Deuterostome Animals

The deuterostomes include the largest-bodied and most morphologically complex of all animals. They range from the sea stars that cling to dock pilings, to the fish that dart in and out of coral reefs, to the wildebeests that migrate across the Serengeti Plains of East Africa.

Most biologists recognize just three phyla of deuterostomes: the Echinodermata, the Hemichordata, and the Chordata. The echinoderms include the sea stars and sea urchins. The hemichordates, or “acorn worms,” are probably unfamiliar—they burrow in marine sands or muds and make their living by deposit feeding or suspension feeding. The chordates include the vertebrates. The vertebrates, in turn, include the sharks, bony fishes, amphibians, reptiles (including birds), and mammals. Vertebrates are animals that have a skull. The vast majority of vertebrates also have a backbone or spinal column. Animals that are not vertebrates are collectively known as invertebrates.

The deuterostomes were initially recognized because they all undergo early embryonic development in a similar way. When a humpback whale, sea urchin, or human is just beginning to grow, the gut starts developing from posterior to anterior—with the anus forming first and the mouth second. Although the events that take place early in embryonic development are diagnostic features that unite the deuterostomes, their adult body plans and their feeding methods, modes of locomotion, and means for reproduction are highly diverse. Let’s explore who the deuterostome animals are and how they diversified, starting with the question of why so many biologists are drawn to studying them.
33.1 Why Do Biologists Study Deuterostome Animals?

If you were to look at data on the number of biologists who study various lineages on the tree of life, you would probably conclude that a disproportionately large number of people study deuterostomes—particularly vertebrates. The charge of disproportionality is valid because, in terms of numbers of species and numbers of individuals, insects and other protostomes are much more successful than deuterostomes. And regarding their ecological impact—meaning their influence on other species and the physical environment—the bacteria, archaea, protists, fungi, and land plants could be considered far more important than the deuterostomes. And yet, thousands of biologists are drawn to the study of vertebrates and other deuterostomes. Why?

The simplest answer to this question is that, because humans are deuterostomes, other species in our lineage interest us. People identify with vertebrates because they are large and mobile. We interact with them extensively as pets or domesticated livestock. We understand their world more intuitively than we do the world of a bacterium or fungus.

In addition to the natural affinity we have for deuterostomes, they are worthy of study because they play important roles in ecological interactions and human economics:

- In marine environments, deuterostomes are key consumers. Echinoderms and ray-finned fishes are important herbivores, and ray-finned fishes, sharks, and mammals important predators. (Ray-finned fishes are distinct from the lobe-finned fishes and coelacanths introduced later in the chapter.) On land, almost all of the large-bodied herbivores and predators are reptiles and mammals. As Figure 33.1 shows, the upper trophic levels of food chains in most ecosystems are dominated by deuterostomes. As a result, understanding deuterostomes is critical to understanding how energy and nutrients flow through both marine and terrestrial ecosystems.

- Humans depend on vertebrates for food and, in preindustrial economies, for power. Ray-finned fishes and domesticated livestock are key sources of protein in many cultures. For many thousands of years, agriculture was based on the power generated by oxen, horses, water buffalo, or mules. Today, preindustrial societies continue to rely on horsepower or oxpower for transportation and agricultural work. In the industrialized world, millions of people birdwatch, plan vacations around seeing large mammals in national parks, or keep vertebrates as pets. All over the world, large numbers of people make their living by caring for vertebrates and studying them.

![Figure 33.1 Deuterostomes Are Important Herbivores and Predators](image-url)

(a) In marine habitats, echinoderms and ray-finned fishes, both of which are deuterostomes, are the most important large herbivores and predators. (b) On land, deuterostomes such as amphibians, reptiles, and mammals play the same role.
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33.2 How Do Biologists Study Deuterostomes?

To understand the events that produced the diversity of deuterostomes we see today, biologists study the comparative morphology of species from each of the three deuterostome phyla, analyze the fossil record of the group, and compare DNA sequences and other traits to infer their phylogeny. There are three central issues: (1) understanding the diversity of body plans observed in echinoderms, hemichordates, and the chordates; (2) exploring how vertebrates evolved from invertebrates; and (3) grasping how the vertebrates made the transition from living in aquatic environments to living on land.

Analyzing Morphological Traits

All deuterostomes are triploblastic and have a coelom (see Chapter 31). Patterns of early embryonic development are also similar among all members of the lineage. But in terms of the basic components of body plans, one of the most remarkable events in animal evolution occurred during the evolution of echinoderms: There was a reversion to a type of radial symmetry. Adult echinoderms have bodies with five-sided radial symmetry, even though both their larvae and their ancestors are bilaterally symmetric (Figure 33.2).

Recall from Chapter 31 that radially symmetric animals do not have well-developed head and posterior regions. As a result, they tend to interact with the environment in all directions at once instead of facing the environment in one direction. If adult echinoderms are capable of movement, they tend to move equally well in all directions instead of only headfirst.

The evolution of radial symmetry in echinoderms was a remarkable event in animal evolution. If echinoderms do not have a head and tail, how is their body organized?

The Water Vascular System of Echinoderms  The unique body plan of echinoderms is based on a unique morphological feature. As Figure 33.3a, shows, the echinoderm body contains a series of continuous fluid-filled tubes and chambers called the water vascular system. One of the tubes is open to the exterior where it meets the body wall, so seawater can flow into and out of the body. (b) Podia project from the underside of the body.
of the system. Inside, fluids move via the beating of cilia that line the interior of the tubes and chambers. In effect, the water vascular system forms a sophisticated hydrostatic skeleton.

Figure 33.3a highlights a particularly important part of the system called tube feet. Tube feet are elongated, fluid-filled structures. Podia ("feet") are sections of the tube feet that project outside the body (Figure 33.3b) and make contact with the substrate. As podia extend and contract in a coordinated way along the base of an echinoderm, they alternately grab and release from the substrate. As a result, the individual moves.

The other noteworthy feature of the echinoderm body is its endoskeleton, which is a hard, supportive structure inside the body (Figure 33.4). As an individual is developing, cells secrete plates of calcium carbonate inside the skin. Depending on the species involved, the plates may remain independent and result in a flexible structure or fuse into a rigid case. This type of endoskeleton is a diagnostic feature of echinoderms, along with radial symmetry and the water vascular system.

**The Origin of Chordates** The phylum Chordata is defined by the presence of four morphological features: (1) openings into the throat called pharyngeal gill slits; (2) a stiff but flexible rod called a notochord, which runs the length of the body; (3) a bundle of nerve cells that runs the length of the body and forms a dorsal hollow nerve cord; and (4) a muscular tail, which extends past the anus.

The hemichordates are not members of the phylum Chordata, because they have just one of these four features. Hemichordates lack a notochord, a dorsal hollow nerve cord, and a tail, although they do have pharyngeal gill slits that function in feeding and gas exchange (Figure 33.5a). Hemichordates are sessile suspension feeders and live in the ocean. As the arrows in Figure 33.5a indicate, water enters the mouths of these animals, flows through structures where oxygen and food particles are extracted, and exits through the pharyngeal gill slits.

**Figure 33.4 Echinoderms Have an Endoskeleton**
The endoskeleton of an echinoderm is located just under the skin.

**Figure 33.5 Four Traits Distinguish the Chordates**
(a) Hemichordata, although closely related to echinoderms, have only one of the four traits that distinguish chordates: pharyngeal gill slits. In chordates, either larvae or adults or both have notochords and muscular tails in addition to pharyngeal gill slits and dorsal hollow nerve cords. The three major chordate lineages are tunicates, lancelets, and vertebrates.
In contrast, pharyngeal gill slits, notochords, dorsal hollow nerve cords, and tails are found in each of the three major lineages of chordates (Figure 33.5b). In the traditional classification schemes introduced in Chapter 1, these groups are considered subphyla. The three groups are (1) urochordates, (2) cephalochordates, and (3) vertebrates. Urochordates are also called tunicates or sea squirts; they are small suspension feeders that as adults live attached to hard substrates in the ocean. Cephalochordates are also called lancelets or amphioxus; they are small, mobile suspension feeders that look a little like fish. Vertebrates include the sharks, bony fishes, reptiles, and mammals.

Adult urochordates are sessile, ocean-dwelling suspension feeders. As Figure 33.5b shows, pharyngeal gill slits are present in both larvae and adults and function in both feeding and gas exchange, much as they do in hemichordates. The notochord, dorsal hollow nerve cord, and tail are present only in the larvae, however. Because the notochord stiffens the tail, muscular contractions on either side of a larva’s tail wag it back and forth and result in swimming movements. As larvae swim or float in the upper water layers of the ocean, they drift to new habitats where food might be more abundant.

Adult cephalochordates live in ocean-bottom habitats, where they burrow in sand and suspension feed with the aid of their pharyngeal gill slits, much like urochordate larvae. The cephalochordates also have a notochord that stiffens their bodies, so that muscle contractions on either side result in fishlike movement when they swim during dispersal or mating.

In vertebrates, the dorsal hollow nerve cord is elaborated into the familiar spinal cord. Structures called pharyngeal pouches are present in all vertebrate embryos. In aquatic species, the creases between pouches open into gill slits and develop into part of the main gas-exchange organ—the gills. In terrestrial species, however, gill slits do not develop after the pharyngeal pouches form. A notochord also appears in all vertebrate embryos. Instead of functioning in body support and movement, however, it helps organize the body plan. Recall from Chapter 22 that cells in the notochord secrete proteins that help induce the formation of somites. Somites are segmental blocks of tissue that form along the length of the body. Although the notochord itself disappears, cells in the somites later differentiate into the vertebrae, ribs, and skeletal muscles of the back, body wall, and limbs. In this way, the notochord is instrumental in the development of the signature adaptation of vertebrates: an endoskeleton made of bone. To understand how bone evolved, let’s delve into the fossil record.

