms and hemichordates, is characterized by a three-part coelom and a bilaterally symmetrical, ciliated larva. The ancestors of the other clade, containing the chordates, had a distinctly different, nonfeeding, tadpole-like larva and a unique dorsal supporting structure.

Echinoderms: Pentaradial Symmetry

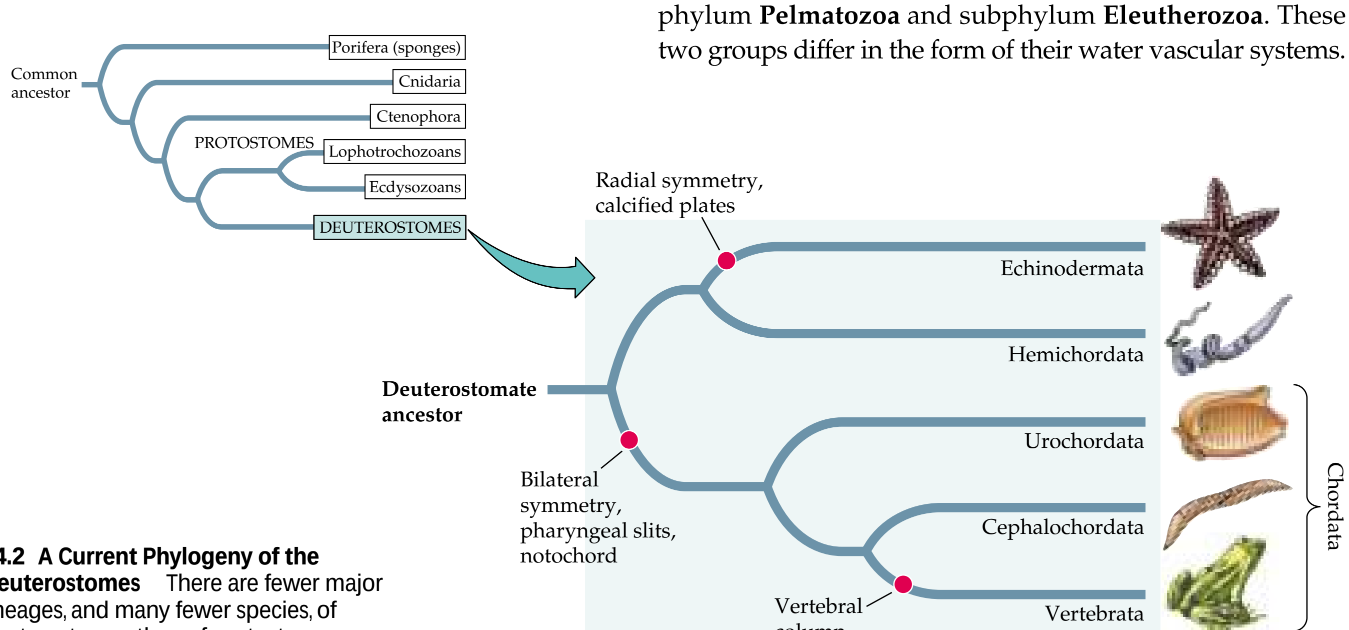


During the evolution of one deuterostomate lineage, the **echinoderms** (phylum **Echinodermata**), two major structural features arose. One was a system of calcified internal plates covered by thin layers of skin and some muscles. The calcified plates of early echinoderms later became enlarged and thickened until they fused inside the entire body, giving rise to an internal skeleton.

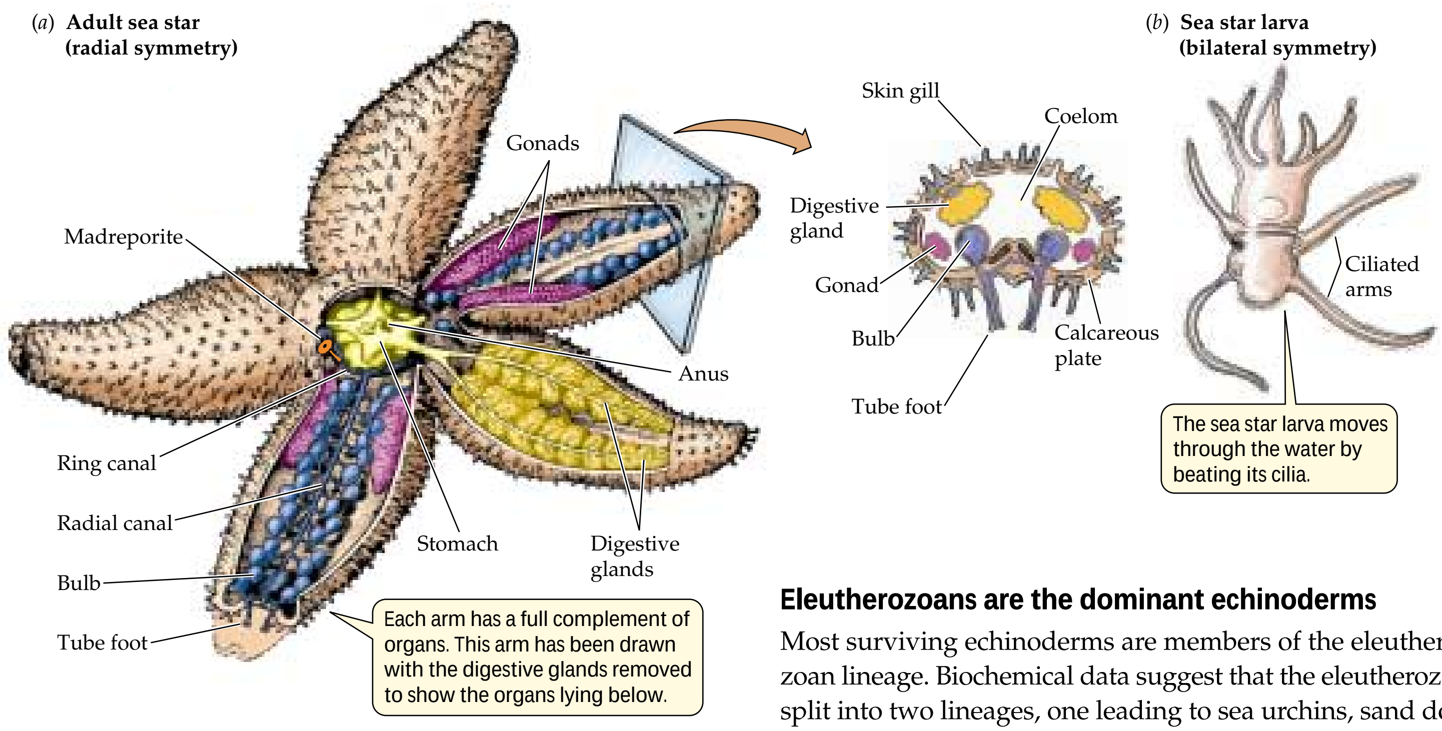
The other feature was a *water vascular system*, a network of water-filled canals leading to extensions called *tube feet*. This system functions in gas exchange, locomotion, and feeding (Figure 34.3*a*). Seawater enters the system through a perforated *madreporite*. A calcified canal leads from the madreporite to another canal that rings the *esophagus* (the tube leading from the mouth to the stomach). Other canals radiate from this *ring canal*, extending through the arms (in species that have arms) and connecting with the tube feet.

The development of these two structural innovations resulted in a striking evolutionary radiation. About 23 classes of echinoderms, of which only 6 survive today, have been described from fossils. The 13,000 species described from their fossil remains are probably only a small fraction of those that actually lived. Nearly all 7,000 species that survive today live only in marine environments. Some have bilaterally symmetrical, ciliated larvae (Figure 34.3*b*) that feed for some time as planktonic organisms before settling and transforming into adults with *pentaradial symmetry* (symmetry in five or multiples of five).

Living echinoderms are members of two lineages: subphylum **Pelmatozoa** and subphylum **Eleutherozoa**. These two groups differ in the form of their water vascular systems.



34.2 A Current Phylogeny of the Deuterostomes There are fewer major lineages, and many fewer species, of deuterostomes than of protostomes.



34.3 Echinoderms Display Two Evolutionary Innovations
(*a*) A dorsal view of a sea star displays the canals and tube feet of the echinoderm water vascular system, as well as a calcified internal skeleton. (*b*) The ciliated sea star larva has bilateral symmetry.

Pelmatozoans have jointed arms

Sea lilies and feather stars (class **Crinoidea**) are the only surviving pelmatozoans. Sea lilies were abundant 300–500 million years ago, but only about 80 species survive today. Most sea lilies attach to a substratum by means of a flexible stalk consisting of a stack of calcareous discs. The main body of the animal is a cup-shaped structure that contains a tubular digestive system. Five to several hundred arms, usually in multiples of five, extend outward from the cup. The jointed calcareous plates of the arms enable them to bend.

A sea lily feeds by orienting its arms in passing water currents. Food particles strike and stick to the tube feet, which are covered with mucus-secreting glands. The tube feet transfer these particles to grooves in the arms, where ciliary action carries the food to the mouth. The tube feet of sea lilies are also used for gas exchange and elimination of nitrogenous wastes.

Feather stars are similar to sea lilies, but they have flexible appendages with which they grasp the substratum (Figure 34.4*a*). Feather stars feed in much the same manner as sea lilies. They can walk on the tips of their arms or swim by rhythmically beating their arms. About 600 living species of feather stars have been described.

Eleutherozoans are the dominant echinoderms

Most surviving echinoderms are members of the eleutherozoan lineage. Biochemical data suggest that the eleutherozoa split into two lineages, one leading to sea urchins, sand dollars, and sea cucumbers, and the second leading to sea stars and brittle stars.

Sea urchins and sand dollars (class **Echinoidea**) lack arms, but they share a five-part body plan with all other echinoderms. Sea urchins are hemispherical animals that are covered with spines attached to the underlying skeleton via ball-and-socket joints (Figure 34.4*b*). The spines of sea urchins come in varied sizes and shapes; a few produce toxic substances. Many sea urchins consume algae, which they scrape from rocks with a complex rasping structure. Others feed on small organic debris that they collect with their tube feet or spines. Sand dollars, which are flattened and disc-shaped, feed on algae and fragments of organic matter found on the seafloor or suspended organic material.

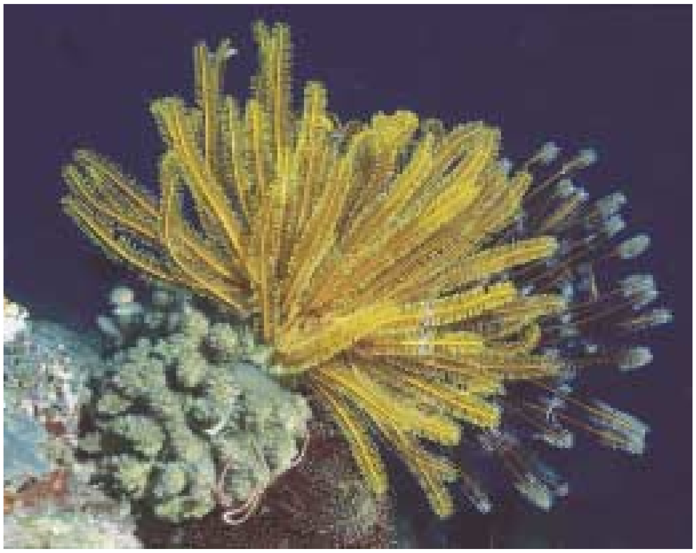
The sea cucumbers (class **Holothuroidea**) lack arms, and their bodies are oriented in an atypical manner for an echinoderm. The mouth is anterior and the anus is posterior, not oral and aboral as in other echinoderms. Sea cucumbers use their tube feet primarily for attaching to the substratum rather than for moving. The anterior tube feet are modified into large, feathery, sticky tentacles that can be protruded from the mouth (Figure 34.4*c*). Periodically, the sea cucumber withdraws the tentacles, wipes off the material that has adhered to them, and digests it.

