Snow monkeys *(Macaca fuscata)*. These snow monkeys, which have the northernmost distribution of any nonhuman primate, are soaking in a hot spring in Japan.

Study Plan

Continued on next page

30 Deuterostomes: Vertebrates and Their Closest Relatives

Why It Matters

In 1798, naturalists at the British Museum skeptically probed a curious specimen that had been sent from Australia. The furry creature—about the size of a housecat—had webbed front feet, a ducklike bill, and a flat, paddlelike tail **(Figure 30.1).** The scientists eagerly searched for evidence that a prankster had stitched together parts from wildly different animals, but they found no signs of trickery and soon accepted the duck-billed platypus *(Ornithorhynchus anatinus)* as a genuine zoological novelty.

Further study has revealed that the platypus is even stranger than those scientists could have imagined. Like other mammals, the platypus is covered with fur, and females produce milk that the offspring lick off the fur on their mother's belly. But like turtles and birds, a platypus has no teeth, and it reproduces by laying eggs instead of giving birth to its offspring. And like turtles, birds, lizards, snakes, and crocodilians, it has a cloaca, a multipurpose chamber through which it releases feces, urine, and eggs. Scientists had never before seen such a weird combination of traits, and they didn't quite know what to make of them.

Continued from previous page

Tom McHugh/Photo Researchers, Inc.

Figure 30.1
A puzzling animal. Because of its strange mixture of traits, the platypus *(Ornithorhynchus anatinus)* amazed the first European zoologists who saw it.

Studies of the platypus under natural conditions have helped biologists make sense of its characteristics. The platypus inhabits streams and lagoons in Australia and Tasmania. It rests in streamside burrows during the day, but at night it slips into the water to hunt for invertebrates. Its dense fur keeps its body warm and dry under water, and its tail serves both as a rudder and as a storehouse for energy-rich fat. It uses its bill to scoop up food and the horny pads that line its jaws to grind up prey. While underwater, the platypus clamps shut its eyes, ears, and nostrils, relying on roughly 800,000 sensory receptors in its bill to detect the movements and weak electrical discharges of nearby prey.

The platypus, with its strange combination of characteristics, illustrates the remarkable diversity of adaptations that enable vertebrates—animals with backbones—to occupy nearly every habitat on Earth. Despite the platypus's mixed characteristics, biologists eventually classified it as a member of the mammal lineage because, like all other mammals, it has hair on its body and produces milk to nourish its offspring. Today biologists know that it is one of just a few remaining survivors of an early lineage of egg-laying mammals.

In this chapter, we survey the Deuterostomia, a monophyletic lineage of animals that dates to the Paleozoic. The deuterostomes are defined by features of early embryological development and molecular sequence data (see Chapter 29). There are three living phyla of deuterostomes; we briefly consider two phyla of invertebrate deuterostomes before focusing on the Phylum Chordata, which includes a few thousand species of invertebrates as well as nearly 50,000 living species of vertebrates.

30.1 Invertebrate Deuterostomes

Deuterostome body plans have been so modified by evolution that a casual observer would not readily group the two phyla of invertebrate deuterostomes—Echinodermata and Hemichordata—together with the Phylum Chordata. However, embryological and molecular analyses agree that all three are indeed closely related.

Echinoderms Have Secondary Radial Symmetry and an Internal Skeleton

The phylum Echinodermata (*echinos* = spiny; *derma* = skin) includes 6600 species of sea stars, sea urchins, sea cucumbers, brittle stars, and sea lilies. These slow moving or sessile, bottom-dwelling animals are important herbivores and predators in shallow coastal waters and, paradoxically, the ocean depths. The phylum was diverse in the Paleozoic, but only a remnant of that fauna remains. Living species vary in size from less than 1 cm to more than 50 cm in diameter.