Using the Fossil Record

Echinoderms and vertebrates are present in the Burgess Shale deposits that formed during the Cambrian explosion 544–515 million years ago (Figure 33.6; see also Chapter 26). The vertebrate fossils in these rocks show that the earliest members of this lineage lived in the ocean about 530 million years ago, had streamlined bodies like fish, and appear to have had a skull, skeletal elements that reinforced the gills, and a notochord made of cartilage. Cartilage is a stiff tissue that consists of scattered cells in a gel-like matrix of polysaccharides and protein fibers. The earliest vertebrates had endoskeletons made of cartilage.

Subsequent to the appearance of vertebrates, the fossil record documents a series of key innovations that occurred as this lineage diversified:

- Fossil vertebrates from the early part of the Ordovician period, about 480 million years ago, are the first fossils to have bone. Bone is a tissue that consists of cells and blood vessels encased in a matrix made primarily of calcium phosphate (CaPO₄), with a small amount of calcium carbonate (CaCO₃)
and protein fibers. When bone first evolved, it did not occur in the endoskeleton. Instead bone was deposited in scalelike plates that formed an exoskeleton—a hard, hollow structure that envelops the body. Based on the fossils’ overall morphology, biologists infer that these animals swam with the aid of a notochord, and that they breathed and fed by gulping water and filtering it through their pharyngeal gill slits. Presumably, the bony plates helped provide protection from predators.

- The first vertebrates with jaws show up in the fossil record about 430 million years ago. The evolution of jaws was significant because it gave vertebrates the ability to bite, meaning that they were no longer limited to suspension feeding or deposit feeding. Instead, they could make a living as herbivores or predators. Soon after, jawbones with teeth appear in the fossil record (Figure 33.6). With jaws and teeth, vertebrates became armed and dangerous. The fossil record shows that a spectacular radiation of jawed fishes followed, filling marine and freshwater habitats.

- The next great event in the evolution of vertebrates was the transition to living on land. The first animals that had limbs and were capable of moving on land are dated to about 357 million years ago. These were the first of the tetrapods (“four-footed”—animals with four limbs (Figure 33.6).

- About 20 million years after the appearance of tetrapods in the fossil record, the first amniotes are present. The Amniota is a lineage of vertebrates that includes all tetrapods other than amphibians. They are named for a signature adaptation: the amniotic egg. An amniotic egg is an egg that has a watertight shell or case enclosing a membrane-bound food
supply, water supply, and waste repository. The evolution of the amniotic egg was significant because it gave vertebrates the ability to reproduce far from water. Amniotic eggs resist drying out, so vertebrates that produce amniotic eggs do not have to return to aquatic habitats to lay their eggs.

To summarize, the fossil record indicates that vertebrates evolved through a series of major steps, beginning about 530 million years ago with vertebrates whose endoskeleton consisted of a notochord. The earliest vertebrates gave rise to cartilaginous fishes (sharks and rays) and fish with bony skeletons and jaws. After the tetrapods emerged and amphibians resembling salamanders began to live on land, the evolution of the amniotic egg paved the way for the evolution of the first truly terrestrial vertebrates. The fossil record indicates that a radiation of reptiles followed, along with the animals that gave rise to mammals. Do phylogenetic trees estimated from analyses of DNA sequence data agree or conflict with these conclusions?

Evaluating Molecular Phylogenies

Figure 33.7 provides a phylogenetic tree that summarizes the relationships among deuterostomes, based on morphological traits and DNA sequence data. The labeled bars on the tree indicate where major innovations occurred during the evolution of deuterostomes. Although the phylogeny of deuterostomes continues to be a topic of intense research, researchers are increasingly confident that the relationships described in Figure 33.7 are accurate.

The overall conclusion from this tree is that the branching sequence inferred from morphological and molecular data...
correlates with the sequence of groups in the fossil record. Reading up from the base of the tree, it is clear that the three groups of deuterostomes that have traditionally been recognized as phyla are indeed monophyletic, and that hemichordates and echinoderms are more closely related to each other than they are to chordates. The closest living relatives of the vertebrates are the cephalochordates. The most basal groups of chordates lack the skull and vertebral column that define the vertebrates, and the most ancient lineages of vertebrates lack jaws and bony skeletons. To understand what happened during the subsequent diversification of echinoderms and vertebrates, let’s explore some of the major innovations involved in feeding, movement, and reproduction in more detail.

CHECK YOUR UNDERSTANDING

Echinoderms are distinguished by their fivefold radial symmetry as adults, water vascular system, and calcium carbonate plates that form an endoskeleton. The water vascular system functions in movement, and the endoskeleton provides protection. You should be able to (1) make a rough sketch of a sea star’s body; include labels indicating the structure and function of the water vascular system and endoskeleton.

Chordates are distinguished by the presence of a notochord, a dorsal hollow nerve cord, pharyngeal gill slits, and a muscular tail. You should be able to (2) sketch the body of a tunicate larva or cephalochordate, and add labels indicating the structure and function of the four diagnostic features. On a phylogeny of the vertebrates, you should be able to (3) map the origin of key traits such as the cartilaginous skeleton, bony skeleton, jaws, limbs, and amniotic egg.

33.3 What Themes Occur in the Diversification of Deuterostomes?

Deuterostomes evolved in marine environments, but their diversification carried them into all of the world’s major habitat types. Echinoderms, hemichordates, urochordates, and cephalochordates are all strictly marine. The most basal groups of chordates are also ocean-dwelling organisms. Lungfish, certain groups of sharks and rays, and about one-third of the ray-finned fishes live in freshwater. All tetrapods, with the exception of marine reptiles and mammals, live in terrestrial habitats, and all must breathe air.

In terms of numbers of species and range of habitats occupied, the most successful lineages of deuterostomes are the echinoderms and the vertebrates. Echinoderms are both widespread and abundant in marine habitats. In some deepwater environments, echinoderms represent 95 percent of the total mass of organisms. Among vertebrates, the most species-rich and ecologically diverse lineages are the ray-finned fishes and the tetrapods (Figure 33.8). Ray-finned fishes occupy habitats ranging from deepwater environments, which are perpetually dark, to shallow ponds that dry up each year. Tetrapods include the large herbivores and predators in terrestrial environments all over the world.

Today there are about 7000 species of echinoderms, 23,700 species of ray-finned fish, and 25,400 species of tetrapods. To understand why these lineages have been so successful, it’s important to recognize that they have unique body plans. Recall that echinoderms are radially symmetric and have a water vascular system, and that ray-finned fishes and tetrapods have a bony endoskeleton. In this light, the situation in deuterostomes appears to be similar to that in protostomes. Recall from Chapter 32 that the most evolutionarily successful protostome lineages are the arthropods and mollusks. A major concept in that chapter was that arthropods and mollusks have body plans that are unique among protostomes. Once their distinctive body plans evolved, evolution by natural selection led to extensive diversification based on novel methods for eating, moving, and reproducing.

Box 33.1 highlights model organisms that biologists have used in experimental work on echinoderms, ray-finned fishes, and tetrapods. To understand how these three groups became so species rich and geographically widespread, let’s take a closer look at the adaptations that allow them to eat, move, and produce offspring in diverse ways.

Feeding

Animals eat to live, and it is logical to predict that the 7000 species of echinoderms and nearly 50,000 species of ray-finned fishes and tetrapods eat different things in different ways. It is also logical to predict that echinoderms and vertebrates have traits that make diverse ways of feeding possible.
Both predictions are correct. Echinoderms have feeding strategies that are unique among marine animals. Many are based on the use of their water vascular system and podia. Ray-finned fishes and tetrapods, in contrast, depend on their jaws.

**Feeding Strategies in Echinoderms** Depending on the lineage and species in question, echinoderms make their living by suspension feeding, deposit feeding, or harvesting algae or other animals. In most cases, the animal’s podia play a key role in obtaining food. Many sea stars, for example, prey on bivalves. Clams and mussels respond to sea star attacks by contracting muscles that close their shells tight. But by clamping onto each shell with their podia and pulling, sea stars are often able to pry the shells apart a few millimeters (Figure 33.10a).

Once a gap exists, the sea star extrudes its stomach from its body and forces the stomach through the opening between the
bivalve’s shells. Upon contacting the visceral mass of the bivalve, the stomach of the sea star secretes digestive enzymes. It then begins to absorb the small molecules released by enzyme action. Eventually, only the unhinged shells of the prey remain.

Podia are also involved in echinoderms that suspension feed (Figure 33.10b). In most cases, podia are extended out into the water. When food particles contact them, the podia flick the food down to cilia, which sweep the particles toward the animal’s mouth. In deposit feeders, podia secrete mucus that is used to sop up food material on the substrate. The podia then roll the food-laden mucus into a ball and move it to the mouth.

**The Vertebrate Jaw**  The most ancient groups of vertebrates have relatively simple mouthparts. For example, hagfish and lampreys lack jaws and cannot bite algae, plants, or animals. They have to make their living as deposit feeders or as ectoparasites.