Sea stars (class **Asteroidea**; Figure 34.4*d*) are the most familiar echinoderms. Their digestive organs and gonads are located in the arms. Their tube feet serve as organs of locomotion, gas exchange, and attachment. Each tube foot of a sea star is also an adhesive organ consisting of an internal ampulla connected by a muscular tube to an external suction

34.1 *Summary of Living Members of the Kingdom Animalia*

PHYLUM	NUMBER OF LIVING SPECIES DESCRIBED	MAJOR GROUPS
Porifera: Sponges	10,000	
Cnidaria: Cnidarians	10,000	Hydrozoa: Hydras and hydroids Scyphozoa: Jellyfishes Anthozoa: Corals, sea anemones
Ctenophora: Comb jellies	100	
PROTOSTOMES		
Lophotrochozoans		
Platyhelminthes: Flatworms	20,000	Turbellaria: Free-living flatworms Trematoda: Flukes (all parasitic) Cestoda: Tapeworms (all parasitic) Monogenea (ectoparasites of fishes)
Rotifera: Rotifers	1,800	
Ectoprocta: Bryozoans	4,500	
Brachiopoda: Lamp shells	340	More than 26,000 fossil species described
Phoronida: Phoronids	20	
Nemertea: Ribbon worms	900	
Annelida: Segmented worms	15,000	Polychaeta: Polychaetes (all marine) Oligochaeta: Earthworms, freshwater worms Hirudinea: Leeches
Mollusca: Mollusks	50,000	Monoplacophora: Monoplacophorans Polyplacophora: Chitons Bivalvia: Clams, oysters, mussels Gastropoda: Snails, slugs, limpets Cephalopoda: Squids, octopuses, nautiloids
Ecdysozoans		
Kinorhyncha: Kinorhynchs	150	
Chaetognatha: Arrow worms*	100	
Nematoda: Roundworms	20,000	
Nematomorpha: Horsehair worms	230	
Onychophora: Onychophorans	80	
Tardigrada: Water bears	600	
Chelicerata: Chelicerates	70,000	Merostomata: Horseshoe crabs Arachnida: Scorpions, harvestmen, spiders, mites, ticks
Crustacea	50,000	Crabs, shrimps, lobsters, barnacles, copepods
Hexapoda	1,500,000	Insects
Myriapoda	13,000	Millipedes, centipedes
DEUTEROSTOMES		
Echinodermata: Echinoderms	7,000	Crinoidea: Sea lilies, feather stars Ophiuroidea: Brittle stars Asteroidea: Sea stars Concentricycloidea: Sea daisies Echinoidea: Sea urchins Holothuroidea: Sea cucumbers
Hemichordata: Hemichordates	95	Acorn worms and pterobranchs
Chordata: Chordates	50,000	Urochordata: Sea squirts Cephalochordata: Lancelets Agnatha: Lampreys, hagfishes Chondrichthyes: Cartilaginous fishes Osteichthyes: Bony fishes Amphibia: Amphibians Reptilia: Reptiles Aves: Birds Mammalia: Mammals

* The position of this phylum is uncertain. Many researchers place them in the deuterostomes.

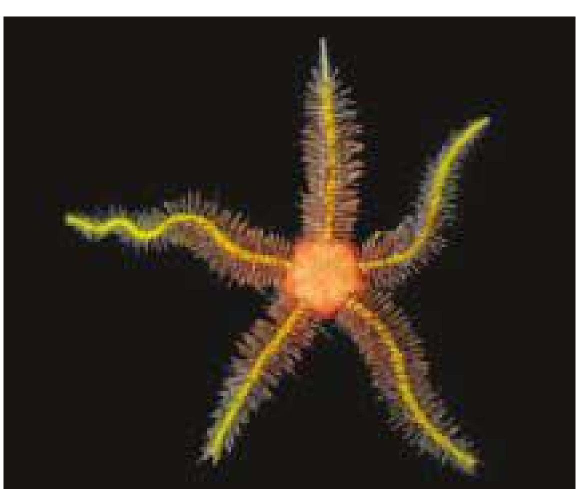


(*a*) *Oxycomanthus bennetti*

(*b*) *Strongylocentrotus purpuratus*

(*c*) *Bohadschia argus*

(*d*) *Henricia leviuscula*



(*e*) *Ophiothrix spiculata*

34.4 Diversity among the Echinoderms (*a*) The flexible arms of this golden feather star are clearly visible. (*b*) Purple sea urchins are important grazers on algae in the intertidal zone of the Pacific Coast of North America. (*c*) This sea cucumber lives on rocky substrata in the seas around Papua New Guinea. (*d*) The blood sea star is typical of many sea stars; some species, however, have more than five arms. (*e*) The arms of the brittle star are composed of hard but flexible plates.

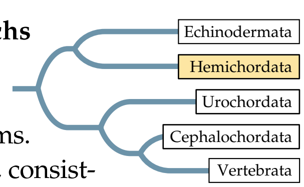
cup. The tube foot is moved by expansion and contraction of the circular and longitudinal muscles of the tube.

Many sea stars prey on polychaetes, gastropods, bivalves, and fish. They are important predators in many marine environments, such as coral reefs and rocky intertidal zones. With hundreds of tube feet acting simultaneously, a sea star can exert an enormous and continuous force. It can grasp a clam in its arms, anchor the arms with its tube feet, and, by steady contraction of the muscles in the arms, gradually exhaust the muscles the clam uses to keep its shell closed. Sea stars that feed on bivalves are able to push the stomach out through the mouth and then through the narrow space between the two halves of the bivalve's shell. The stomach secretes enzymes that digest the prey.

Brittle stars (class **Ophiuroidea**) are similar in structure to sea stars, but their flexible arms are composed of jointed hard plates (Figure 34.4*e*). Brittle stars generally have five arms, but each arm may branch a number of times. Most of the 2,000 species of brittle stars ingest particles from the upper regions of sediments and assimilate the organic material from them, but some species remove suspended food particles from the water; others capture small animals. Brittle stars eject the indigestible particles through their mouths because, unlike most other echinoderms, they have only one opening to the digestive tract.

An additional group, the sea daisies (class **Concentricycloidea**) were discovered only in 1986, and little is known about them. They have tiny disc-shaped bodies with a ring of marginal spines, and two ring canals, but no arms. Sea daisies are found on rotting wood in ocean waters. They apparently eat prokaryotes, which they digest outside their bodies and absorb either through a membrane that covers the oral surface or via a shallow, saclike stomach. Recent molecular data suggest that they are greatly modified sea stars.

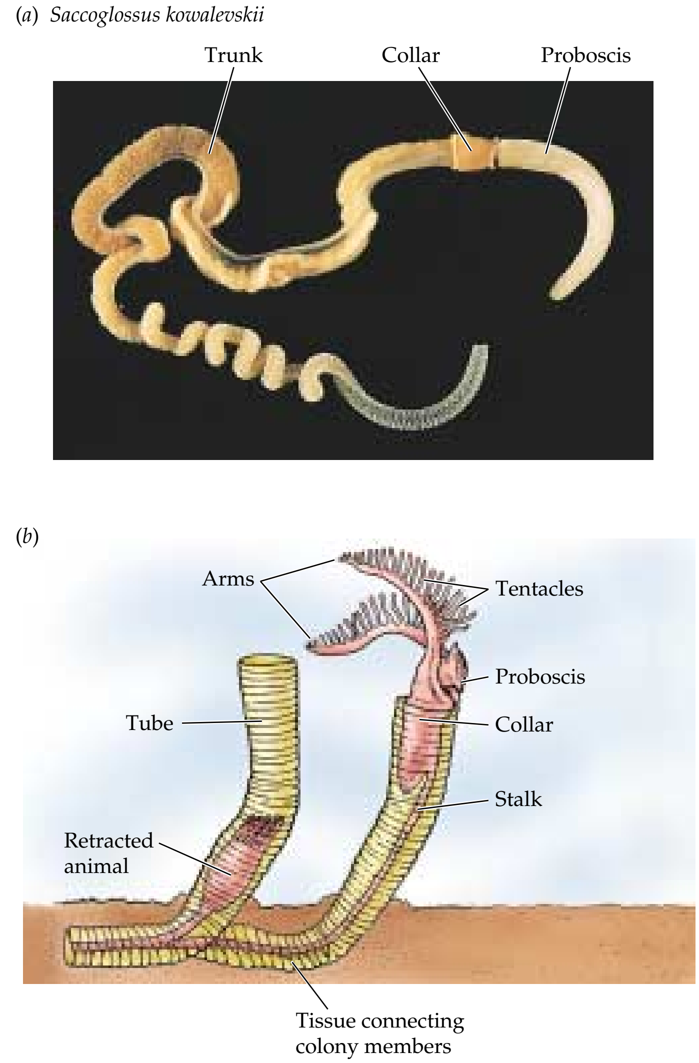
Hemichordates: Conservative Evolution



Acorn worms and **pterobranchs** (phylum **Hemichordata**) are probably similar in form to the ancestor they share with the echinoderms. They have a three-part body plan, consisting of a proboscis, a collar, and a trunk.

The 70 species of acorn worms range up to 2 meters in length. They live in burrows in muddy and sandy marine sediments. The large proboscis of an acorn worm is a digging organ (Figure 34.5*a*). It is coated with a sticky mucus that traps small organisms in the sediment. The mucus and its attached prey are conveyed by cilia to the mouth. In the esophagus, the food-laden mucus is compacted into a ropelike mass that is moved through the digestive tract by ciliary action. Behind the mouth is a muscular *pharynx*, a tube that connects the mouth to the intestine. The pharynx opens to the outside through a number of *pharyngeal slits* through which water can exit. Highly vascularized tissue surrounding the pharyngeal slits serves as a gas exchange apparatus. An acorn worm breathes by pumping water into its mouth and out through its pharyngeal slits.

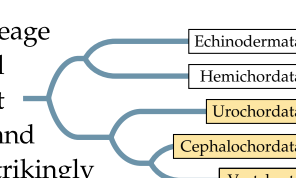
The 10 living species of pterobranchs are sedentary animals up to 12 mm in length that live in a tube secreted by the proboscis. Some species are solitary; others form colonies of individuals joined together. Behind the proboscis is a collar



34.5 Hemichordates (*a*) The proboscis of this acorn worm is modified for digging. This individual has been extracted from its burrow. (*b*) Pterobranchs may be colonial or solitary.

with 1–9 pairs of arms, bearing long tentacles that capture prey and function in gas exchange (Figure 34.5*b*).

Chordates: New Ways of Feeding



Members of the second major lineage of deuterostomes evolved several modifications of the coelom that provided new ways of capturing and handling food. They evolved a strikingly different body plan, characterized by an internal dorsal supporting structure. The pharyngeal slits, which originally functioned as sites for the uptake of O_2 and elimination of CO_2, and for eliminating water, were further enlarged. The result was a phylum (Chordata) of bilaterally (*a*) *Rhopalaea crassa* (*b*) *Pegea socia*

34.6 Urochordates (*a*) The tunic is clearly visible in this transparent sea squirt. (*b*) A chainlike colony of salps floats in tropical waters.

symmetrical animals with body plans characterized by the following shared features at some stage in their development:

- *Pharyngeal slits*
- A dorsal, hollow *nerve cord*
- A ventral *heart*
- A *tail* that extends beyond the anus
- A dorsal supporting rod, the *notochord*

The **notochord** is the distinctive derived trait of the lineage. It is composed of a core of large cells with turgid fluid-filled vacuoles that make it rigid but flexible. In some urochordates, the notochord is lost during metamorphosis to the adult stage. In vertebrates, it is replaced by other skeletal structures that provide support for the body.

The **tunicates** (subphylum **Urochordata**) may be similar to the ancestors of the chordates. All 2,500 species of tunicates are marine animals, most of which are sessile as adults. Their swimming, tadpole-like larvae reveal the close evolutionary relationship between tunicates and chordates (as Darwin realized; see Figure 25.4).

In addition to its pharyngeal slits, a tunicate larva has a dorsal, hollow nerve cord and a notochord that is restricted to the tail region. Bands of muscle surround the notochord, providing support for the body. After a short time swimming in the water, the larvae of most species settle to the seafloor and transform into sessile adults. The tunicate pharynx is enlarged into a *pharyngeal basket*, with which the animal feeds by extracting plankton from the water. Some urochordates are solitary, but others produce colonies by asexual budding from a single founder.

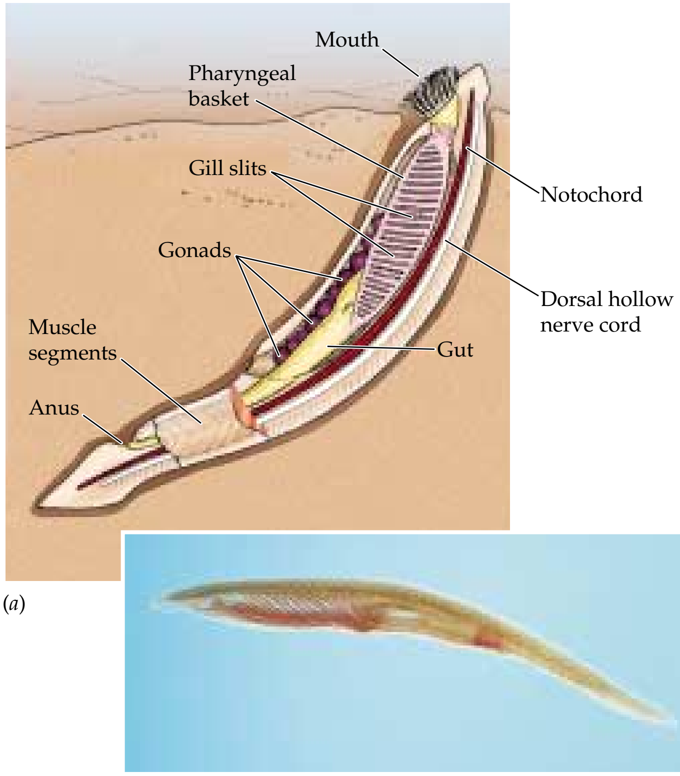
There are three major urochordate groups: ascidians, thaliaceans, and larvaceans. More than 90 percent of the known species of tunicates are *ascidians* (sea squirts). Individual sea squirts range in size from less than 1 mm to 60 cm in length, but colonies may measure several meters across. The baglike body of an adult ascidian is enclosed in a tough tunic that is secreted by epidermal cells. The tunic is composed of proteins and a complex polysaccharide. Much of the body is occupied by a large pharyngeal basket lined with cilia, whose beating moves water through the animal (Figure 34.6*a*).