Echinoderms develop from a bilaterally symmetrical, free-swimming larva. As a larva develops, it assumes a secondary radial symmetry, often organized around five rays or "arms" **(Figure 30.2).** Many echinoderms have an *oral surface,* with the mouth facing the substrate, and an *aboral surface* facing in the opposite direction. Virtually all echinoderms have an internal skeleton made of calcium-stiffened *ossicles* that develop from mesoderm. In some groups, fused ossicles form a rigid container called a *test.* In most, spines or bumps project from the ossicles.

The internal anatomy of echinoderms is unique among animals **(Figure 30.3).** They have a well-defined coelom and a complete digestive system (see Figure 30.3a), but no excretory or respiratory systems, and most have only a minimal circulatory system. In many, gases are exchanged and metabolic wastes eliminated through projections of the epidermis and peritoneum near the base of the spines. Given their radial symmetry, there is no head or central brain; the nervous system is organized around nerve cords that encircle the mouth and branch into the rays. Sensory cells are abundant in the skin.

Echinoderms move using a unique system of fluid-filled canals, the *water vascular system* (see Figure 30.3b). In a sea star, for example, water enters the system through the *madreporite,* a sievelike plate on the aboral surface. A short tube connects it to the *ring canal,* which surrounds the esophagus. The ring canal branches into five *radial canals* that extend into the arms. Each radial canal is connected to numerous *tube feet* that protrude through holes in the plates. Each tube foot has a mucus-covered, suckerlike tip and a small muscular bulb, the *ampulla,* that lies inside the body. When an ampulla contracts, fluid is forced into the tube foot, causing it to lengthen and attach to the substrate (see Figure 30.3c). The tube foot then contracts, pulling the animal along. As the tube foot shortens, water is forced back into the ampulla, and the tube foot releases its grip on the substrate. The tube foot can then take another step forward, reattaching to the substrate. Although each tube foot has limited strength, the coordinated action of hundreds or even thousands of them is so strong that they can hold an echinoderm to a substrate even against strong wave action.

Echinoderms have separate sexes, and most reproduce by releasing gametes into the water. Radial cleavage is so clearly apparent in the transparent eggs of some sea urchins that they are commonly used for demonstrations of cleavage in introductory biology laboratories. A few echinoderms also reproduce asexually by splitting in half and regenerating the missing parts; some can regenerate body parts lost to predators.

Echinoderms are divided into six groups, one of which, the sea daisies (Concentricycloidea) was discovered only in 1986. These small, medusa-shaped animals occupy sunken, waterlogged wood in the deep sea. In the following sections, we describe the five other groups, which are more diverse and better known.

Asteroidea. The 1500 species of sea stars (Asteroidea, from *asteroeides* = starlike) live from rocky shorelines to depths of 10,000 m. The body consists of a central disk surrounded by 5 to 20 radiating "arms" (see Figure 30.2a), with the mouth centered on the oral surface. The ossicles of the endoskeleton are not fused, permitting flexibility of the arms and disk. Small pincers, **pedicellariae,** at the base of short spines remove debris that falls onto the animal's surface (see Figure 30.3c). Many sea stars feed on invertebrates and small fishes. Species that consume bivalve mollusks pry apart the two valves using their tube feet and slip their everted stomachs between the bivalve's shells. The stomach secretes digestive enzymes that dissolve the mollusk's tissues. Some sea stars are destructive predators of corals, endangering many reefs.

Ophiuroidea. The 2000 species of brittle stars and basket stars (Ophiuroidea, from *ophioneos* = snakelike) occupy roughly the same range of habitats as sea stars. Their bodies have a well-defined central disk and slender, elongate arms that are sometimes branched (see Figure 30.2b). Ophiuroids can crawl fairly swiftly across substrates by moving their arms in coordinated fashion. As their common name implies, the arms are delicate and easily broken, an adaptation that allows them to escape from predators with only minor losses. Brittle stars feed on small prey, suspended plankton, or detritus that they extract from muddy deposits.