Vertebrates were not able to harvest food by biting until jaws evolved. The leading hypothesis for the origin of the jaw proposes that natural selection acted on mutations that affected the morphology of **gill arches**, which are curved regions of tissue between the gills. The jawless vertebrates have bars of cartilage that stiffen these gill arches. The gill-arch hypothesis proposes that mutation and natural selection increased the size of an arch and modified its orientation slightly, producing the first working jaw (Figure 33.11). Three lines of evidence, drawn from comparative anatomy and embryology, support the gill-arch hypothesis:

1. Both gill arches and jaws consist of flattened bars of bony or cartilaginous tissue that hinges and bends forward.
2. Unlike most other parts of the vertebrate skeleton, both jaws and gill arches are derived from specialized cells in the embryo called neural crest cells.
3. The muscles that move jaws and that move gill arches are derived from the same population of embryonic cells.

Taken together, these data support the hypothesis that jaws evolved from gill arches.

To explain why ray-finned fishes are so diverse in their feeding methods, biologists point to important modifications of the jaw. In ray-finned fishes, for example, the jaw is protrusible—meaning it can be extended to nip or bite out at food. In addition, several particularly species-rich lineages of ray-finned fishes have a set of pharyngeal jaws. The **pharyngeal jaw** consists of modified gill arches that function as a second set of jaws, located in the back of the mouth. Pharyngeal jaws are important because they make food processing particularly efficient. (For more on the structure and function of pharyngeal jaws, see Chapter 43.)

To summarize, the radiation of ray-finned fishes was triggered in large part by the evolution of the jaw, modifications that made it possible to protrude the jaw, and the origin of the pharyngeal jaw. The story of tetrapods is different, however.

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**FIGURE 33.11 A Hypothesis for the Evolution of the Jaw**

(a) Gill arches support the gills in jawless vertebrates. (b) In the fossil record, jawbones appear first in fossil fish called acanthodians. (c) Fossil sharks that appeared later had more elaborate jaws.

**QUESTION** The transition from the gill arches to the jaws of acanthodian fishes is complex, and intermediate forms have yet to be found in the fossil record. Would intermediate stages in the evolution of the jaw have any function?

Although jaw structure varies somewhat among tetrapod groups, the adaptation that triggered their initial diversification involved the ability to get to food, not to bite it and process it.

**Movement**

The signature adaptations of echinoderms and tetrapods involve locomotion. We’ve already explored the water vascular system and tube feet of echinoderms; here let’s focus on the tetrapod limb.

Most tetrapods live on land and use their limbs to move. But for vertebrates to succeed on land, not only did they have to be able to move out of water, but they also had to breathe air and avoid drying out. To understand how this was accomplished, consider the morphology and behavior of their closest living relatives, the lungfish (Figure 33.12). Most living species of lungfish inhabit shallow, oxygen-poor water. To supplement the oxygen taken in by their gills, they have lungs and breathe...
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EVOLUTION OF THE LIMB

Both the fossil fish and the early tetrapod are from the Devonian period, about 375 million years ago. The number and arrangement of bones in the fins and limbs of these two fossil organisms agree with the general form of Paleozoic tetrapods as well as the modern tetrapod limb. The color coding indicates homologous elements.

FIGURE 33.13 Fossil Evidence for a Fin-to-Limb Transition
Both the fossil fish and the early tetrapod are from the Devonian period, about 375 million years ago. The number and arrangement of bones in the fins and limbs of these two fossil organisms agree with the general form of Paleozoic tetrapods as well as the modern tetrapod limb. The color coding indicates homologous elements.

Some also have fleshy fins supported by bones and are capable of walking short distances along watery mudflats or the bottoms of ponds. In addition, some species can survive extended droughts by burrowing in mud.

Fossils provide strong links between lungfish and the earliest land-dwelling vertebrates. Figure 33.13 shows three of the species involved. The first, an aquatic animal related to today’s lungfishes, is from the Devonian period—about 375 million years ago. The second is one of the oldest tetrapods, or limbed vertebrates, found to date. The third is a more recent tetrapod fossil, dated to about 350 million years ago. The figure highlights the numbers and arrangement of bones in the fossil fish fin and the numbers and arrangement of bones in the limbs of early tetrapods. The color coding emphasizes that each fin or limb has a single bony element that is proximal (closest to the body) and then two bones that are distal (farther from the body) and arranged side by side, followed by a series of distal elements. Because the structures are similar and because no other groups have limb bones in this arrangement, the evidence for homology is strong. Based on the lifestyle of living lungfish, biologists suggest that mutation and natural selection gradually transformed fins into limbs as the first tetrapods became more and more dependent on terrestrial habitats.

The hypothesis that tetrapod limbs evolved from fish fins has also been supported by molecular genetic evidence. Recall from Chapter 26 that several regulatory proteins involved in the development of zebrafish fins and the upper parts of mouse limbs are homologous. Specifically, the proteins produced by Hox genes and the homeotic locus Sonic hedgehog (Shh) are found at the same times and in the same locations in fins and limbs. These data suggest that these appendages are patterned by the same genes. As a result, the data support the hypothesis that tetrapod limbs evolved from fins.

Once the tetrapod limb evolved, natural selection elaborated it into structures that are used for running, gliding, crawling, burrowing, or swimming. In addition, wings and the ability to fly evolved independently in three lineages of tetrapods: the extinct flying reptiles called pterosaurs (pronounced TARE-ob-sors), birds, and bats. Tetrapods and insects are the only animals that have taken to the skies. Box 33.2 (page 760) explores how flight evolved in birds.

To summarize, the evolution of the jaw gave tetrapods the potential to capture and process a wide array of foods. With limbs, they could move efficiently on land in search of food. Another challenge remained, however: producing offspring that could survive out of water.
In 2003 Xing Xu and colleagues published an analysis of a fossilized dinosaur called *Microraptor gui*, which had feathers on both its legs and wings (Figure 33.14). This paper was the culmination of a spectacular series of feathered dinosaur species that Xu’s group has discovered. Taken together, the newly discovered species answer several key questions about the evolution of birds, feathers, and flight:

- **Did birds evolve from dinosaurs?** On the basis of skeletal characteristics, all of these recently discovered fossil species clearly belong to a lineage of dinosaurs called the *dromaeosaurs*. The fossils definitively link the dromaeosaurs and the earliest known fossil birds.

- **How did feathers evolve?** The fossils support Xu’s model that feathers evolved in a series of steps, beginning with simple projections from the skin and culminating with the complex structures observed in today’s birds (Figure 33.15). *Microraptor gui*, for example, has simple feathers. It is controversial, however, whether the original function of feathers was for courtship or other types of display or for insulation. In today’s birds, feathers function in display, insulation, and flight.

- **Did birds begin flying from the ground up or from the trees down?** More specifically, did flight evolve with running species that began to jump and glide or make short flights, with the aid of feathers to provide lift? Or did flight evolve from tree-dwelling species that used feathers to glide from tree to tree, much as flying squirrels do today? Because it is unlikely that *Microraptor gui* could run efficiently with feathered legs, Xu and colleagues propose that flight evolved from tree-dwelling gliders.

Once dinosaurs evolved feathers and took to the air as gliders, the fossil record shows that a series of adaptations made powered, flapping flight
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Reproduction
Chapter 31 summarized the diversity of reproductive methods observed in fish. Recall that a few species undergo only asexual reproduction and that when sexual reproduction occurs, it may be based on internal or external fertilization and oviparity, viviparity, or ovoviviparity. In addition, parental care is extensive in some fish species, and often involves guarding eggs from predators and fanning them to keep oxygen levels high. All fish lay their eggs or give birth in water, however. Tetrapods were the first vertebrates that were able to breed on land.

Three major evolutionary innovations gave tetrapods the ability to produce offspring successfully in terrestrial environments: (1) the amniotic egg, (2) the placenta, and (3) elaboration of parental care. Let’s explore each of these innovations in turn.

The Amniotic Egg   Amniotic eggs have shells that minimize water loss as the embryo develops inside. The first tetrapods, like today’s amphibians (frogs, toads, and salamanders), lacked amniotic eggs. Although their eggs were encased by a membrane, the first tetrapods laid eggs that would dry out and die unless they were laid in water. This fact limited the range of habitats that these animals could exploit. Like today’s amphibians, the early tetrapods were largely restricted to living in or near marshes, lakes, or ponds.

In contrast, reptiles and the egg-laying mammals produce amniotic eggs. The eggshell is leathery in turtles, crocodiles, and snakes and lizards but hard—due to deposition of the calcium carbonate—in birds and the egg-laying mammals. In addition to having a shell that is largely watertight, an amniotic egg contains a membrane-bound supply of water in a protein-rich solution called albumen (Figure 33.17). The embryo is enveloped in a protective inner membrane known as the amnion. The yolk sac is a membranous pouch that contains nutrients for the growing embryo, and the allantois is a membranous pouch that holds waste materials. A middle membrane, the chorion, separates the...
amnion, yolk sac, and allantois from the albumen and provides a surface where gas exchange can take place between the embryo and the surrounding air. (Oxygen and carbon dioxide diffuse freely across the shell.) Inside an amniotic egg, the embryo is bathed in fluid. The egg itself is highly resistant to drying.

The evolution of the amniotic egg was a key event in the diversification of tetrapods because it allowed turtles, snakes, lizards, crocodiles, birds, and the egg-laying mammals to reproduce in any terrestrial environment—even habitats as dry as deserts. Members of the lineage called Amniota now occupy all types of terrestrial environments. But during the evolution of mammals, a second major innovation in reproduction occurred that eliminated the need for any type of egg laying: the placenta.