Thaliaceans (salps and others) float in tropical and subtropical oceans at all depths down to 1,500 meters (Figure 34.6*b*). They live singly or in chainlike colonies up to several meters long. *Larvaceans* are solitary planktonic animals usually less than 5 mm long. They retain their notochords and nerve cords throughout their lives.

The 25 species of **lancelets** (subphylum **Cephalochordata**) are small, fishlike animals that rarely exceed 5 cm in length. Their notochord extends the entire length of the body throughout their lives. Lancelets live partly buried in soft marine sediments. They extract small prey from the water with their pharyngeal baskets (Figure 34.7).

A jointed vertebral column replaced the notochord in vertebrates

In another chordate lineage, the enlarged pharyngeal basket came to be used to extract prey from mud. This lineage gave rise to the **vertebrates** (subphylum **Vertebrata**) (Figure 34.8). Vertebrates take their name from the jointed, dorsal **vertebral column** that replaced the notochord as their primary sup-



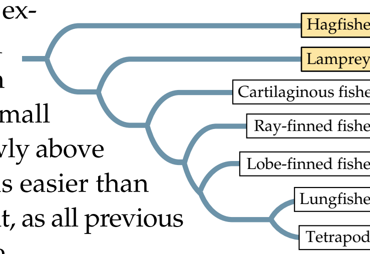
34.7 Lancelets (*a*) The internal structure of a lancelet. Note the large pharyngeal basket with gill slits. (*b*) This lancelet, which is about 6 cm long, has been excavated from the sediment to show its entire body.

port. The vertebrate body plan (Figure 34.9) can be characterized as follows:

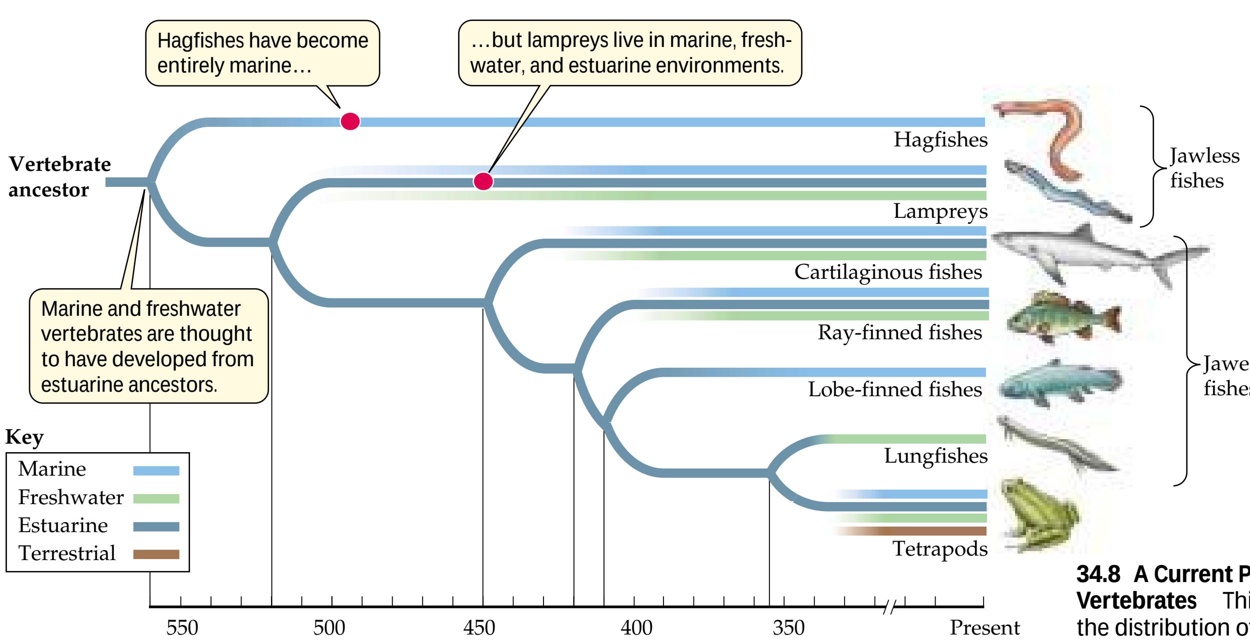
- A rigid *internal skeleton*, with the vertebral column as its anchor, that provides support and mobility
- Two pairs of *appendages* attached to the vertebral column
- An anterior *skull* with a large *brain*
- Internal organs suspended in a large *coelom*
- A well-developed *circulatory system*, driven by contractions of a ventral *heart*

The ancestral vertebrates lacked jaws. They probably swam over the bottom, sucking up mud and straining it through the pharyngeal basket to extract microscopic food particles. The vascularized tissues of the basket also served a gas-exchange function. These animals gave rise to the jawless fishes.

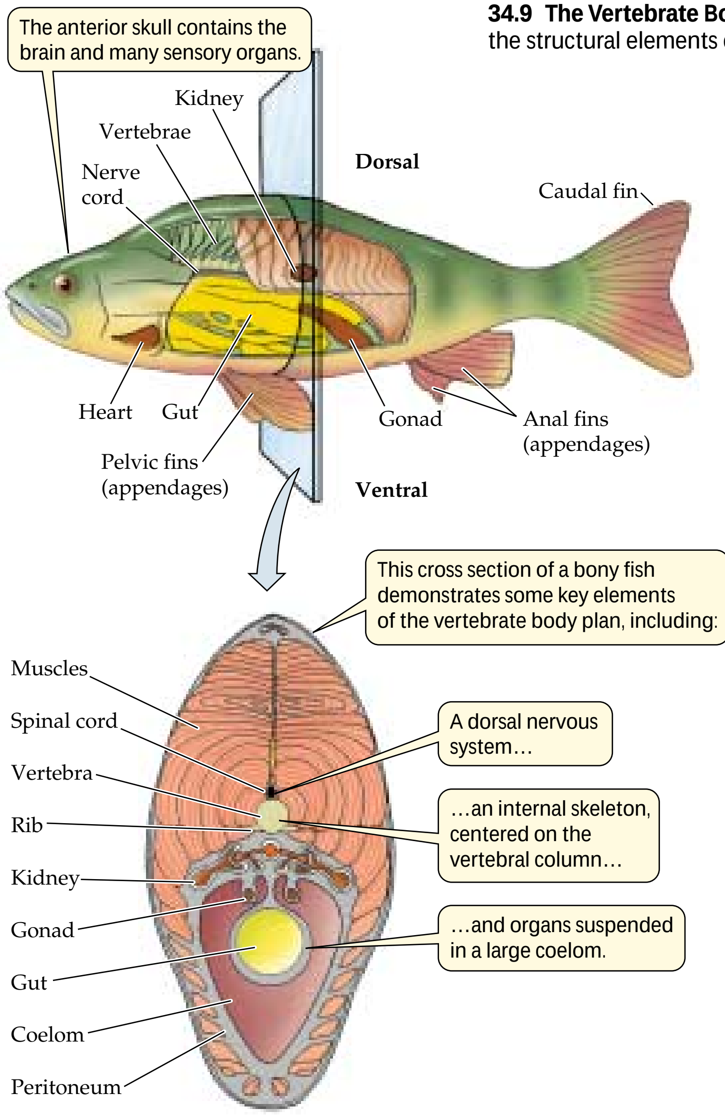
One group of jawless fishes, called **ostracoderms** ("shell-skinned"), evolved a bony external armor that protected them from predators. With their heavy armor, these small fish could safely swim slowly above the substratum, which was easier than having to burrow through it, as all previous sediment feeders had done.



Jawless fishes could attach to dead organisms and use suction created by the pharynx to pull fluids and partly decomposed tissues into the mouth. Hagfishes and lampreys, the only jawless fishes to survive beyond the Devonian, feed on both dead and living organisms in this way (Figure 34.10). These fishes, often placed in the class **Agnatha**, have tough skins instead of external armor. They lack paired appendages



34.8 A Current Phylogeny of the Vertebrates This phylogeny shows the distribution of lineages over the major types of environments.



34.9 The Vertebrate Body Plan A ray-finned fish is used here to illustrate the structural elements common to all vertebrates.

(fins). The round mouth is a sucking organ with which the animals attach to their prey and rasp at the flesh. The lineages leading to modern hagfishes probably diverged from other groups first (see Figure 34.8). The 60 species of hagfishes are entirely marine, but the 50 species of lampreys live in both fresh and salt water.

Jaws improved feeding efficiency

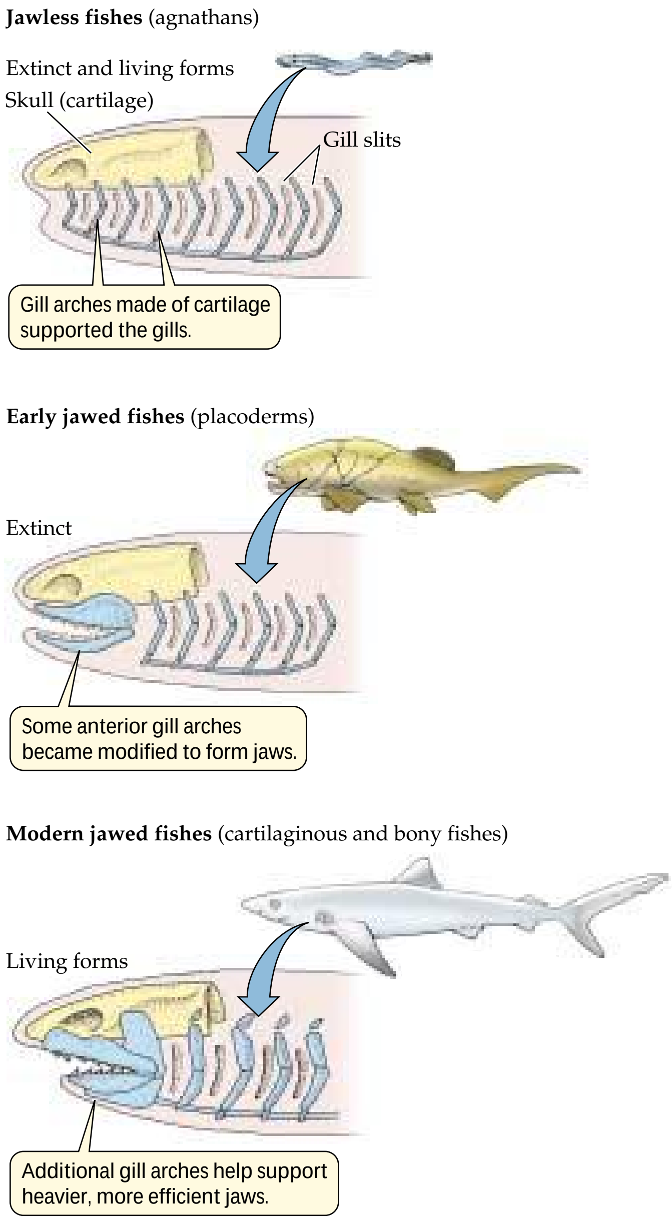
During the Devonian period, many new kinds of fishes evolved in the seas, estuaries, and fresh waters. Although most of these fishes were jawless, in one lineage, some of the skeletal arches that supported the gills evolved into jaws (Figure 34.11). A fish with jaws can grasp and subdue large prey. Further development of jaws and teeth enabled some fishes to chew both soft and hard body parts of prey. Chewing aided chemical digestion and improved the fishes' ability to extract nutrients from their prey.

The dominant early jawed fishes were the heavily armored **placoderms** (class **Placodermi**). Some of these fishes evolved elaborate fins and relatively sleek body forms that improved their ability to maneuver in open water. A few became huge (10 m long) and, together with squids (cephalopod mollusks), were probably the major predators in the Devonian oceans. Despite their early abundance, however, most placoderms had disappeared by the end of the Devonian period; none survived to the end of the Paleozoic era.

34.10 Modern Jawless Fishes (*a*) The Pacific hagfish. (*b*) Two sea lampreys using their large, jawless mouths to suck blood and flesh from a trout. The sea lamprey can live in either fresh or saltwater.

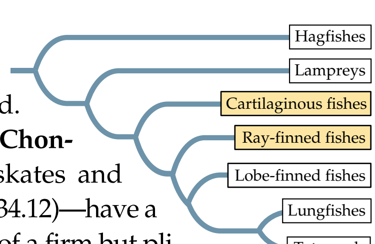
(*a*) *Eptatretus stouti*

(*b*) *Petromyzon marinus*



34.11 Jaws from Gill Arches This series of diagrams illustrates one probable scenario for the evolution of jaws from the anterior gill arches of fishes.

Fins improved mobility



Several other groups of fishes became abundant during the Devonian period. **Cartilaginous fishes** (class **Chondrichthyes**)—the sharks, skates and rays, and chimaeras (Figure 34.12)—have a skeleton composed entirely of a firm but pliable material called *cartilage*. Their skin is flexible and leathery, sometimes bearing scales that give it the consistency of sandpaper.