Echinoidea. The 950 species of sea urchins and sand dollars (Echinoidea, "having spines") lack arms altogether (see Figure 30.2c). Their ossicles are fused into solid tests, which provide excellent protection but restrict flexibility. The test is spherical in sea urchins and flattened in sand dollars. Five rows of tube feet, used primarily for locomotion, emerge through pores in the test. Most echinoids have movable spines, some with poison glands; a jab from certain tropical species can cause severe pain and inflammation to a careless swimmer. Echinoids graze on algae and other organisms that cling to marine surfaces. In the center of an

Figure 30.2
Echinoderm diversity. Echinoderms exhibit secondary radial symmetry, usually organized as five rays around an oral-aboral axis.

a. Asteroidea: This sea star *(Fromia milleporella)* lives in the intertidal zone.

b. Ophiuroidea: A brittle star *(Ophiothrix swensonii)* perches on a coral branch.

c. Echinoidea: A sea urchin *(Strongylocentrotus purpuratus)* grazes on algae.

d. Holothuroidea: A sea cucumber *(Cucumaria miniata)* extends its tentacles, which are modified tube feet, to trap particulate food.

e. Crinoidea: A feather star *(Himerometra robustipinna)* feeds by catching small particles with its numerous arms.

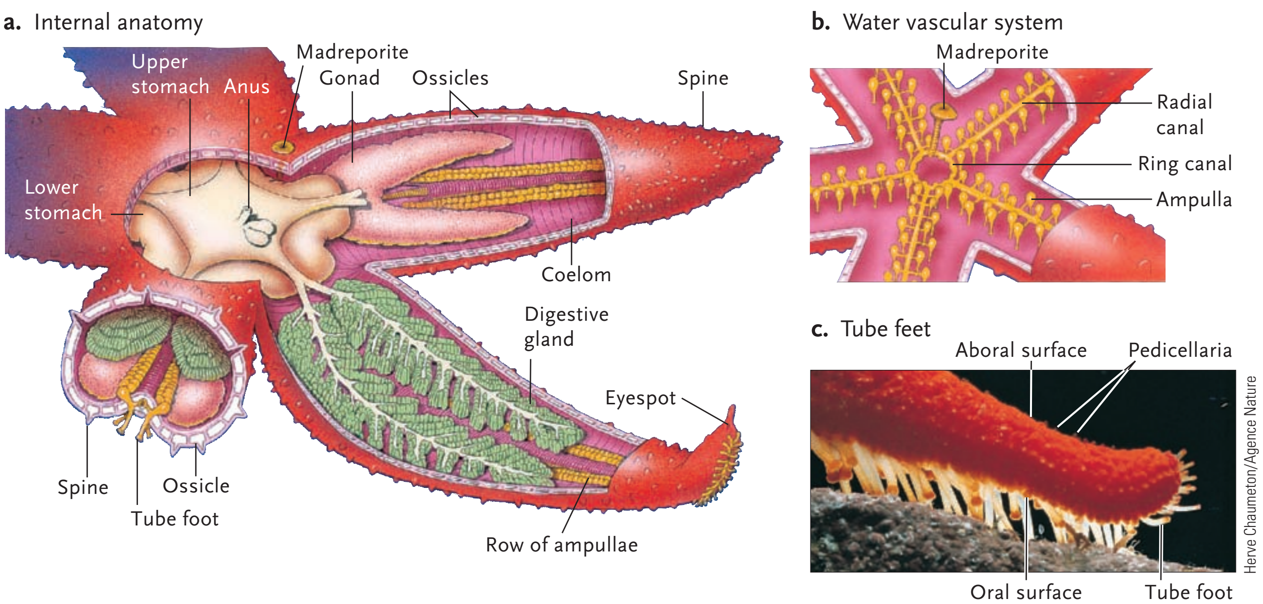


Figure 30.3
Internal anatomy of a sea star. (a) The coelom is well developed in echinoderms, as illustrated by this cutaway diagram of a sea star. **(b)** The water vascular system, unique in the animal kingdom, operates the tube feet **(c),** which are responsible for locomotion. Note the pedicellariae on the upper surface of the sea star's arm **(c).**

urchin's oral surface is a five-part nipping jaw that is controlled by powerful muscles. Some species damage kelp beds, disrupting the habitat of young lobsters and other crustaceans. But echinoid ovaries are a delicacy in many countries, making these animals a prized natural resource.