The Placenta  Recall from Chapter 31 that egg-laying animals are said to be oviparous, while species that give birth are termed viviparous. In many viviparous animals, females produce an egg that contains a nutrient-rich yolk. Instead of laying the egg, however, the mother retains it inside her body. In these ovoviviparous species, the developing offspring depends on the resources in the egg yolk. In most mammals, however, the eggs that females produce lack yolk. After fertilization occurs and the egg is retained, the mother produces a placenta within her uterus. The placenta is an organ that is rich in blood vessels and that facilitates a flow of oxygen and nutrients from the mother to the developing offspring (Figure 33.18). After a development period called gestation, the embryo emerges from the mother’s body.

Why did viviparity and the placenta evolve? Biologists have formulated an answer to this question by pointing out that females have a finite amount of time and energy available to invest in reproduction. As a result, a female can produce a large number of small offspring or a small number of large offspring but not a large number of large offspring. Stated more formally, every female faces a trade-off between the quantity of offspring she can produce and their size. In some lineages, natural selection has favored traits that allow females to produce a small number of large, well-developed offspring. Viviparity and the placenta are two such traits. Compared with female insects or echinoderms, which routinely lay thousands or even millions of eggs over the course of a lifetime, a female mammal produces just a few offspring. But because those offspring are protected inside her body and fed until they are well developed, they are much more likely to survive than sea star or insect embryos. Even after birth, many mammals continue to invest time and energy in rearing their young.

Parental Care  The term parental care encompasses any action by a parent that improves the ability of its offspring to survive, including supplying food, keeping young warm and dry, and protecting them from danger. In some insect and frog species, mothers carry around eggs or newly hatched young; in fishes, parents commonly guard eggs during development and fan them with oxygen-rich water.

The most extensive parental care observed among animals is provided by mammals and birds. In both groups, the mother and often the father continue to feed and care for individuals after birth or hatching—sometimes for many years (Figure 33.19). Female mammals also lactate—meaning that they produce nutrient-rich fluid called milk and use it to feed their offspring after birth. With the combination of the placenta and lactation, placental mammals make the most extensive investment of time and energy in offspring known. The evolution of extensive parental care is hypothesized to be a major reason for the evolutionary success of mammals and birds.

CHECK YOUR UNDERSTANDING

The diversification of echinoderms and vertebrates was based on innovations that made it possible for species to feed, move, and reproduce in novel ways. Most echinoderms use their podia to move, but they feed in a wide variety of ways—including using their podia to pry open bivalves, suspension feed, or deposit feed. An array of key innovations occurred during the evolution of vertebrates: Jaws made it possible to bite and process food, limbs allowed tetrapods to move on land, and amniotic eggs could be laid on land. You should be able to (1) explain how the jaw and limb evolved, (2) diagram the structure of an amniotic egg, and (3) explain the role of increased parental care in the evolution of birds and mammals.
(a) Mammal mothers feed and protect newborn young.

(b) Many bird species have extensive parental care.

FIGURE 33.19 Parental Care Is Extensive in Mammals and Birds
(a) Female mammals feed and protect embryos inside their bodies until the young are well developed. Once the offspring is born, the mother feeds it milk until it is able to eat on its own. In some species, parents continue to feed and protect young for many years. (b) In birds, one or both parents may incubate the eggs, protect the nest, and feed the young after hatching occurs.

33.4 Key Lineages: Echinodermata

The echinoderms (“spiny-skins”) were named for the spines or spikes observed in many species. They are bilaterally symmetric as larvae but undergo metamorphosis and develop into radially symmetric adults. They all have a water vascular system and produce calcium carbonate plates under their skin to form an endoskeleton.

The echinoderms living today make up five major lineages, traditionally recognized as classes: (1) feather stars and sea lilies, (2) brittle stars and basket stars, (3) sea cucumbers, (4) sea stars, and (5) sea urchins and sand dollars. Most feather stars and sea lilies are sessile suspension feeders (Figure 33.20a). Brittle stars and basket stars have five long arms that radiate out from a small central disk (Figure 33.20b). They use these arms to suspension feed, deposit feed by sopping up material with mucus, or capture small prey animals. Sea cucumbers are sausage-shaped animals that suspension feed or deposit feed with the aid of tentacles arranged in a whorl around their mouths (Figure 33.20c). Sea stars and sea urchins are described in detail in the text that follows.
The 1700 known species of sea stars have bodies with five or more long arms—in some species up to 300—radiating from a central region that contains the mouth, stomach, and anus (Figure 33.21). They range in size from less than 1 cm in diameter when fully grown to 1 m across. They live on hard or soft substrates along the coasts of all the world’s oceans. Although the spines that are characteristic of echinoderms are reduced to knobs on the surface of most sea stars, the crown-of-thorns star and a few other species have prominent, upright, movable spines.

**Feeding**  Sea stars are predators or scavengers. Some species pull bivalves apart with their tube feet and evert their stomach into the prey’s visceral mass. Sponges, barnacles, and snails are also common prey. The crown-of-thorns sea star specializes in feeding on corals and is native to the Indian Ocean and western Pacific Ocean. Its population has skyrocketed recently—possibly because people are harvesting their major predator, a large snail called the triton, for its pretty shell. Large crown-of-thorns star populations have led to the destruction of large areas of coral reef.

**Movement**  Sea stars crawl with the aid of their tube feet. Any one of the five or more arms may be in “front” as the animal moves.

**Reproduction**  Sexual reproduction predominates, and sexes are separate. At least one sea star arm is filled with reproductive organs that produce massive amounts of gametes—millions of eggs per female, in some species. Species that are native to habitats in the far north, where conditions are particularly harsh, care for their offspring by holding fertilized eggs on their body until the eggs hatch. Most sea stars are capable of regenerating arms that are lost in predator attacks or storms. Some species can reproduce asexually by dividing the body in two, with each of the two individuals then regenerating the missing half.

There are about 800 species of echinoids living today; most are sea urchins or sand dollars. Sea urchins have globe-shaped bodies and long spines and crawl along substrates (Figure 33.22a). Sand dollars are flattened and disk-shaped, have short spines, and burrow in soft sediments (Figure 33.22b).

**Feeding**  Sand dollars use their mucus-covered podia to collect food particles in sand or in other soft substrates. Most types of sea urchins are herbivores. In some areas of the world, urchins are extremely important grazers on kelp and other types of algae. In fact, when urchin populations are high, their grazing can prevent the formation of kelp forests. Most echinoids have a unique, jaw-like feeding structure in their mouths that is made up of five calcium carbonate teeth attached to muscles. In many species, this apparatus can extend and retract as the animal feeds.

**Movement**  Using their podia, sea urchins crawl and sand dollars burrow. Sea urchins can also move their spines to aid in crawling along a substrate.

**Reproduction**  Sexual reproduction predominates. Fertilization is external, and sexes are separate.
Chordata ▶ Myxinoidea (Hagfish) and Petromyzontoidea (Lampreys)

Although recent phylogenetic analyses indicate that hagfish and lampreys may belong to two independent lineages, some data suggest that they are a single group called the Agnatha (“not-jawed”). Because these animals are the only vertebrates that lack jaws, the 110 species in the two groups are still referred to as the jawless fishes. The hagfish and lampreys—several of which are known only from fossils—are the only surviving members of the earliest branches at the base of the vertebrates.

Hagfish and lampreys have long, slender bodies and are aquatic. Most species are less than a meter long when fully grown. Hagfish lack any sort of vertebral column, but lampreys have small pieces of cartilage along the length of their dorsal hollow nerve cord.

Feeding  Hagfish are scavengers and predators (Figure 33.23a). They deposit feed in the carcasses of dead fish and whales, and some are thought to burrow through ooze at the bottom of the ocean, feeding on polychaetes and other buried prey. Lampreys, in contrast, are ectoparasites. They attach to the sides of fish or other hosts by suction, then use spines in their mouth and tongue to rasp a hole in the side of their victim (Figure 33.23b). Once the wound is open, they suck blood and other body fluids.

Movement  Hagfish and lampreys have a well-developed notochord and swim by making undulating movements. Lampreys can also move themselves upstream, against the flow of water, by attaching their suckers to rocks and looping the rest of their body forward, like an inchworm. Although lampreys have fins that aid in locomotion, their fins do not occur in pairs as they do in jawed fish.

Reproduction  Virtually nothing is known about hagfish mating or embryonic development. Lampreys are anadromous, meaning that they spend their adult life in large lakes or the ocean but swim up streams to breed. Fertilization is external, and adults die after breeding once. Lamprey eggs hatch into larvae that look and act like lancelets. The larvae burrow into sediments and suspension feed for several years before metamorphosing into free-swimming adults.
The 840 species in this lineage are distinguished by their cartilaginous skeleton (*chondrus* is the Greek word for cartilage), the presence of jaws, and the existence of paired fins. Paired fins were an important evolutionary innovation, because they stabilize the body during rapid swimming—keeping it from pitching up or down, yawing to one side or the other, or rolling.

Most sharks, rays, and skates are marine, though a few species live in freshwater. Sharks have streamlined, torpedo-shaped bodies and an asymmetrical tail—the dorsal portion is longer than the ventral portion (*Figure 33.24a*). In contrast, the dorsal-ventral plane of the body in rays and skates is strongly flattened (*Figure 33.24b*).

**Feeding** A few species of ray and shark suspension feed on plankton, but most species in this lineage are predators. Skates and rays lie on the ocean floor and ambush passing animals; electric rays capture their prey by stunning them with electric discharges of up to 200 volts. Most sharks, in contrast, are active hunters that chase down prey in open water and bite them. The larger species of shark feed on large fish or marine mammals. Sharks are referred to as the “top predator” in many marine ecosystems, because they are at the top of the food chain—nothing eats them. Yet the largest of all sharks, the whale shark, is a suspension feeder. Whale sharks filter plankton out of water as it passes over their gills.