Cartilaginous fishes control their movement with pairs of unjointed appendages called *fins:* a pair of pectoral fins just behind the gill slits and a pair of pelvic fins just in front of the anal region (see Figure 34.9). A dorsal median fin stabilizes the fish as it moves. Sharks move forward by means of lateral undulations of their bodies and tail fins. Skates and rays propel themselves by means of vertical undulating movements of their greatly enlarged pectoral fins.

Most sharks are predators, but some feed by straining plankton from the water. The world's largest fish, the whale shark (*Rhincodon typhus*), is a filter feeder. It may grow to more than 12 meters in length and weigh more than 12,000 kilograms. Most skates and rays live on the ocean floor, where they feed on mollusks and other invertebrates buried in the sediments. Nearly all cartilaginous fishes live in the oceans, but a few are estuarine or migrate into lakes and rivers. One group of stingrays is found only in river systems of South America. The chimaeras are found in deep ocean waters and are seen less often than the sharks and rays.

Swim bladders allowed control of buoyancy

Ray-finned fishes (class **Actinopterygii**) have internal skeletons of calcified, rigid bone rather than flexible cartilage. The outer surface of most species of ray-finned fishes is covered with flat, thin, lightweight scales that provide some protection or enhance their movement through the water.

The gills of ray-finned fishes open into a single chamber covered by a hard flap. Movement of the flap improves the flow of water over the gills, where gas exchange takes place. Early ray-finned fishes also evolved gas-filled sacs that supplemented the action of the gills in respiration. These features enabled early ray-finned fishes to live where oxygen was periodically in short supply, as it often is in freshwater environments. The lunglike sacs evolved into *swim bladders*, which function as organs of buoyancy in most ray-finned fishes today. By adjusting the amount of gas in its swim bladder, a fish can control the depth at which it is suspended in the water without expending energy.

Ray-finned fishes radiated during the Tertiary into about 24,000 species, encompassing a remarkable variety of sizes, shapes, and lifestyles (Figure 34.13). The smallest are less than 1 cm long as adults; the largest weigh up to 900 kilograms. Ray-finned fishes exploit nearly all types of aquatic food sources. In the oceans they filter plankton from the water, rasp algae from rocks, eat corals and other colonial invertebrates, dig invertebrates from soft sediments, and prey upon virtually all other fishes. In fresh water they eat plankton, devour insects of all aquatic orders, eat fruits that fall into the water in flooded forests, and prey on other aquatic vertebrates and, occasionally, terrestrial vertebrates.

(*a*) *Triaenodon obesus*

(*b*) *Trygon pastinaca*

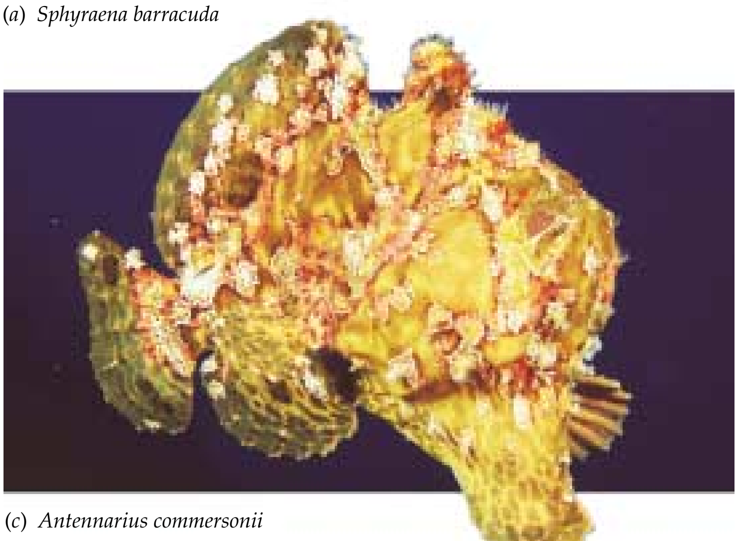
(*c*) *Chimaera* sp.

34.12 Cartilaginous Fishes (*a*) Most sharks, such as this whitetip reef shark, are active marine predators. (*b*) Skates and rays, represented here by a stingray, feed on the ocean bottom. Their modified pectoral fins are used for propulsion. (*c*) A chimaera, or ratfish. These deep-ocean fish often possess poisonous dorsal fins.

34.13 Diversity among Ray-Finned Fishes (*a*) The barracuda has the large teeth and powerful jaws of a predator. (*b*) The coral grouper lives on tropical coral reefs. (*c*) Commerson's frogfish can change its color over a range from pale yellow to orange-brown to deep red, thus enhancing its camouflage abilities. (*d*) This weedy sea dragon is difficult to see when it hides in vegetation. It is a larger relative of the more familiar seahorse.

(*a*) *Sphyraena barracuda*

(*b*) *Plectorhinchus chaetodonoides*



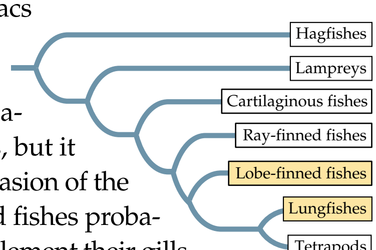
(*c*) *Antennarius commersonii*

(*d*) *Phyllopteryx taeniolatus*

Some fishes live buried in soft sediments, capturing passing prey or emerging at night to feed. Many fishes are solitary, but in open water others form large aggregations called *schools*. Many fishes perform complicated behaviors by means of which they maintain schools, build nests, court and choose mates, and care for their young.

Although ray-finned fishes can readily control their positions in open water, their eggs tend to sink. A few species produce small eggs that are buoyant enough to complete their development in the open water. However, most marine fishes move to food-rich shallow waters to lay their eggs, which is why coastal waters and estuaries are so important in the life cycles of many species. Some, such as salmon, actually abandon salt water when they breed, ascending rivers to spawn in freshwater streams and lakes.

Colonizing the Land: Obtaining Oxygen from the Air



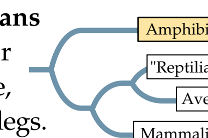
The evolution of lunglike sacs in fishes appears to have been a response to the inadequacy of gills for respiration in oxygen-poor waters, but it also set the stage for the invasion of the land. Some early ray-finned fishes probably used their lungs to supplement their gills when oxygen levels in the water were low, as lungfishes do today. This ability would also have allowed them to leave the water temporarily and breathe air when pursued by predators unable to do so. But with their unjointed fins, these fishes could only flop around on land, as most fish out of water do today. Changes in the structure of the fins allowed these fishes to move on land.

The **lobe-finned fishes** (class **Actinistia**) were the first lineage to evolve jointed fins. Lobe-fins flourished from the Devonian period until about 65 million years ago, when they were thought to have become extinct. However, in 1938, a living lobe-fin was caught by commercial fishermen off South Africa. Since that time, several dozen specimens of this extraordinary fish, *Latimeria chalumnae*, have been collected. *Latimeria*, a predator on other fish, reaches a length of about 1.8 meters and weighs up to 82 kilograms (Figure 34.14*a*). Its skeleton is mostly composed of cartilage, not bone. A second species, *L. menadoensis*, was discovered in 1998 off the Indonesian island of Sulawesi.

Lungfishes (class **Dipnoi**) were important predators in shallow-water habitats in the Devonian, but most lineages died out. The three surviving species live in stagnant swamps and muddy waters in the Southern Hemisphere, one each in South America, Africa, and Australia (Figure 34.14*b*). Lungfishes have both gills and lungs. When ponds dry up, they can burrow deep into the mud and survive for many months in an inactive state.

It is believed that descendants of some lungfishes began to use terrestrial food sources, became more fully adapted to life on land, and eventually evolved to become the **tetrapods**—the four-legged amphibians, reptiles, birds, and mammals.

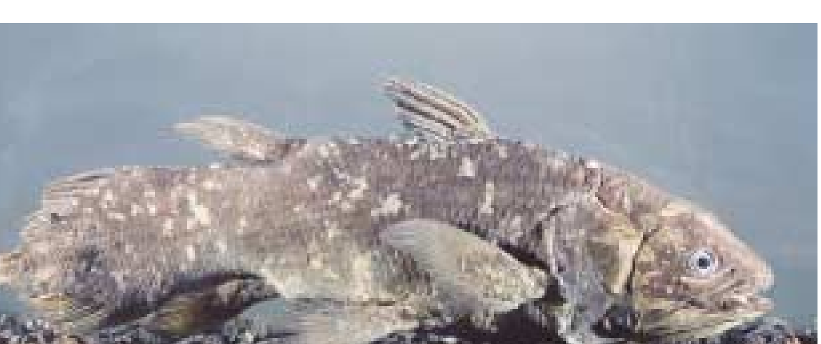
Amphibians invaded the land



During the Devonian period, **amphibians** (class **Amphibia**) arose from an ancestor they shared with lungfishes. In this lineage, stubby, jointed fins evolved into walking legs. The basic design of these legs has remained largely unchanged throughout the evolution of terrestrial vertebrates.

The Devonian predecessors of amphibians were probably able to crawl from one pond or stream to another by slowly pulling themselves along on their finlike legs, as do some modern species of catfishes. They gradually evolved the ability to live in swamps and, eventually, on dry land. Modern

34.14 Fishes with Jointed Fins (*a*) This lobe-fin fish, found in deep waters of the Indian Ocean, represents one of two surviving species of a lineage that was once thought to be extinct. (*b*) All surviving lungfish lineages live in the Southern Hemisphere.



(*a*) *Latimeria chalumnae*

(*b*) *Neoceratodus forsteri*

(*a*) *Dermophis mexicanus*

(*b*) *Gyrinophilus porphyriticus*

(*c*) *Scaphiophryne gottlebei*

34.15 Diversity among the Amphibians (*a*) Burrowing caecilians superficially look more like worms than amphibians. (*b*) A Kentucky spring salamander. (*c*) This rare frog species was discovered in a national park on the island of Madagascar.

amphibians have small lungs, and most species exchange gases through their skins as well. Most terrestrial species are confined to moist environments because they lose water rapidly through their skins when exposed to dry air, and because they require water for reproduction.

About 4,500 species of amphibians live on Earth today, many fewer than the number known only from fossils. Living amphibians belong to three orders (Figure 34.15): the wormlike, limbless, tropical, burrowing caecilians (order Gymnophiona), the frogs and toads (order Anura, which means "tailless"), and the salamanders (order Urodela, which means "tailed"). Most species of frogs and toads live in tropical and warm temperate regions, although a few are found at very high latitudes and altitudes. Some toads have tough skins that enable them to live for long periods of time in dry places. Salamanders are most diverse in temperate regions, but many species are found in cool, moist environments in Central American mountains. Many salamanders that live in rotting logs or moist soil lack lungs. They exchange gases entirely through the skin and mouth lining. Amphibians are the focus of much attention today because populations of many species are declining rapidly (see Chapter 1).

Most species of amphibians live in water at some time in their lives. In the typical amphibian life cycle, part or all of the adult stage is spent on land, but adults return to fresh water to lay their eggs (Figure 34.16). Amphibian eggs can survive only in moist environments because they are enclosed within delicate envelopes that cannot prevent water loss in dry conditions. The fertilized eggs of most species give rise to larvae that live in water until they undergo metamorphosis to become terrestrial adults. Some amphibians, however, are entirely aquatic, never leaving the water at any stage of their lives. Others are entirely terrestrial, laying their eggs in moist places on land and skipping the aquatic larval stage.

Amniotes colonized dry environments

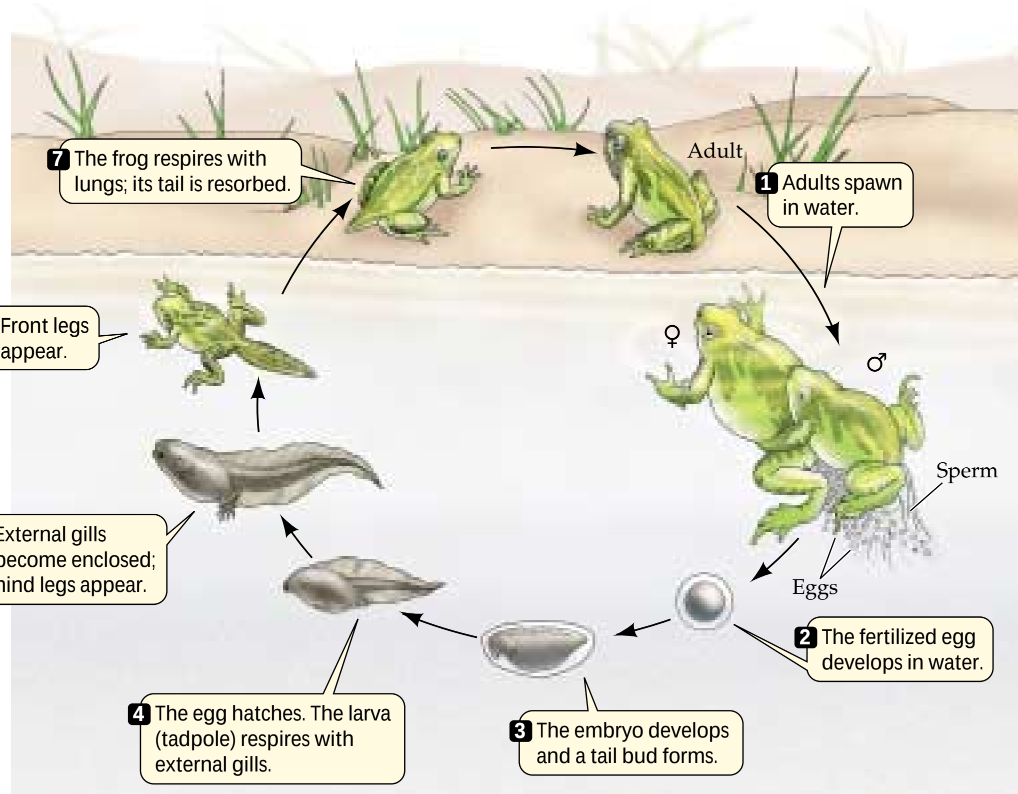
Two morphological changes contributed to the ability of one lineage of tetrapods to control water loss and, therefore, to exploit a wide range of terrestrial habitats:

- Evolution of an egg with a shell that is relatively impermeable to water
- A combination of traits that included a tough skin impermeable to water and kidneys that could excrete concentrated urine

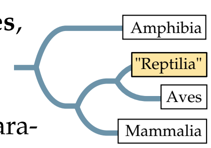
The vertebrates that evolved both of these traits are called **amniotes**. They were the first vertebrates to become widely distributed over the terrestrial surface of Earth.