Holothuroidea. The 1500 species of sea cucumbers (Holothuroidea, from *holothourion* = water polyp) are elongate animals that lie on their sides on the ocean bottom (see Figure 30.2d). Although they have five rows of tube feet, their endoskeleton is reduced to widely separated microscopic plates. The body, which is elongated along the oral-aboral axis, is soft and fleshy, with a tough, leathery covering. Modified tube feet form a ring of tentacles around the mouth, which points to the side or upward. Some species secrete a mucous net that traps plankton or other food particles. The net and tentacles are inserted into the mouth where the net and trapped food are ingested. Other species extract food from bottom sediments. Many sea cucumbers exchange gases through an extensively branched *respiratory tree* that arises from the rectum, the part of the digestive system just inside the anus at the aboral end of the animal. A well-developed circulatory system distributes oxygen and nutrients to tissues throughout the body.

Crinoidea. The 600 living species of sea lilies and feather stars (Crinoidea, from *krinon* = lily) are the surviving remnants of a fauna that was diverse and abundant 500 million years ago (see Figure 30.2e). Most species occupy marine waters of medium depth. The central disk and mouth point upward rather than toward the substrate. Between five and several hundred branched arms surround the disk; new arms are added as a crinoid grows larger. The branches of the arms are covered with tiny mucus-coated tube feet, which trap suspended microscopic organisms. The sessile sea lilies have the central disk attached to a flexible stalk that can reach a meter in length. Adult feather stars can swim or crawl weakly, attaching temporarily to substrates.

Acorn Worms Use Gill Slits and a Pharynx to Acquire Food and Oxygen

The 80 species of acorn worms (phylum Hemichordata, from *hemi* = half and *chorda* referring to the phylum Chordata) are sedentary marine animals that live in U-shaped tubes or burrows in coastal sand or mud. Their soft bodies, which range from 2 cm to 2 m in length, are organized into an anterior proboscis, a tentacled collar, and an elongate trunk **(Figure 30.4).** They use their muscular, mucus-coated proboscis to construct burrows and trap food particles. Acorn worms also have pairs of **gill slits** in the pharynx, the part of the digestive system just posterior to the mouth. Beating cilia create a flow of water, which enters the pharynx through the mouth and exits through the gill slits. As water passes through, suspended food is trapped and shunted into the digestive system, and gases are exchanged across the partitions between gill slits. The coupling of feeding and respiration—as well as a dorsal nerve cord—reflects the close evolutionary relationship between hemichordates and chordates, the phylum that we consider next.