**Movement** Rays and skates swim by flapping their greatly enlarged pectoral fins. (*Pectoral fins* are located on the sides of an organism; *dorsal fins* are located on the dorsal surface.) Sharks swim by undulating their bodies and beating their large tail.

**Reproduction** Sharks have internal fertilization, and fertilized eggs may be shed into the water or retained until the young are hatched and well developed. In some viviparous species, embryos are attached to the mother by specialized tissues in a mammal-like placenta, where the exchange of gases, nutrients, and wastes takes place. Skates are oviparous, but rays are viviparous.

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**Chordata ➤ Chondrichthyes (Sharks, Rays, Skates)**

*Prionace glauca*

**Chondrichthyes (Sharks, Rays, Skates)**

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**Actinopterygii (Ray-Finned Fishes)**

*Actinopterygii* (pronounced *ack-tin-op-teh-RIJ-i*) means “ray-finned.” Logically enough, these fish have fins that are supported by long, bony rods arranged in a ray pattern. They are the most ancient living group of vertebrates that have a skeleton made of bone. Their bodies are covered with interlocking scales that provide a stiff but flexible covering, and they avoid sinking in the water with the aid of a gas-filled *swim bladder*. The evolution of the swim bladder was an important innovation, because this structure allowed ray-finned fishes to float. Tissues are heavier than water, so the bodies of aquatic organisms tend to sink. Sharks and rays, for example, have to swim to avoid sinking. But ray-finned fishes have a bladder that changes in volume, depending on the individual’s position. Gas is added to the bladder when a ray-finned fish swims down; gas is removed when the fish swims up. In this way, ray-finned fishes maintain neutral buoyancy in water of various depths and thus pressures.

The actinopterygians are the most successful vertebrate lineage based on number of species, duration in the fossil record, and extent of habitats occupied. Almost 24,000 species of ray-finned fishes have been identified. In traditional classifications, Actinopterygii is considered a class.

The most important major lineage of ray-finned fishes is the Teleostei, which includes some 20,000 species. Most of the fish that you are familiar with, such as tuna, trout, cod, and goldfish, are teleosts (*Figure 33.25*).

(Continued on next page)
Feeding  Teleosts can suck food toward their mouths, grasp it with their protrusible jaws, and then process it with teeth on their jaws and with pharyngeal jaws in their throat. The size and shape of the mouth, the jaw teeth, and the pharyngeal jaw teeth all correlate with the type of food consumed. For example, most predatory teleosts have long, spear-shaped jaws armed with spiky teeth, as well as bladelike teeth on their pharyngeal jaws. In addition to being major predators, ray-finned fishes are the most important large herbivores in both marine and freshwater environments.

Movement  Ray-finned fishes swim by alternately contracting muscles on the left and right sides of their bodies from head to tail, resulting in rapid, side-to-side undulations. Their bodies are streamlined to reduce drag in water. Teleosts have a flexible, symmetrical tail, which reduces the need to use their pectoral (side) fins as steering and stabilizing devices during rapid swimming.

Reproduction  Most species rely on external fertilization and are oviparous; some species have internal fertilization with external development; still others have internal fertilization and are viviparous. Although it is common for fish eggs to be released in the water and left to develop on their own, parental care occurs in some species. Parents may carry fertilized eggs on their fins, in their mouth, or in specialized pouches to guard them until the eggs hatch. In freshwater teleosts, offspring develop directly, but marine species have larva that are very different from adult forms. As they develop, marine fish larvae undergo a metamorphosis to the juvenile form, which then grows into an adult.

Although coelacanths (pronounced SEEL-uh-kanths) and lungfish represent independent lineages, they are sometimes grouped together and called lobe-finned fishes. Lobe-finned fishes are common and diverse in the fossil record in the Devonian period, about 400 million years ago, but only eight species are living today. They are important, however, because they represent a crucial evolutionary link between the ray-finned fishes and the tetrapods. Instead of having fins supported by rays of bone, their fins are fleshy lobes supported by an array of bones and muscles—similar to those observed in the limbs of tetrapods.

Coelacanths are marine and occupy habitats 150–700 m below the surface (Figure 33.26). In contrast, lungfish live in shallow, freshwater ponds (see Figure 33.12). As their name implies, lungfish have lungs and breathe air when oxygen levels in their habitats drop. Some species burrow in mud and enter a quiescent state when their habitat dries up during each year’s dry season.

Feeding  Coelacanths prey on fish. Lungfish are omnivorous (“all-eating”), meaning that they eat algae and plant material as well as animals.

Movement  Coelacanths swim by waving their pectoral and pelvic (“hip”) fins in the same sequence that tetrapods use in walking with their limbs. Lungfish swim by waving their body, and they can use their fins to walk along pond bottoms.

Reproduction  Sexual reproduction is the rule, with fertilization internal in coelacanths and external in lungfish. Coelacanths are ovoviviparous; lungfish lay eggs. Lungfish eggs hatch into larvae that resemble juvenile salamanders.
The 4800 species of amphibians living today form three distinct clades traditionally termed orders: (1) frogs and toads, (2) salamanders, and (3) caecilians (pronounced suh-SILL-ee-uns). Amphibians are found throughout the world and occupy ponds, lakes, or moist terrestrial environments (Figure 33.27a). Translated literally, their name means “both-sides-living.” The name is appropriate because adults of most species of amphibian feed on land, but many species lay their eggs in water. When amphibians live on land, gas exchange occurs exclusively or in part across their moist, mucus-covered skin.

**Feeding**  Adult amphibians are carnivores. Most frogs are sit-and-wait predators that use their long, extensible tongues to capture passing prey. Salamanders also have an extensible tongue, which some species use in feeding. Terrestrial caecilians prey on earthworms and other soil-dwelling animals; aquatic forms eat vertebrates and small fish.

**Movement**  Most amphibians have four well-developed limbs. In water, frogs and toads move by kicking their hind legs to swim; on land they kick their hind legs out to jump or hop. Salamanders walk on land; in water they undulate their body to swim like fish. Caecilians lack limbs and eyes; terrestrial forms burrow in moist soils (Figure 33.27b).

**Reproduction**  Frogs are oviparous and have external fertilization, but salamanders and caecilians have internal fertilization. Most salamanders are oviparous, but many caecilians are viviparous. In some species of frogs, parents may guard or even carry eggs. In many frogs, young develop in the water and suspension feed on plant or algal material. Salamander larvae are carnivorous. Later the larvae undergo a dramatic metamorphosis into land-dwelling adults. For example, the fishlike tadpoles of frogs and toads develop limbs and replace their gills with lungs.

**Chordata: Mammalia (Mammals)**

Mammals are easily recognized by the presence of hair or fur, which serves to insulate the body. Like birds, mammals are endotherms that maintain high body temperatures by oxidizing large amounts of food and generating large amounts of heat. Instead of insulating themselves with feathers, though, mammals retain heat because the body surface is covered with layers of hair or fur. Endothermy evolved independently in birds and mammals. In both groups, endothermy is thought to be an adaptation that enables individuals to maintain high levels of activity—particularly at night or during cold weather.

In addition to being endothermic and having fur, mammals have mammary glands—a unique structure that makes lactation possible. The evolution of mammary glands gave mammals the ability to provide their young with particularly extensive parental care. Mammals are also the only vertebrates with facial muscles and lips and the only vertebrates that have jaws formed from a single bone. In traditional classifications, Mammalia is designated as a class.

Mammals evolved when dinosaurs and other reptiles were the dominant large herbivores and predators in terrestrial and aquatic environments. The earliest mammals in the fossil record appear about 195 million years ago; they were small animals that were probably active only at night. Presumably because of their ancestry, most of the 4500 species of mammal living today have good nocturnal vision and a strong sense of smell. The adaptive radiation that gave rise to today’s diversity of mammals did not take place until after the dinosaurs went extinct about 65 million years ago. After the dinosaurs were gone, the mammals diversified into lineages of small and large herbivores, small and large predators, or marine hunters—ecological roles that had once been filled by dinosaurs and mosasaurs.
The monotremes are the most ancient lineage of mammals living today, and they are found only in Australia and New Zealand. They lay eggs and have lower metabolic rates than other mammals do. Three species exist: one species of platypus and two species of echidna.

**Feeding** Monotremes have a leathery beak or bill. The platypus feeds on insect larvae, mollusks, and other small animals in streams (Figure 33.28a). Echidnas feed on ants, termites, and earthworms (Figure 33.28b).

**Movement** Platypuses swim with the aid of their webbed feet. Echidnas walk on their four legs.

**Reproduction** Platypuses lay their eggs in a burrow, while echidnas keep their eggs in a pouch on their belly. The young hatch quickly, and the mother must continue keeping them warm and dry for another four months.

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The 275 known species of marsupials live in the Australian region and the Americas (Figure 33.29). Although females have a placenta that nourishes embryos during development, the young are born after a short embryonic period and are poorly developed. They crawl from the opening of the female’s reproductive tract to the female’s nipples, where they suck milk. They stay attached to their mother until they grow large enough to move independently.

**Feeding** Marsupials are herbivores, omnivores, or carnivores (“meat-eaters”). Many more cases of convergent evolution have occurred than for placental mammals. For example, the recently extinct Tasmanian wolf was a long-legged, social hunter similar to the timber wolves of North America and northern Eurasia. A species of marsupial native to Australia specializes in eating ants and looks and acts much like the South American anteater, which is not a marsupial.