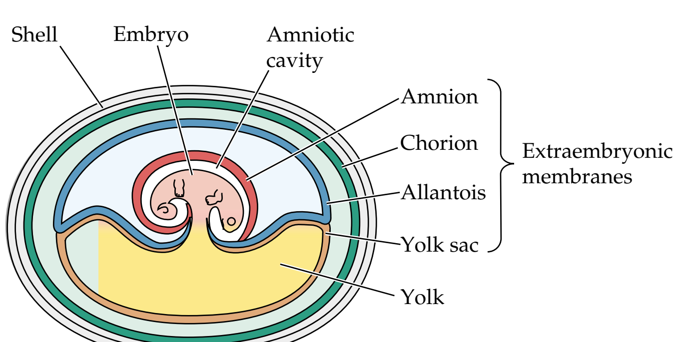
The amniote egg has a leathery or a brittle, calcium-impregnated shell that retards evaporation of the fluids inside but permits O_2 and CO_2 to pass through. Such an egg does not require a moist environment and can be laid anywhere. Within the shell and surrounding the embryo are membranes that protect the embryo from desiccation and assist its respiration and excretion of waste nitrogen. The egg also stores large quantities of food as *yolk*, permitting the embryo to attain a relatively advanced state of development before it hatches and must feed itself (Figure 34.17).

34.16 In and Out of the Water Most stages in the life cycle of temperate-zone frogs take place in water. The aquatic tadpole is transformed into a terrestrial adult through metamorphosis.



An early amniote lineage, the **reptiles**, arose from a tetrapod ancestor in the Carboniferous period (Figure 34.18). The class "Reptilia," as we use the term here, is a paraphyletic group because some reptiles (crocodilians) are in fact more closely related to the birds than they are to lizards, snakes, and turtles (see Figure 25.8). However, because all members of "Reptilia" are structurally similar, it serves as a convenient group for discussing the characteristics of amniotes. Therefore, we use the traditional classification of "Reptilia" as a basis for our discussion while recognizing that, technically, the birds should be included within it.





34.17 An Egg for Dry Places The evolution of the amniote egg, with its shell, four extraembryonic membranes, and embryo-nourishing yolk, was a major step in the colonization of the terrestrial environment.

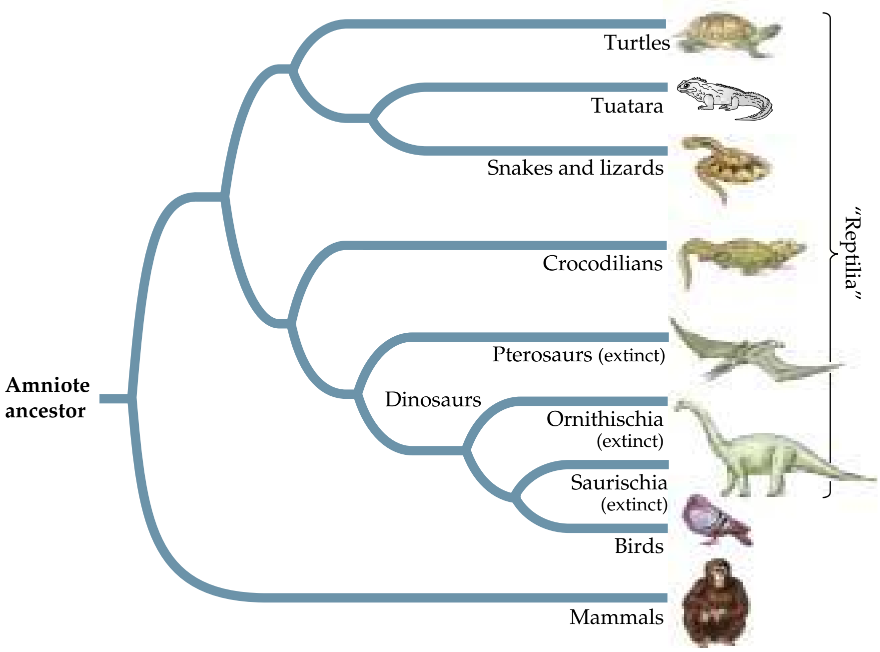
About 6,000 species of reptiles live today. Most reptiles do not care for their eggs after laying them. In some species, the eggs do not develop shells, but are retained inside the female's body until they hatch. Some of these species evolved a structure called the *placenta* that nourishes the developing embryos.

The skin of a reptile is covered with horny scales that greatly reduce loss of water from the body surface. These scales, however, make the skin unavailable as an organ of gas exchange. In reptiles, gases are exchanged almost entirely by the lungs, which are proportionally much larger in surface area than those of amphibians. A reptile forces air into and out of its lungs by bellows-like movements of its ribs. The reptilian heart is divided into three and one-half or four chambers that partially separate oxygenated from unoxygenated blood. With this type of heart, reptiles can generate higher blood pressures than amphibians, which have three-chambered hearts, and can sustain higher levels of muscular activity.

Reptilian lineages diverged

The lineages leading to modern reptiles began to diverge about 250 mya. One lineage that has changed very little over the intervening millenia is the turtles (subclass **Testudines**). Turtles have a combination of ancestral traits and highly specialized characteristics that they do not share with any other vertebrate group. For this reason, their phylogenetic relationships are uncertain.

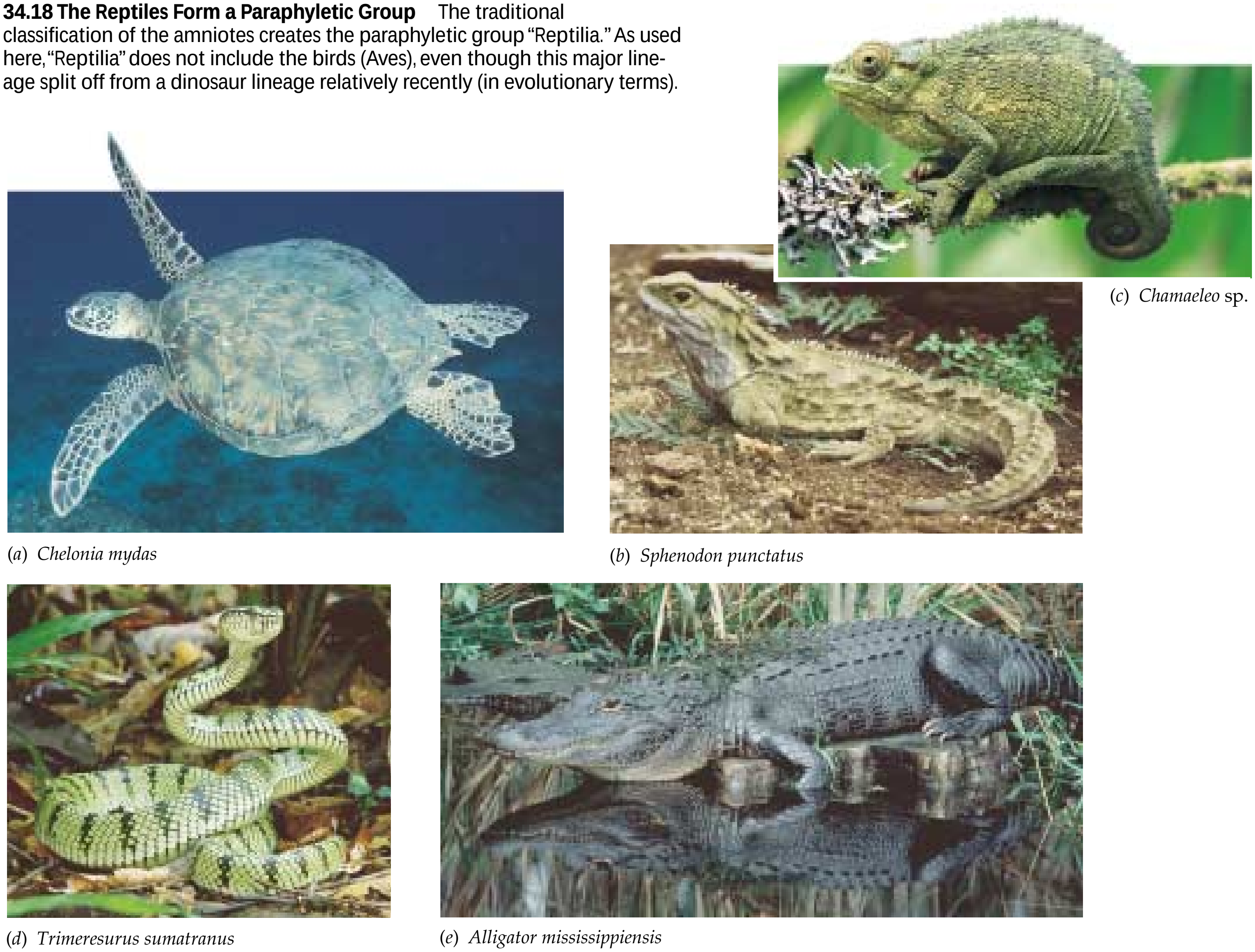
The dorsal and ventral bony plates of modern turtles and tortoises form a shell into which the head and limbs can be



34.18 The Reptiles Form a Paraphyletic Group The traditional classification of the amniotes creates the paraphyletic group "Reptilia." As used here, "Reptilia" does not include the birds (Aves), even though this major lineage split off from a dinosaur lineage relatively recently (in evolutionary terms).

withdrawn (Figure 34.19*a*). Most turtles live in lakes and ponds, but tortoises are terrestrial; some live in deserts. Sea turtles spend their entire lives at sea except when they come ashore to lay eggs. All seven species of sea turtles are endangered. A few species of turtles and tortoises are carnivores, but most species are omnivores that eat a variety of aquatic and terrestrial plants and animals.

The subclass **Squamata** includes lizards and snakes as well as the amphisbaenians (a group of legless, wormlike, burrowing animals with greatly reduced eyes). The tuataras (subclass **Sphenodontida**) are a sister group to the lizards and snakes. Sphenodontids were diverse dur-



34.19 Reptilian Diversity (*a*) The green sea turtle is widely distributed in tropical oceans. (*b*) This tuatara represents one of only two surviving species in a lineage that separated from lizards long ago. (*c*) The African chameleon, a lizard, has large eyes that move independently in their sockets. (*d*) This venomous Sumatran pit viper is coiled to strike. (*e*) Alligators live in warm temperate environments in China and, like this one, in the southeastern United States.

ing the Mesozoic era, but today they are represented only by two species restricted to a few islands off the coast of New Zealand (Figure 34.19*b*). Tuataras superficially resemble lizards, but differ from them in tooth attachment and several internal anatomical features.