**Movement** Marsupials move by crawling, gliding, walking, running, or hopping.

**Reproduction** Marsupial young spend more time developing while attached to their mother’s nipple than they do inside her body being fed via the placenta.
The approximately 4300 species of placental mammals are distributed worldwide. They are far and away the most species-rich and morphologically diverse group of mammals.

Biologists group mammals into 18 lineages called orders. The six most species-rich mammalian orders are the rodents (rats, mice, squirrels; 1814 species), bats (986 species), insectivores (hedgehogs, moles, shrews; 390 species), artiodactyls (pigs, hippos, whales, deer, sheep, cattle; 293 species), carnivores (dogs, bears, cats, weasels, seals; 274 species), and primates (lemurs, monkeys, apes, humans; 235 species).

**Feeding**  The size and structure of the teeth correlate closely with the diet of placental mammals. Herbivores have large, flat teeth for crushing leaves and other coarse plant material; predators have sharp teeth that are efficient at biting and tearing flesh. Omnivores, such as humans, usually have several distinct types of teeth. The structure of the digestive tract also correlates with the placental mammals’ diet. In some plant-eaters, for example, the stomach hosts unicellular organisms that digest cellulose and other complex polysaccharides.

**Movement**  In placental mammals, the structure of the limb correlates closely with the type of movement performed. Eutherians fly, glide, run, walk, swim, burrow, or swing from trees (Figure 33.30). Limbs are reduced or lost in aquatic groups such as whales and dolphins, which swim by undulating their bodies.

**Reproduction**  In mammals, both fertilization and development are internal. Thus, eutherians are viviparous. An extensive placenta develops from a combination of maternal and fetal tissues, and gestation is relatively long. At birth, young are much better developed than in marsupials—some are able to walk or run minutes after birth. All eutherians feed their offspring milk until the young have grown large enough to process solid food. A prolonged period of parental care, extending beyond the nursing stage, is common as offspring learn how to escape predators and find food.

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**Chordata: Reptilia (Turtles, Snakes and Lizards, Crocodiles, Birds)**

The reptiles are a monophyletic group and represent one of the two major living lineages of amniotes—the other lineage consisting of the extinct mammal-like reptiles and today’s mammals. The major feature distinguishing the reptilian and mammalian lineages is the number and placement of openings in the skull. These openings are used by jaw muscles that make sophisticated biting and chewing movements possible.

Several features adapt reptiles for life on land. Their skin is made watertight by a layer of scales made of the protein keratin, which is the same protein as that found in mammalian hair. They breathe air through well-developed lungs and lay shelled, amniotic eggs that resist drying out. In turtles, the egg has a leathery shell; in other reptiles, the shell is made of stiff calcium carbonate. Because sperm and egg must fuse before the amniotic membrane and shell form, fertilization in reptiles is internal.

The reptiles include the dinosaurs, pterosaurs (flying reptiles), mosasaurians (marine reptiles), and other extinct lineages that flourished from about 250 million years ago until the mass extinction at the end of the Cretaceous, 65 million years ago. Today, the Reptilia are represented by four major lineages, traditionally recognized as subclasses: (1) turtles, (2) snakes and lizards, (3) crocodiles and alligators, and (4) birds. With the exception of birds, all of these groups are **ectothermic** (“outside-heated”)—meaning that individuals do not use internally generated heat to regulate their body temperature. It would be a mistake, however, to conclude that reptiles other than birds do not regulate their body temperature closely. Reptiles bask in sunlight, seek shade, and perform other behaviors to keep their body temperature at a preferred level.
The 271 known species of turtles and tortoises inhabit freshwater, marine, and terrestrial environments throughout the world. The testudines are distinguished by a shell composed of bony plates that fuse to the vertebrae and ribs (Figure 33.31). Their skulls are highly modified versions of the skulls of other reptiles. Turtles and tortoises lack teeth, but their jawbone and lower skull form a bony beak.

**Feeding**  Turtles are either herbivorous or carnivorous—feeding on whatever animals they can capture and swallow. They may also scavenge dead material. Most marine turtles are carnivorous. Leatherback turtles, for example, feed primarily on jellyfish, such as the Portuguese man-of-war, and are only mildly affected by the jellyfish’s stinging cnidocytes. Tortoises are plant eaters.

**Movement**  Turtles swim, walk, or burrow. Aquatic species usually have feet that are modified to function as flippers.

**Reproduction**  All turtles are oviparous. Other than digging a nest prior to depositing eggs, parental care is lacking. The sex of a baby turtle is often not determined by sex chromosomes. Instead, in many species the temperature at which the egg develops determines gender. High temperatures produce mostly males, while low temperatures produce mostly females.

Most squamates are small reptiles with elongated bodies and scaly skin. Most lizards have well-developed jointed legs, but snakes are limbless (Figure 33.32). The hypothesis that snakes evolved from limbed ancestors is supported by the presence of vestigial hip and leg bones in boas and pythons. There are about 6800 species of lizards and snakes alive now.

**Feeding**  Small lizards prey on insects. Although most of the larger lizard species are herbivores, the 3-meter-long monitor lizard from the island of Komodo is a predator that kills and eats deer. Snakes are carnivores; some subdue their prey with the aid of poison that is injected via modified teeth called fangs. Snakes prey primarily on small mammals, amphibians, and invertebrates, which they swallow whole (usually headfirst).

**Movement**  Lizards crawl or run on their four limbs. Snakes and limbless lizards burrow through soil, crawl over the ground, or climb trees by undulating their bodies.

**Reproduction**  Although most squamates lay eggs, many are oviparous. Most squamates are bisexual, but asexual reproduction, via the production of eggs by mitosis, is known to occur in six groups of lizards and one snake lineage.
Chordata ▶ Reptilia ▶ Crocodilia (Crocodiles, Alligators)

Only 21 species of crocodile and alligator are known. Most are tropical and live in freshwater or marine environments. They have eyes located on the top of their heads and nostrils located at the top of their long snouts—adaptations that allow them to sit semi-submerged in water for long periods of time (Figure 33.33).

Feeding Crocodilians are predators. Their jaws are filled with conical teeth that are continually replaced as they fall out during feeding. The usual method of killing small prey is by biting through the body wall. Large prey are usually subdued by drowning. Crocodilians eat amphibians, turtles, fish, birds, and mammals.

Movement Crocodiles and alligators walk or gallop on land. In water they swim with the aid of their large, muscular tails.

Reproduction Although crocodilians are oviparous, parental care is extensive. Eggs are laid in earth-covered nests that are guarded by the parents. When young inside the eggs begin to vocalize, parents dig them up and carry the newly hatched young inside their mouths to nearby water. Crocodilian young can hunt when newly hatched but stay near their mother for up to three years.

Chordata ▶ Reptilia ▶ Aves (Birds)

The fossil record provides conclusive evidence that birds descended from a lineage of dinosaurs that had a unique trait: feathers. In dinosaurs, feathers are hypothesized to have functioned as insulation and in courtship or aggressive displays. In birds, feathers insulate and are used for display but also furnish the lift, power, and steering required for flight. Birds have other adaptations that make flight possible, including large breast muscles used to flap the wings. Bird bodies are lightweight, because they have a reduced number of bones and organs and because their hollow bones are filled with air sacs, linked to the lungs. Instead of teeth, birds have a horny beak. They are endotherms ("within-heating")—they have a high metabolic rate and use the heat produced, along with the insulation provided by feathers, to maintain a constant body temperature. The 9700 bird species today occupy virtually every habitat, including the open ocean (Figure 33.34).

Feeding Plant-eating birds usually feed on nectar or seeds. Most birds are omnivores, although many are predators that capture insects, small mammals, fish, other birds, lizards, mollusks, or crustaceans. The size and shape of a bird’s beak correlates closely with its diet. For example, predatory species such as falcons have sharp, hook-shaped beaks; finches and other seedeaters have short, stocky bills that can crack seeds and nuts; fish-eating species such as the great blue heron have spear-shaped beaks.

Movement Although flightlessness has evolved repeatedly during the evolution of birds, almost all species can fly. The size and shape of birds’ wings correlate closely with the type of flying they do. Birds that glide or hover have long, thin wings; species that specialize in explosive takeoffs and short flights have short, stocky wings. Many seabirds are efficient swimmers, using their webbed feet or wings under water. Ground-dwelling birds such as ostrich and pheasants can run long distances at high speed.

Reproduction Birds are oviparous but provide extensive parental care. In most species, one or both parents build a nest and incubate the eggs. After the eggs hatch, parents feed offspring until they are large enough to fly and find food on their own.
33.6 Key Lineages: The Hominin Radiation

Although humans occupy a tiny twig on the tree of life, there has been a tremendous amount of research on human origins. This section introduces the lineage of mammals called the Primates, the fossil record of human ancestors, and data on the relationships among human populations living today.

The Primates

The lineage called Primates consists of two main groups: prosimians and anthropoids. The prosimians (“before-monkeys”) consist of the lemurs, found in Madagascar, and the tarsiers, pottos, and lorises of Africa and south Asia. Most prosimians live in trees and are active at night (Figure 33.35a). The anthropoids (“human-like”) include the New World monkeys found in Central and South America, the Old World monkeys that live in Africa and tropical regions of Asia, the gibbons of the Asian tropics, and the great apes—orangutans, gorillas, chimpanzees, and humans (Figure 33.35b). The phylogenetic tree in Figure 33.35c shows the evolutionary relationships among these groups.