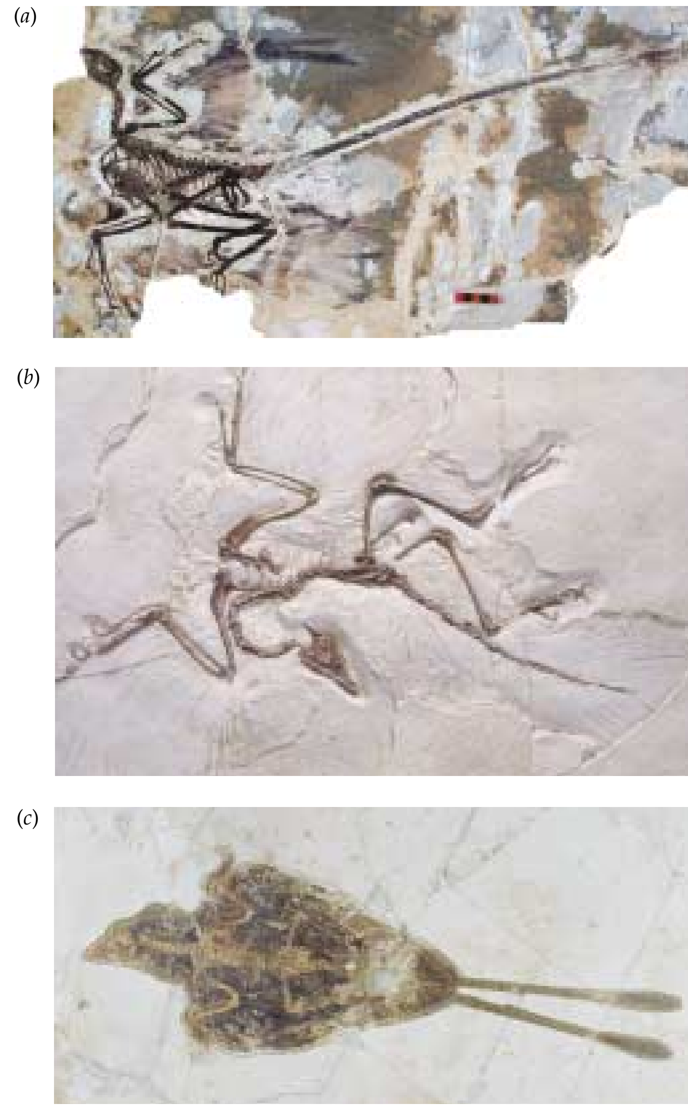
Most lizards are insectivores, but some are herbivores; a few prey on other vertebrates. The largest lizards, growing as long as 3 meters, are certain monitor lizards (such as the Komodo dragon) that live in the East Indies. Most lizards walk on four limbs (Figure 34.19*c*), but some are limbless, as are all snakes, which are descendants of burrowing lizards.

All snakes are carnivores; many can swallow objects much larger than themselves. This is the mode of feeding of the largest snakes, the pythons, which can grow to more than 10 meters long. Several snake lineages evolved a combination of venom glands and the ability to inject venom rapidly into their prey (Figure 34.19*d*).

A separate diverging lineage led to the crocodilians (subclass **Crocodylia**) and to the dinosaurs. The crocodilians—crocodiles, caimans, gharials, and alligators—are confined to tropical and warm temperate environments (Figure 34.19*e*). Crocodilians spend much of their time in water, but they build nests on land or on floating piles of vegetation. The eggs are warmed by heat generated by decaying organic matter that the parents place in the nest. Typically the female guards the eggs until they hatch. All crocodilians are carnivorous; they eat vertebrates of all classes, including large mammals.

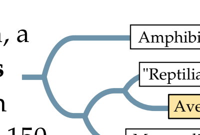
The **dinosaurs** rose to prominence about 215 mya and dominated terrestrial environments for about 150 million years. During that time, virtually all terrestrial animals more than a meter in length were dinosaurs. Some of the largest dinosaurs weighed up to 100 tons. Many were agile and could run rapidly. The ability to breathe and run simultaneously, which we take for granted, was a major innovation in the evolution of terrestrial vertebrates. Not until the evolution of the lineages leading to the mammals, dinosaurs, and birds did the legs assume vertical positions directly under the body, which reduced the lateral forces on the body during locomotion. Special muscles that enabled the lungs to be filled and emptied while the limbs moved also evolved. We can infer the existence of such muscles in dinosaurs from the structure of the vertebral column in fossils and the capacity of many dinosaurs for bounding, bipedal (two-legged) locomotion.

Several fossil dinosaurs discovered recently in early Cretaceous deposits in Liaoning Province, in northeastern China, clearly show that in some small predatory dinosaurs, the scales had been highly modified to form feathers. One of these dinosaurs, *Microraptor gui*, had feathers on all four limbs, and those feathers were structurally similar to those of modern birds (Figure 34.20*a*).



34.20 Mesozoic Birds and Their Ancestors Fossil remains demonstrate the probable evolution of birds from reptilian ancestors. (*a*) *Microraptor gui*, a feathered dinosaur from the early Cretaceous (about 140 mya). (*b*) *Archaeopteryx*, the oldest known bird. (*c*) The elongated tail feathers of a male *Confuciusornis sanctus* ("sacred bird of Confucius") fossil suggest that the males used them in courtship displays.

Birds: More Feathers and Better Flight



During the Mesozoic era, about 175 mya, a dinosaur lineage gave rise to the **birds** (subclass **Aves**). The oldest known avian fossil, *Archaeopteryx*, which lived about 150 mya, had teeth, unlike modern birds, but was covered with feathers that are virtually identical to those of modern birds. It also had well-developed wings, a long tail (Figure 34.20*b*), and a furcula, or "wishbone," to which some of the flight muscles were probably attached. *Archaeopteryx* had clawed fingers on its forelimbs, but it also had typical perching bird claws, suggesting that it lived in trees and shrubs and used the fingers to assist it in clambering over branches. Because the avian lineage separated from other reptiles long before *Archaeopteryx* lived, existing data are insufficient to identify the ancestors of birds with certainty. Most paleontologists believe that birds evolved from feathered terrestrial bipedal dinosaurs that used their forelimbs for capturing prey.

Many remains of other early birds have been discovered in 120–125-million-year-old fossil beds in northeastern China. One of these birds, *Confuciusornis sanctus*, is known from hundreds of complete specimens. The males had greatly elongated tail feathers (Figure 34.20*c*), which they probably used in communal courtship displays. Large numbers of individuals have been found together, as would be expected if many males assembled on communal display grounds, as some birds do today.

Birds range in size from the 2-gram bee hummingbird of the West Indies to the 150-kilogram ostrich (Figure 34.21). Some flightless birds of Madagascar and New Zealand known from fossils were even larger. These birds were exterminated by humans soon after they colonized those islands. There are about 9,600 species of living birds, more than in any other major vertebrate group except ray-finned fishes.

As a group, birds eat almost all types of animal and plant material. A few aquatic species have bills modified for filtering small food particles from water. Insects are the most important dietary items for terrestrial species. Birds are major predators of flying insects during the day, and some species exploit that food source at night. In addition, birds eat fruits and seeds, nectar and pollen, leaves and buds, carrion, and other vertebrates. By eating the fruits and seeds of plants, birds serve as major agents of seed dispersal.

The feathers developed by some dinosaurs may originally have had thermoregulatory or display functions. Birds also use them for flying. Large quills that arise from the skin of the fore-

34.21 Diversity among the Birds (*a*) Penguins such as these gentoos are widespread in the cold waters of the Southern Hemisphere. They are expert swimmers, although they have lost the ability to fly. (*b*) Perching birds, represented here by a male northern cardinal, are the most species-rich of all the bird lineages. (*c*) Parrots are a diverse group of birds, especially in the Tropics of Asia, South America, and Australia. This king parrot is one member of Australia's rich parrot fauna. (*d*) The flightless ostrich is the largest bird species in existence today.

(*a*) *Pygoscelis papua*

(*b*) *Cardinalis cardinalis*

(*c*) *Alisterus scapularis*

(*d*) *Struthio camelus*

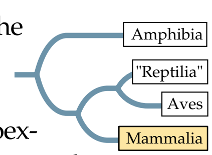
limbs create the flying surfaces of wings. Other strong feathers sprout like a fan from the shortened tail and serve as stabilizers during flight. The feathers that cover the body, along with an underlying layer of down feathers, provide insulation.

The bones of birds are modified for flight. They are hollow and have internal struts for strength. The *sternum* (breastbone) forms a large, vertical keel to which the flight muscles are attached. These muscles pull the wings downward during the main propulsive movement in flight. Flight is metabolically expensive. A flying bird consumes energy at a rate about 15–20 times faster than a running lizard of the same weight! Because birds have such high metabolic rates, they generate large amounts of heat. They control the rate of heat loss using their feathers, which may be held close to the body or elevated to alter the amount of insulation they provide.

The brain of a bird is larger in proportion to its body than a lizard or crocodile brain, primarily because the cerebellum, the center of sight and muscular coordination, is enlarged.

Most birds lay their eggs in a nest, where they are warmed by heat from an adult that sits on them. Because birds have such high body temperatures, the eggs of most species hatch within a few weeks. The offspring of many species are *altricial* (hatch at a relatively helpless stage) and are fed for some time by their parents. The young of other bird species, such as chickens, sandpipers, and ducks, are *precocial* (can feed themselves shortly after hatching). Adults of nearly all species attend their offspring for some time, warning them of and protecting them from predators, protecting them from bad weather, leading them to good foraging places, and feeding them.

The Origin and Diversity of Mammals



Mammals (class **Mammalia**) appeared in the early part of the Mesozoic era, about 225 million years ago, branching from a lineage of mammal-like reptiles. Small mammals coexisted with reptiles and dinosaurs for at least 150 million years. After the large reptiles and dinosaurs disappeared during the mass extinction at the close of the Mesozoic era, mammals increased dramatically in numbers, diversity, and size. Today, mammals range in size from tiny shrews and bats weighing only about 2 grams to the endangered blue whale, which measures up to 33 meters long and weighs up to 160,000 kilograms—the largest animal ever to live on Earth.

Skeletal simplification accompanied the evolution of early mammals from their larger reptilian ancestors. During mammalian evolution, some bones from the lower jaw were incorporated into the middle ear, leaving a single bone in the lower jaw. The number of bones in the skull also decreased. The bulk of both the limbs and the bony girdles from which they are suspended was reduced. Mammals have far fewer, but more highly differentiated, teeth than reptiles do. Differences in the number, type, and arrangement of teeth in mammals reflect their varied diets.

Skeletal features are readily preserved as fossils, but the soft parts of animals are seldom fossilized. Therefore, we do not know when mammalian features such as mammary glands, sweat glands, hair, and a four-chambered heart evolved. Mammals are unique among animals in supplying their young with a nutritive fluid (milk) secreted by mammary glands. Mammalian eggs are fertilized within the female's body, and the embryos undergo a period of development, called *gestation*, within a specialized organ, the *uterus*, prior to being born. In many species, the embryos are connected to the uterus and nourished by a placenta. In addition, mammals have a protective and insulating covering of hair, which is luxuriant in some species but has been almost entirely lost in whales, dolphins, and humans. In whales and dolphins, thick layers of insulating fat (blubber) replace hair as a heat-retention mechanism. Clothing assumes the same role for humans. The approximately 4,000 species of living mammals are divided into two major subclasses: Prototheria and Theria. The subclass **Prototheria** contains a single order, the Monotremata, with a total of three species, which are found only in Australia and New Guinea. These mammals, the duck-billed platypus and the spiny anteaters, or echidnas, differ from other mammals in lacking a placenta, laying eggs, and having legs that poke out to the side (Figure 34.22). Monotremes supply milk for their young, but they have no nipples on their mammary glands; rather, the milk simply oozes out and is lapped off the fur by the offspring.

Members of the other subclass, **Theria**, are further divided into two groups. In most species of the first group, the **Marsupialia**, females have a ventral pouch in which they carry and feed their offspring (Figure 34.23*a*). Gestation in marsupials is short; the young are born tiny but with well-developed forelimbs, with which they climb to the pouch. They attach to a nipple, but cannot suck. The mother ejects milk into the tiny offspring until they grow large enough to suckle. Once her offspring have left the uterus, a female marsupial may become sexually receptive again. She can then carry fertilized eggs capable of initiating development and replacing the offspring in her pouch should something happen to them.

There are about 240 living species of marsupials. At one time marsupials were found on all continents, but today the majority of species are restricted to the Australian region, with a modest representation in South America (Figure 34.23*b*). One species, the Virginia opossum, is widely distributed in the United States. Marsupials radiated to become terrestrial herbivores, insectivores, and carnivores, but no marsupial species live in the oceans or can fly, although some are gliders. The largest living marsupial is the red kangaroo of Australia (Figure 34.23*a*), which weighs up to 90 kilo-

(*a*) *Tachyglossus aculeata*

(*b*) *Ornithorhynchus anatinus*

34.22 Monotremes (*a*) The short-beaked echidna is one of the two surviving species of echidnas. (*b*) The duck-billed platypus is the other surviving monotreme species.

grams. Much larger marsupials existed in Australia until they were exterminated by humans soon after they reached the continent (about 50,000 years ago).

Most living mammals belong to the second therian group, the **eutherians**. (Eutherians are sometimes called *placental mammals*, but this name is not accurate because some marsupials also have placentas.) Eutherians are more developed at birth than are marsupials, and no external pouch houses them after birth. The nearly 4,000 species of eutherians are placed into 16 major groups (Figure 34.24), the largest of which is the rodents (order Rodentia) with about 1,700 species. The next largest group, the bats (order Chiroptera), has about 1,000 species, followed by the moles and shrews (order Insectivora) with slightly more than 400 species.

Eutherians are extremely varied in their form and ecology. Several lineages of terrestrial eutherians subsequently colonized marine environments to become whales, dolphins, seals, and sea lions. Eutherian mammals are—or were, until they were greatly reduced in numbers by humans—the most important grazers and browsers in most terrestrial ecosystems. Grazing and browsing have been an evolutionary force intense enough to select for the spines, tough leaves, and difficult-to-eat growth forms found in many plants—a striking example of coevolution.

Primates and the Origin of Humans

A eutherian lineage that has had dramatic effects on ecosystems worldwide is the **primate** lineage, which has undergone extensive recent evolutionary radiation. Primates probably

(*a*) *Macropus rufus*

(*b*) *Caluromys philander*

(*c*) *Sarcophilus harrisii*

34.23 Marsupials (*a*) Australia's red kangaroos are the largest living marsupials. The marsupial radiation also produced (*b*) arboreal species, such as this South American opossum, and (*c*) carnivores, such as the Tasmanian devil.

(*a*) *Citellus parryi*

(*b*) *Carollia perspicillata*

(*c*)

(*d*) *Rangifer tarandus*

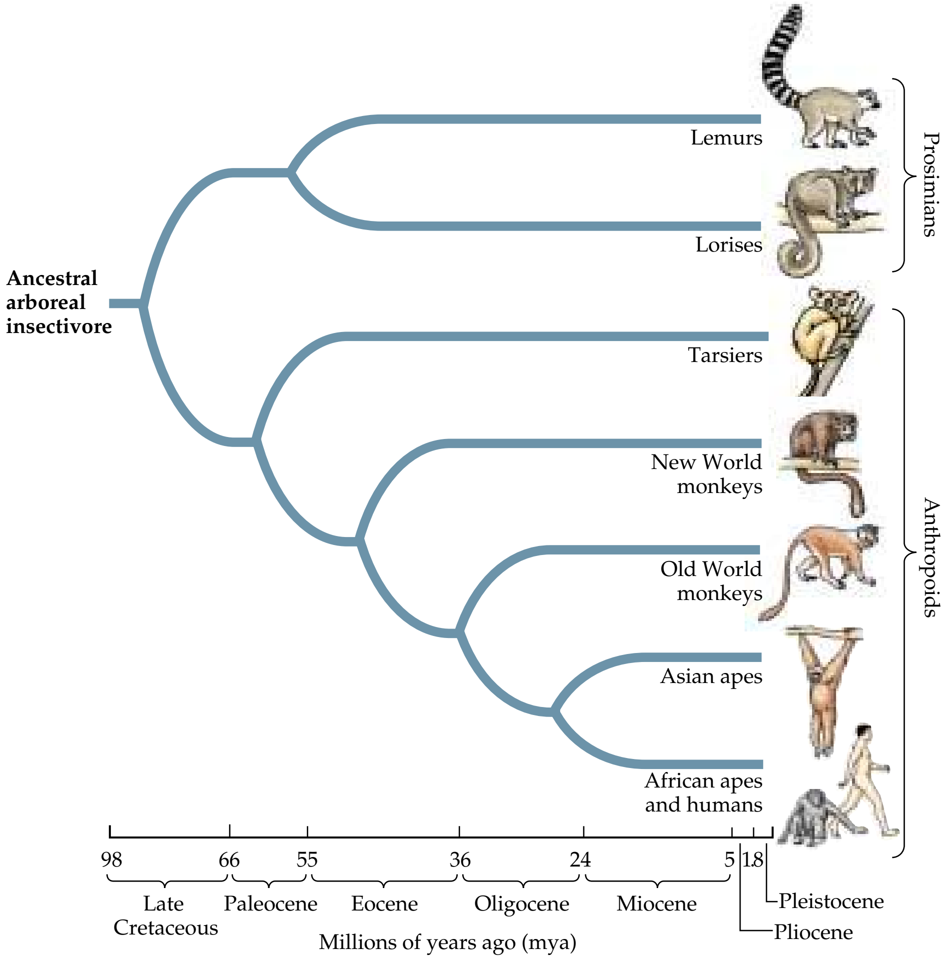
34.24 Diversity among the Eutherians (*a*) The Arctic ground squirrel is one of the many species of small, diurnal rodents found in North America. (*b*) Temperate-zone bats are all insectivores, but many tropical bats, such as this leaf-nosed bat, eat fruit. (*c*) These Hawaiian spinner dolphins represent a eutherian lineage that colonized the marine environment. (*d*) Large hoofed mammals are important herbivores in terrestrial environments. This caribou bull is grazing by himself, although caribou are often seen in huge herds.

descended from small *arboreal* (tree-living) insectivorous mammals early in the Cretaceous period. A nearly complete fossil of an early primate species, *Carpolestes*, from Wyoming, dated at 56 mya, had grasping feet with an opposable big toe that had a nail rather than a claw. Such grasping limbs are one of the major adaptations to arboreal life that distinguish primates from other mammals. However, *Carpolestes* did not have eyes positioned on the front of the face to provide good depth perception, as all modern primates do.

Early in its evolutionary history, the primate lineage split into two main branches, the prosimians and the anthropoids (Figure 34.25). **Prosimians**—lemurs, pottos, and lorises—once lived on all continents, but today they are restricted to Africa, Madagascar, and tropical Asia (Figure 34.26). All of the mainland prosimian species are arboreal and nocturnal. However, on the island of Madagascar, the site of a remarkable prosimian radiation, there are also diurnal and terrestrial species.

The **anthropoids**—tarsiers, monkeys, apes, and humans—evolved from an early primate lineage about 55 million years ago in Africa or Asia. New World monkeys diverged from Old World monkeys early enough that they could have reached South America from Africa when those two continents were still close to each other. All New World monkeys are arboreal (Figure 34.27*a*). Many of them have long, *prehensile* (grasping) tails with which they can hold onto branches. Many Old World primates are arboreal as well, but a number of species are terrestrial. Some of these species, such as baboons and macaques, live and travel in large groups (Figure 34.27*b*). No Old World primates have prehensile tails.

About 22 million years ago, the lineage that led to modern **apes** separated from the other Old World primates. Between 22 and 5.5 mya, as many as 100 species of apes ranged over Europe, Asia, and Africa. About 9 mya, members of one European ape lineage, *Dryopithecus*, migrated to Africa and became the ancestors of the modern African apes—gorillas and chimpanzees (Figure 34.28*a*,*b*)—and of humans. The Asian apes—gibbons and orangutans (Figure 34.28*c*,*d*)—are a different ape lineage, descendants of *Sirapithecus*.



34.25 A Current Phylogeny of the Primates Too few fossil primates have been discovered to reveal with certainty their evolutionary relationships, but this phylogenetic tree is consistent with the existing evidence.

(*a*) *Eulemur fulvus*

(*b*) *Loris tardigradus*

34.26 Prosimians (*a*) The brown lemur is one of the many lemur species found in Madagascar, where they are part of a unique assemblage of plants and animals. (*b*) The slender loris is found in India. Its large eyes tell us that it is nocturnal.

(*a*) *Leontopithecus rosalia*

(*b*) *Macaca sylvanus*

34.27 Monkeys (*a*) Golden lion tamarins are endangered New World monkeys living in coastal Brazilian rainforests. (*b*) Many Old World species, such as these Barbary macaques, live in social groups. Here two members of a group groom each other.

(*a*) *Gorilla gorilla*

(*b*) *Pan troglodytes*

(*c*) *Hylobates lar*

(*d*) *Pongo pygmaeus*

34.28 Apes (*a*) Gorillas, the largest apes, are restricted to humid African forests. This male is a lowland gorilla. (*b*) Chimpanzees, our closest relatives, are found in forested regions of Africa. (*c*) Gibbons are the smallest of the apes. The common gibbon is found in Asia, from India to Borneo. (*d*) Orangutans live in the forests of Indonesia.

Human ancestors evolved bipedal locomotion

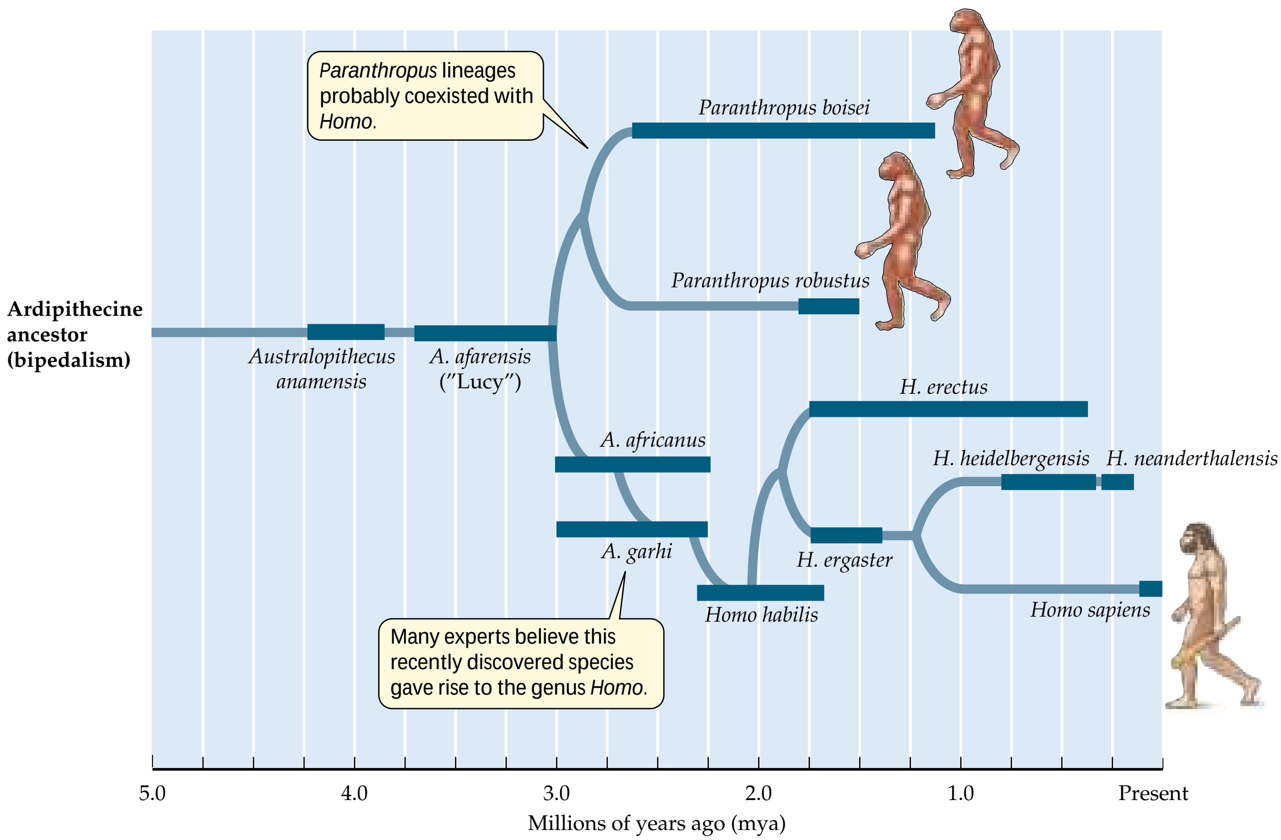
The **hominids**—the lineage that led to humans—separated from other ape lineages about 6 mya in Africa. The earliest protohominids, known as **ardipithecines**, had distinct morphological adaptations for **bipedalism**—locomotion in which the body is held erect and moved exclusively by movements of the hind legs. Bipedal locomotion frees the forelimbs to manipulate objects and to carry them while walking. It also elevates the eyes, enabling the animal to see over tall vegetation to spot predators and prey. At walking rates, bipedal movement is also energetically much more economical than quadrupedal (four-legged) locomotion. All three advantages were probably important for the ardipithecines and their descendants, the **australopithecines**.

The first australopithecine skull was found in South Africa in 1924. Since then, australopithecine fossils have been found in many sites in Africa. The most complete fossil skeleton of an australopithecine, approximately 3.5 million years old, was discovered in Ethiopia in 1974. That individual, a young female known to the world as Lucy, was assigned to the species *Australopithecus afarensis*. Fossil remains of more than 100 *A. afarensis* have now been discovered. During the past 5 years, fossils of other australopithecines that lived in Africa 4–5 million years ago have been unearthed.

Experts disagree over how many species are represented by the australopithecine fossils, but it is clear that several million years ago, at least two distinct types lived together over much of eastern Africa. The larger type (about 40 kilograms) is represented by at least two species (*Paranthropus robustus* and *P. boisei*), both of which died out suddenly about 1.5 million years ago.

Humans arose from australopithecine ancestors

Early members of the genus *Homo* lived contemporaneously with australopithecines for perhaps half a million years (Figure 34.29). The oldest fossils of the genus, an extinct species called *H. habilis*, were discovered in the Olduvai Gorge, Tanzania. These fossils are estimated to be 2 million years old. Other fossils of *H. habilis* have been found in Kenya and Ethiopia. Associated with the fossils are tools that these early hominids used to obtain food.



34.29 A Current Phylogeny of *Homo sapiens* At times in the past, more than one species of hominid lived on Earth. The heavy dark blue lines indicate the time frame over which each species lived.

Another extinct species of our genus, *Homo erectus*, evolved in Africa about 1.6 mya. Soon thereafter it had spread as far as eastern Asia. As it expanded its range and increased in abundance, *H. erectus* may have exterminated *H. habilis*. Members of *H. erectus* were as large as modern people, but their bones were considerably heavier. *Homo erectus* used fire for cooking and for hunting large animals, and made characteristic stone tools that have been found in many parts of the Old World. Although *H. erectus* survived in Eurasia until about 250,000 years ago, it was replaced in tropical regions by our species, *Homo sapiens*, about 200,000 years ago.