Primates are distinguished by having eyes located on the front of the face. Eyes that look forward provide better depth perception than do eyes on the sides of the face. Primates also tend to have hands and feet that are efficient at grasping, flattened nails instead of claws on the fingers and toes, brains that are large relative to overall body size, complex social behavior, and extensive parental care of offspring. The anthropoids are distinguished from the prosimians by having a fully opposable thumb—meaning a thumb that can touch the tips of all the other fingers—which makes grasping particularly efficient.

The lineage in Figure 33.35c that is composed of the great apes, including humans, is known as the hominids. From extensive comparisons of DNA sequence data, it is now clear that humans are most closely related to the chimpanzees and that our next nearest living relative is the gorilla.

Compared with most types of primate, the great apes are relatively large bodied and have long arms, short legs, and no tail.
Although all of the great ape species except for the orangutans live primarily on the ground, they have distinct ways of walking. When orangutans do come to the ground, they occasionally walk with their knuckles pressed to the ground. More commonly, though, they “fist walk”—that is, they walk with the backs of their hands pressed to the ground. Gorillas and chimpanzees, in contrast, only “knuckle-walk.” They also occasionally rise up on two legs—usually in the context of displaying aggression. Humans are the only great ape that is fully bipedal (“two-footed”)—meaning they walk upright on two legs. Bipedalism is, in fact, the shared derived character that defines the group called hominins.

**Fossil Humans**

According to the fossil record, the common ancestor of chimps and humans lived in Africa 6–7 million years ago. As a group, all the species on the branch leading to contemporary humans are called hominins. The fossil record of hominins, though not nearly as complete as investigators would like, is rapidly improving. About 14 species have been found, and new fossils that inform the debate over the ancestry of humans are discovered every year. Although naming the hominin species and interpreting their characteristics remain intensely controversial, most researchers agree that they can be organized into four groups:

1. **Australopithecus** Four species of small apes called gracile australopithecines have been identified to date (Figure 33.36a). The adjective gracile, or “slender,” is appropriate because these organisms were slightly built. The genus name *Australopithecus* (“southern ape”) was inspired by the earliest specimens, which came from South Africa. Several lines of evidence support the hypothesis that the gracile australopithecines were bipedal. For example, the hole in the back of their skulls where the spinal cord connects to the brain is oriented downward, just as it is in our species, *Homo sapiens*. In chimps, gorillas, and other vertebrates that walk on four feet, this hole is oriented backward.

2. **Paranthropus** Three species are grouped in the genus *Paranthropus* (“beside-human”). Like the gracile australopithecines, these robust australopithecines were bipedal. But as Figure 33.36b illustrates, their skulls were much broader and more robust than those of the gracile forms. All three species had massive cheek teeth and jaws, very large cheekbones, and a sagittal crest—a flange of bone at the top of the skull. Because muscles that work the jaw attach to the sagittal crest and cheekbones, researchers conclude that these organisms made their living by crushing large seeds or coarse plant materials. One species is nicknamed “nutcracker man.” The name *Paranthropus* was inspired by the hypothesis that the three known species are a monophyletic group that was a side branch during human evolution—an independent lineage that went extinct.

3. **Early Homo** Species in the genus *Homo* are called humans. As Figure 33.36c shows, species in this genus have flatter...
and narrower faces, smaller jaws and teeth, and larger braincases than the earlier hominins do. (The braincase is the portion of the skull that encloses the brain.) The appearance of early members of the genus *Homo* in the fossil record coincides closely with the appearance of tools made of worked stone—most of which are interpreted as handheld choppers or knives. Although the fossil record does not exclude the possibility that *Paranthropus* made tools, many researchers favor the hypothesis that extensive toolmaking was a diagnostic trait of early *Homo*.

4. Recent *Homo* The recent species of *Homo* date from 1.2 million years ago to the present. As Figure 33.36d shows, these species have even flatter faces, smaller teeth, and larger braincases than the early *Homo* species do. The 30,000-year-old fossil in the figure, for example, is from a population of *Homo sapiens* called the Cro-Magnons. The Cro-Magnons were accomplished painters and sculptors who buried their dead in carefully prepared graves. There is also evidence that Neanderthals (*Homo neanderthalensis*) made art and buried their dead in a ceremonial fashion.

Table 33.1 summarizes data on the geographic range, braincase volume, and body size of selected species within these four groups. Figure 33.37 provides the time range of each species in the fossil record. Although researchers do not have a solid understanding of the phylogenetic relationships among the hominin species, several points are clear from the available data. First, the shared, derived character that defines the hominins is bipedalism. Second, several species from the lineage were present simultaneously during most of hominin evolution. For example, about 1.8 million years ago there may have been as many as five hominin species living in eastern and southern Africa. Because fossils from more than one species have been found in the same geographic location in rock strata of the same age, it is almost certain that different hominin species lived in physical contact. Finally, compared with the gracile and robust australopithecines and the great apes, species in the genus *Homo* have extremely large brains relative to their overall body size.

Why did humans evolve such gigantic brains? The leading hypothesis on this question is that early *Homo* began using symbolic spoken language along with initiating extensive tool use. The logic here is that increased toolmaking and language use triggered natural selection for the capacity to reason and communicate, which required a larger brain. To support this

<table>
<thead>
<tr>
<th>Species</th>
<th>Location of Fossils</th>
<th>Estimated Average Braincase Volume (cm³)</th>
<th>Estimated Average Body Size (kg)</th>
<th>Associated with Stone Tools?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australopithecus afarensis</td>
<td>Africa</td>
<td>450</td>
<td>36</td>
<td>no</td>
</tr>
<tr>
<td><em>A. africanus</em></td>
<td>Africa</td>
<td>450</td>
<td>36</td>
<td>no</td>
</tr>
<tr>
<td>Paranthropus boisei</td>
<td>Africa</td>
<td>510</td>
<td>44</td>
<td>no?</td>
</tr>
<tr>
<td><em>Homo habilis</em></td>
<td>Africa</td>
<td>550</td>
<td>34</td>
<td>yes</td>
</tr>
<tr>
<td><em>H. ergaster</em></td>
<td>Africa, Asia</td>
<td>850</td>
<td>58</td>
<td>yes</td>
</tr>
<tr>
<td><em>H. erectus</em></td>
<td>Africa, Asia</td>
<td>1000</td>
<td>57</td>
<td>yes</td>
</tr>
<tr>
<td><em>H. heidelbergensis</em></td>
<td>Africa, Europe</td>
<td>1200</td>
<td>62</td>
<td>yes</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>Middle East, Europe, Asia</td>
<td>1500</td>
<td>76</td>
<td>yes</td>
</tr>
<tr>
<td><em>H. sapiens</em></td>
<td>Middle East, Europe, Asia</td>
<td>1350</td>
<td>53</td>
<td>yes</td>
</tr>
</tbody>
</table>

**TABLE 33.1 Characteristics of Selected Hominins**

**FIGURE 33.37 A Timeline of Human Evolution**
Plot of the ages of selected fossil hominins. QUESTION How many species of hominin existed 2.2 million years ago, 1.8 million years ago, and 100,000 years ago?
hypothesis, researchers point out that, relative to the brain areas of other hominins, the brain areas responsible for language were enlarged in the earliest Homo species. There is even stronger fossil evidence for extensive use of speech in Homo neanderthalensis and early Homo sapiens:

- The hyoid bone is a slender bone in the voice box of modern humans that holds muscles used in speech. In Neanderthals and early Homo sapiens, the hyoid is vastly different in size and shape from a chimpanzee’s hyoid bone. Researchers recently found an intact hyoid bone associated with a 60,000-year-old Neanderthal individual and showed that it is virtually identical to the hyoid of modern humans.
- Homo sapiens colonized Australia by boat between 60,000 and 40,000 years ago. An expedition of that type could not be planned and carried out in the absence of symbolic speech.

To summarize, Homo sapiens is the sole survivor of an adaptive radiation that took place over the past 3.5 million years. From a common ancestor shared with chimpanzees, hominins evolved the ability to walk upright, make tools, and talk.

### The Out-of-Africa Hypothesis

The first fossils of Homo sapiens appear in African rocks that date to about 160,000 years ago. For some 100,000 years thereafter, the fossil record indicates that our species occupied Africa while H. neanderthalensis resided in Europe and the Middle East. Some evidence suggests that H. erectus may still have been present in Asia at that time. Then, in rocks dated between 60,000 and 30,000 years ago, H. sapiens fossils are found throughout the Old World and Australia. But H. neanderthalensis and H. erectus have disappeared by this time.

Phylogenies of Homo sapiens estimated from DNA sequence data agree with the pattern in the fossil record. In phylogenetic trees that show the relationships among human populations living today, the first lineages to branch off lead to descendant populations that live in Africa today (Figure 33.38). Based on this observation, it is logical to infer that the ancestral population of modern humans also lived in Africa. The tree shows that lineages subsequently branched off to form three monophyletic groups. Because the populations within each of these clades live in a distinct area, the three lineages are thought to represent three major waves of migration that occurred as Homo sapiens populations dispersed from Africa to (1) southeast Asia and the South Pacific, (2) central Asia and Europe, and (3) northeast Asia and the Americas (Figure 33.39). To summarize, the data suggest that modern humans originated in Africa and then spread throughout the world in a series of three major migrations.