Human brains became larger

The earliest members of *Homo sapiens* had larger brains than members of the earlier species of *Homo*. Brain size in the lineage increased rapidly, reaching modern size by about 160,000 years ago. This striking change was probably favored by an increasingly complex social life. The ability of group members to communicate with one another would have been valuable in cooperative hunting and gathering and for improving one's status in the complex social interactions that must have characterized early human societies, just as they do ours today. But why did brains become larger only in the human lineage?

A clue to the answer is provided by brain chemistry. The human brain is a fat-rich organ. About 60 percent of its structural material is made up of lipids, most of them long-chain polyunsaturated omega-3 and omega-6 fatty acids. Humans must consume omega fatty acids in their diet because the body cannot synthesize these molecules fast enough from the other fatty acids found in vegetables, nuts, and seeds to supply their brains. Animal brains and livers contain omega fatty acids, but fish and shellfish are by far the best sources.

Therefore, because savannas and open woodlands provide few sources of omega fatty acids, the traditional view that early human evolution took place in those environments is being questioned. In contrast, the shores of Africa's many lakes would have been rich sources of fish and mollusks. Thus, access to fat-rich foods from aquatic environments may have been the key factor that supported the dramatic expansion of the human brain. The archeological record of the past 100,000 years includes hundreds of piles of mollusk shells and fish bones, as well as carved points used for fishing. Chimpanzees remained in the forest and ate fruits and nuts. They may have lacked food sources to support much larger brains.

Several *Homo* species existed during the mid-Pleistocene epoch, from about 1.5 million to about 300,000 years ago. All were skilled hunters of large mammals, but plants continued to be important components of their diets. During this period another distinctly human trait emerged: rituals and a concept of life after death. Deceased individuals were buried with tools and clothing, presumably supplies for their existence in the next world.

One species, *Homo neanderthalensis*, was widespread in Europe and Asia between about 75,000 and 30,000 years ago. Neanderthals were short, stocky, and powerfully built humans whose massive skulls housed brains somewhat larger than our own. They manufactured a variety of tools and hunted large mammals, which they probably ambushed and subdued in close combat. For a short time, their range overlapped that of the *H. sapiens* known as Cro-Magnons, but then the Neanderthals abruptly disappeared. Many scientists believe that they were exterminated by the Cro-Magnons, just as *H. habilis* may have been exterminated by *H. erectus*.

Cro-Magnon people made and used a variety of sophisticated tools. They created the remarkable paintings of large mammals, many of them showing scenes of hunting, that have been discovered in European caves (Figure 34.30). The animals depicted were characteristic of the cold steppes and grasslands that occupied much of Europe during periods of glacial expansion. Cro-Magnon people spread across Asia, reaching North America perhaps as early as 20,000 years ago, although the date of their arrival in the New World is still uncertain. Within a few thousand years, they had spread southward through North America to the southern tip of South America.

34.30 Hunting Inspires Art Cro-Magnon cave drawings such as those found in Lascaux Cave, France, typically depict the large mammals that these people hunted.

Humans evolved language and culture

As our ancestors evolved larger brains, their behavioral capabilities increased, especially the capacity for language. Most animal communication consists of a limited number of signals, which refer mostly to immediate circumstances and are associated with changed emotional states induced by those circumstances. Human language is far richer in its symbolic character than any other animal vocalizations. Our words can refer to past and future times and to distant places. We are capable of learning thousands of words, many of them referring to abstract concepts. We can rearrange words to form sentences with complex meanings.

The expanded mental abilities of humans are largely responsible for the development of **culture**, the process by which knowledge and traditions are passed along from one generation to another by teaching and observation. Culture can change rapidly because genetic changes are not necessary for a cultural trait to spread through a population. A potential disadvantage of culture is that its norms must be taught to each generation.

Cultural learning greatly facilitated the spread of domestic plants and animals and the resultant conversion of most human societies from ones in which food was obtained by hunting and gathering to ones in which *pastoralism* (herding large animals) and *agriculture* dominated.

The development of agriculture led to an increasingly sedentary life, the growth of cities, greatly expanded food supplies, rapid increases in the human population, and the appearance of occupational specializations, such as artisans, shamans, and teachers.

Deuterostomes and Protostomes: Shared Evolutionary Themes

The evolution of deuterostomes paralleled the evolution of protostomes in several important ways. Both lineages exploited the abundant food supplies buried in soft marine substrata, attached to rocks, or suspended in water. Many groups of both lineages developed elaborate structures for moving water and extracting prey from it.

In some lineages of both groups, the body cavity became divided into compartments that allowed better control of shape and movement. Some members of both groups evolved mechanisms for controlling their buoyancy in water using gas-filled internal spaces. Planktonic larval stages evolved in marine members of many protostomate and deuterostomate phyla.

Both protostomes and deuterostomes colonized the land, but the consequences were very different. The jointed external skeletons of arthropods, although they provide excellent support and protection in air, cannot support large animals, as the internal skeletons developed by deuterostomes can.

Terrestrial deuterostomes recolonized aquatic environments a number of times. Suspension feeding evolved once again in several of these lineages. The largest living animals, baleen (toothless) whales, feed upon small prey only a few centimeters long, which they extract from the water with large straining structures in their mouths.

Chapter Summary

Origins of the Deuterostomes

▶ The deuterostomate lineage separated from the protostomate lineage early in animal evolution. The ancestral deuterostome had external gills. **Review Figure 34.1**

▶ There are only two major deuterostomate lineages, and there are fewer species of deuterostomes than protostomes, but as members of the lineage, we have a special interest in its members. **Review Figure 34.2. See Web/CD Activity 34.1**

Echinoderms: Pentaradial Symmetry

▶ Echinoderms have a pentaradially symmetrical body plan, a unique water vascular system, and a calcified internal skeleton. **Review Figure 34.3*a***

▶ Nearly all living species of echinoderms have a bilaterally symmetrical, ciliated larva that feeds as a planktonic organism. **Review Figure 34.3*b***

▶ Six major groups of echinoderms survive today, but 23 other lineages existed in the past. Some groups of echinoderms have arms, but others do not.

Hemichordates: Conservative Evolution

▶ Acorn worms and pterobranchs are similar to ancestral deuterostomes. **Review Figure 34.5**

Chordates: New Ways of Feeding

▶ Members of another deuterostomate lineage evolved enlarged pharyngeal slits used as feeding devices and a dorsal supporting rod, the notochord.

▶ Most urochordates are sessile as adults and filter prey from seawater with large pharyngeal baskets. But some species retain their notochords and nerve cords as planktonic adults.

Evolution of the Chordates

▶ Cephalochordates probably resemble the ancestors of all other chordates. **Review Figure 34.7**

▶ Vertebrates evolved jointed internal skeletons that enabled them to swim rapidly. Early vertebrates used the pharyngeal basket to filter small animals from mud. **Review Figures 34.8, 34.9**

▶ Jaws, which evolved from anterior gill arches, enabled their possessors to grasp and chew their prey. Jawed fishes rapidly became dominant animals in both marine and fresh waters. **Review Figure 34.11**

▶ Fishes evolved two pairs of unjointed fins, with which they control their swimming movements and stabilize themselves in the water, and swim bladders, which help keep them suspended in open water.

▶ Ray-finned fishes come in a wide variety of sizes and shapes. Many species have complex social systems.

Colonizing the Land: Obtaining Oxygen from the Air

▶ Two lineages of fishes—lobe-finned fishes and lungfishes—evolved jointed fins.

▶ Amphibians, the first terrestrial vertebrates, arose from lungfish ancestors.

▶ The 4,500 species of amphibians living today belong to three groups: caecilians, frogs and toads, and salamanders.

▶ Most amphibians live in water at some time in their lives, and their eggs must remain moist. **Review Figure 34.16. See Web/CD Tutorial 34.1**

▶ Amniotes evolved eggs with shells impermeable to water and thus became the first vertebrates to be independent of water for reproduction. **Review Figure 34.17. See Web/CD Activity 34.2**

▶ Modern reptiles are members of four lineages: snakes and lizards, tuataras, turtles and tortoises, and crocodilians. **Review Figure 34.18**

▶ Dinosaurs rose to dominance about 215 mya and dominated terrestrial environments for about 150 million years until they became extinct about 65 mya.

▶ Some dinosaurs evolved feathers and were capable of flight.

Birds: More Feathers and Better Flight

▶ Birds arose about 175 mya from feathered dinosaur ancestors.

▶ The 9,600 species of birds are characterized by feathers, high metabolic rates, and parental care.

The Origin and Diversity of Mammals

▶ Mammals evolved during the Mesozoic era, about 225 mya.

▶ The eggs of mammals are fertilized within the body of the female, and embryos develop for some time within a uterus before being born. Mammals are unique in suckling their young with milk secreted by mammary glands.

▶ The three species of mammals in subclass Prototheria lay eggs, but all other mammals give birth to live young.

▶ Therian mammals are divided into two major groups: the marsupials, which give birth to tiny young that are, in most species, raised in a pouch on the female's belly, and the eutherians, which give birth to relatively well-developed offspring.

Primates and the Origin of Humans

▶ The primates split into two major lineages, one leading to the prosimians (lemurs and lorises) and the other leading to the tarsiers, monkeys, apes, and humans. **Review Figure 34.25**

▶ Hominids evolved in Africa from terrestrial, bipedal ancestors. **Review Figure 34.29**

▶ Early humans evolved large brains, language, and culture. They manufactured and used tools, developed rituals, and domesticated plants and animals. In combination, these traits enabled humans to increase greatly in number and to transform the face of Earth.

Deuterostomes and Protostomes: Shared Evolutionary Themes

▶ Both protostomes and deuterostomes evolved structures to filter prey from the water, mechanisms to control their buoyancy in water, and planktonic larval stages.

See Web/CD Activity 34.3 for a concept review of this chapter.

Self-Quiz

1. Which of the following deuterostomate groups have a three-part body plan?
   a. Acorn worms and tunicates
   b. Acorn worms and pterobranchs
   c. Pterobranchs and tunicates
   d. Pterobranchs and lancelets
   e. Tunicates and lancelets
2. The structure used by adult ascidians to capture food is a
   a. pharyngeal basket.
   b. proboscis.
   c. lophophore.
   d. mucus net.
   e. radula.
3. The pharyngeal gill slits of chordates originally functioned as sites for
   a. uptake of oxygen only.

b. release of carbon dioxide only.
c. both uptake of oxygen and release of carbon dioxide.
d. removal of small prey from the water.
e. forcible expulsion of water to move the animal.

4. The key to the vertebrate body plan is a
a. pharyngeal basket.
b. vertebral column to which internal organs are attached.
c. vertebral column to which two pairs of appendages are attached.
d. vertebral column to which a pharyngeal basket is attached.
e. pharyngeal basket and two pairs of appendages.

5. Which of the following fishes do *not* have a cartilaginous skeleton?
a. Chimaeras
b. Lungfishes
c. Sharks
d. Skates
e. Rays

6. In most fishes, lunglike sacs evolved into
a. pharyngeal gill slits.
b. true lungs.
c. coelomic cavities.
d. swim bladders.
e. none of the above

7. Most amphibians return to water to lay their eggs because
a. water is isotonic to egg fluids.
b. adults must be in water while they guard their eggs.
c. there are fewer predators in water than on land.
d. amphibians need water to produce their eggs.
e. amphibian eggs quickly lose water and desiccate if their surroundings are dry.

8. The horny scales that cover the skin of reptiles prevent them from
a. using their skin as an organ of gas exchange.
b. sustaining high levels of metabolic activity.
c. laying their eggs in water.
d. flying.
e. crawling into small spaces.

9. Which statement about bird feathers is *not* true?
a. They are highly modified reptilian scales.
b. They provide insulation for the body.
c. They exist in two layers.
d. They help birds fly.
e. They are important sites of gas exchange.

10. Monotremes differ from other mammals in that they
a. do not produce milk.
b. lack body hair.
c. lay eggs.
d. live in Australia.
e. have a pouch in which the young are raised.

11. Bipedalism is believed to have evolved in the human lineage because bipedal locomotion is
a. more efficient than quadrupedal locomotion.
b. more efficient than quadrupedal locomotion, and it frees the forelimbs to manipulate objects.
c. less efficient than quadrupedal locomotion, but it frees the forelimbs to manipulate objects.
d. less efficient than quadrupedal locomotion, but bipedal animals can run faster.
e. less efficient than quadrupedal locomotion, but natural selection does not act to improve efficiency.

For Discussion

1. In what animal phyla has the ability to fly evolved? How do the structures used for flying differ among these animals?
2. Extracting suspended food from the water column is a common mode of foraging among animals. Which groups contain species that extract prey from the air? Why is this mode of obtaining food so much less common than extracting prey from the water?
3. Large size both confers benefits and poses certain risks. What are these risks and benefits?
4. Amphibians have survived and prospered for many millions of years, but today many species are disappearing and populations of others are declining seriously. What features of amphibian life histories might make them especially vulnerable to the kinds of environmental changes now happening on Earth?
5. The body plan of most vertebrates is based on four appendages. Describe the varied forms that these appendages take and how they are used. How do the vertebrates that have kept their four appendages move?
6. Compare the ways that different animal lineages colonized the land. How were those ways influenced by the body plans of animals in the different lineages?