What happened to the Neanderthals and to Homo erectus as H. sapiens expanded its range? This simple question has provoked years of heated controversy. Currently, the debate boils down to two possibilities: (1) Either H. sapiens interbred with the other two hominid groups as it moved into Europe and Asia, or (2) it did not. The first possibility is called the assimilation hypothesis. It implies that the genetic composition and morphological features of H. sapiens are a mixture of ancient traits from Neanderthals and H. erectus and recent traits from H. sapiens. The second possibility is called the out-of-Africa hypothesis. It contends that H. sapiens evolved independently of the European and Asian species of Homo—meaning there was no interbreeding between H. sapiens and Neanderthals or H. erectus. Stated another way, the out-of-Africa hypothesis proposes that H. sapiens evolved its distinctive traits in Africa, then dispersed throughout the world. The assimilation hypothesis proposes that Homo sapiens acquired its distinctive traits at least in part through extensive interbreeding with H. neanderthalensis or H. erectus, or both.

If the assimilation hypothesis is correct, then modern humans should contain genes descended from H. neanderthalensis or H. erectus, or both. Recall from Chapter 19 that researchers have tested this prediction by extracting DNA from the fossilized bones of four Neanderthal individuals from three differ-
ent locations in Eurasia. In each case, the researchers ground samples from the intact bone, extracted DNA, and used the polymerase chain reaction to copy a 379-base-pair section of the mitochondrial genome. When they sequenced the Neanderthal DNA and compared it with sequences from about a thousand humans living today, the results were striking: The Neanderthal DNA was extremely different from the DNA of living humans. For example, when sequences from any two randomly chosen *H. sapiens* are compared with each other, an average of 8 bases are unalike. But when randomly chosen *H. sapiens* sequences are compared to the *H. neanderthalensis* DNA, there is an average of over 25 differences. Further, the sequence differences observed in the Neanderthal DNA are unique—none of the *H. sapiens* sequences contained the nucleotide substitutions found in *H. neanderthalensis*. These results support the hypothesis that *H. sapiens* and *H. neanderthalensis* did not interbreed.

Unfortunately, it has been impossible so far to extract DNA from *H. erectus* fossils and perform the same test. Although the weight of evidence currently tips the scales in favor of the out-of-Africa hypothesis, research continues.

**FIGURE 33.39 Homo sapiens Originated in Africa and Spread throughout the World**
The phylogeny in Figure 33.38 supports the hypothesis that humans originated in Africa and spread out in three major migrations: to southeast Asia and the Pacific Islands, to Europe, and to northeast Asia and the New World.

**ESSAY So Human an Animal**

From a biological point of view, what is a human being? Historically, scientists and philosophers have answered this question by arguing that humans have one or more unique, defining characteristics that set us apart from other organisms. For decades this defining characteristic was thought to be tool use. But then Jane Goodall, who pioneered the study of common chimpanzees in the field, observed that chimps collect and modify twigs to “fish” for termites or ants and eat them (Figure 33.40, page 778). Later, Goodall and other biologists reported additional examples of tool use by common chimps, bonobos (also known as pygmy chimps), baboons, sea otters, and various birds.

In response, some observers began to argue that the defining characteristic of humans was not toolmaking but the use of symbolic speech—language based on the abstract symbols we call words and letters. But researchers have since taught chimps rudimentary aspects of the American Sign Language, and the shape of a recently discovered Neanderthal bone located in the larynx suggests that Neanderthals, too, could speak. These results have a key message: The ability to learn and to use abstract symbols and grammatical rules is not unique to humans.

In short, there may be no single characteristic that “defines” humans. Instead, most contemporary biologists would characterize our

*(Continued on next page)*
The most prominent deuterostome lineages are the echinoderms and the vertebrate groups called ray-finned fishes and tetrapods. Echinoderms, ray-finned fishes, and tetrapods are the most species-rich groups of deuterostomes and are the most important large-bodied predators and herbivores in marine and terrestrial environments.

Echinoderms and vertebrates have unique body plans. Echinoderms are radially symmetric as adults and have a water vascular system. All vertebrates have a skull, and most have an extensive endoskeleton made of cartilage or bone. Echinoderm larvae are bilaterally symmetric but undergo a metamorphosis into radially symmetric adults. Their water vascular system is composed of fluid-filled tubes and chambers and extends from the body wall in projections called podia. Podia can extend and retract in response to muscle contractions that move fluid inside the water vascular system.

Chordates are distinguished by the presence of a notochord, a dorsal hollow nerve cord, pharyngeal gill slits, and a muscular tail that extends past the anus. Vertebrates are distinguished by the presence of a cranium; most species also have vertebrae. In more recent groups of vertebrates, the body plan features an extensive endoskeleton composed of bone.

The diversification of echinoderms was triggered by the evolution of appendages called podia; the diversification of vertebrates was driven by the evolution of the jaw and limbs. Most echinoderms move via their podia, and many species suspension feed, deposit feed, or act as predators with the aid of their podia. Ray-finned fishes and tetrapods use their jaws to bite food and process it with teeth. Species in both groups move when muscles attached to their endoskeletons contract or relax. Ray-finned fishes called teleosts are efficient swimmers because their flexible, symmetrical tail stabilizes their body during rapid movement. Tetrapods can move on land because their limbs enable walking, running, or flying. The evolution of the amniotic egg allowed tetrapods to lay eggs on land. Parental care was an important adaptation in some groups of ray-finned fishes and tetrapods—particularly mammals.

Recently, research in molecular genetics has furnished a new perspective on the question, Who are humans? When Svante Pääbo and co-workers sequenced a 10,156-base-pair segment from the X chromosomes of humans and common chimpanzees, the team found that the sequences were identical at almost 99 percent of the 10,156 sites.

These findings prompt a question: Which 1 to 2 percent of the human genome is responsible for the morphological and behavioral differences between chimps and humans? Will it be possible to identify the alleles responsible for our bipedal posture, large brains, slow rate of sexual maturation, and huge capacity for learning? Researchers have only begun to tackle these questions. But, with a variety of genome analysis projects now under way, answers may soon be forthcoming.
Humans are a tiny twig on the tree of life. Chimpanzees and humans diverged from a common ancestor that lived in Africa 6–7 million years ago. Since then, at least 14 humanlike species have existed.

The fossil record of the past 3.5 million years contains at least 14 distinct species of hominins. Several of these organisms lived in Africa at the same time, and some lineages went extinct without leaving descendant populations. Thus, Homo sapiens is the sole surviving representative of an adaptive radiation. The phylogeny of living humans, based on comparisons of DNA sequences, agrees with evidence in the fossil record that H. sapiens originated in Africa and later spread throughout Europe, Asia, and the Americas. DNA sequences recovered from the fossilized bones of H. neanderthalensis suggest that H. sapiens replaced this species in Europe without interbreeding.

**Questions**

**Content Review**

1. If you found an organism on a beach, what characteristics would allow you to declare that the organism is an echinoderm?
   a. radially symmetric adults, spines, and presence of tube feet
   b. notochord, dorsal hollow nerve cord, pharyngeal Gill slits, and muscular tail
   c. exoskeleton and three pairs of appendages; distinct head and body (trunk) regions
   d. mouth forms second (after the anus) during gastrulation

2. What is the diagnostic trait of vertebrates?
   a. cranium
   b. jaws
   c. endoskeleton constructed of bone
   d. endoskeleton constructed of cartilage

3. Why are the pharyngeal jaws found in many ray-finned fishes important?
   a. They allow the main jaw to be protrusible (extendible).
   b. They make it possible for individuals to suck food toward their mouths.
   c. They give rise to teeth that are found on the main jawbones.
   d. They can bite down on food and help process it.

4. Which of the following lineages make up the living Amniota?
   a. reptiles and mammals
   b. viviparous fishes
   c. frogs, salamanders, and caecilians
   d. hagfish, lampreys, and cartilaginous fishes (sharks and rays)

5. Which of the following does not occur in either cartilaginous fishes or ray-finned fishes?
   a. internal fertilization and viviparity or ovoviviparity
   b. external fertilization and oviparity
   c. formation of a placenta
   d. feeding of young

6. Researchers agree that modern Homo sapiens originated in Africa and then spread throughout Europe, Asia, and eventually the Americas. What do they disagree about?
   a. whether the original African population of H. sapiens left any descendants
   b. whether H. sapiens members interbred with H. erectus members
   c. whether the Neanderthals represent a distinct species from H. sapiens
   d. whether H. neanderthalensis and H. erectus died out concurrently

**Conceptual Review**

1. Explain how the water vascular system of echinoderms functions as a type of hydrostatic skeleton.

2. List the four morphological traits that distinguish chordates. How are these traits involved in locomotion and feeding in larvae or adults?

3. Describe evidence that supports the hypothesis that jaws evolved from gill arches in fish.

4. Describe evidence that supports the hypothesis that the tetrapod limb evolved from the fins of lobe-finned fishes.

5. The text claims that “Homo sapiens is the sole survivor of an adaptive radiation that took place over the past 3.5 million years.” Do you agree with this statement? Why or why not?

6. Explain how the evolution of the placenta and lactation in mammals improved the probability that their offspring would survive. Over the course of a lifetime, why are female mammals expected to produce fewer eggs than do female fish?

**Group Discussion Problems**

1. A growing number of biologists maintain that only monophyletic groups should be given names. According to these researchers, there is no such thing as a fish. Explain this statement.

2. Compare and contrast adaptations that triggered the diversification of the three most species-rich animal lineages: mollusks, arthropods, and vertebrates.

3. Aquatic habitats occupy 73 percent of Earth’s surface area. How does this fact relate to the success of ray-finned fishes? How does it relate to the success of coelacanths and other lobe-finned fishes?

4. Mammals and birds are endothermic. Did they inherit this trait from a common ancestor, or did endothermy evolve independently in these two lineages? Provide evidence to support your answer.

Answers to Multiple-Choice Questions  
1. a; 2. a; 3. d; 4. a; 5. d; 6. b

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