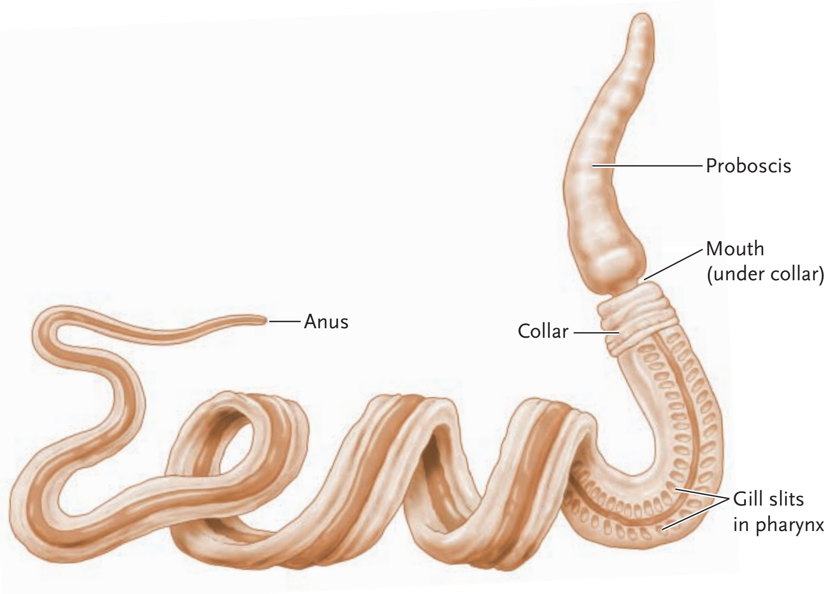


Figure 30.4 Phylum Hemichordata. Acorn worms draw food- and oxygen-laden water in through the mouth and expel it through gill slits in the anterior region of the trunk.

Study Break

1. What organ system is unique to echinoderms, and what is its function?
2. How does a perforated pharynx enable hemichordates to acquire food and oxygen from seawater?

30.2 Overview of the Phylum Chordata

The phylum Chordata contains three subphyla: two lineages of invertebrates, Urochordata and Cephalochordata, and a diverse lineage of vertebrates, Vertebrata.

Key Morphological Innovations Distinguish Chordates from Other Deuterostome Phyla

Chordates are distinguished from other deuterostomes by a set of key morphological innovations: a *notochord, segmental muscles in the body wall and tail,* a *dorsal hollow nerve chord,* and a *perforated pharynx* **(Figure 30.5).** These structures foster higher levels of activity, unique modes of aquatic locomotion, and more efficient feeding and oxygen acquisition.

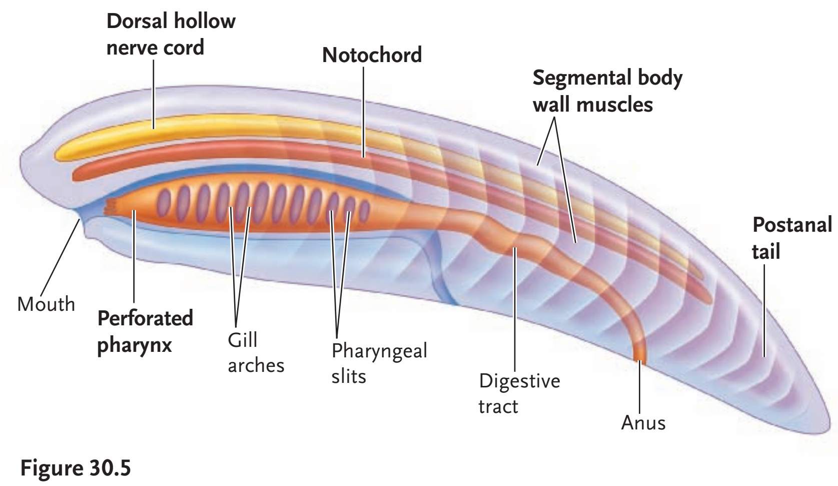


Figure 30.5
Diagnostic chordate characters. Chordates have a notochord; a muscular postanal tail; a segmental body wall and tail muscles; a dorsal, hollow nerve cord; and a perforated pharynx.

Notochord. Early in chordate development, mesoderm that is dorsal to the developing digestive system forms a **notochord** (*noton* = the back; *chorda* = string). This flexible rod, constructed of fluid-filled cells surrounded by tough connective tissue, supports the embryo from head to tail. The notochord forms the skeleton of invertebrate chordates. Their body wall muscles are anchored to the notochord, and when these muscles contract, the notochord bends, but it does not shorten. As a result, the chordate body swings left and right during locomotion, propelling the animal forward; unlike annelids and other nonchordate invertebrates, the chordate body does not shorten when the animal is moving. Remnants of the notochord persist as gelatinous disks in the backbones of adult vertebrates.

Segmental Body Wall and Tail Muscles. Chordates evolved in water, and they swim by contracting segmentally arranged blocks of muscles in the body wall and tail. The chordate tail, which is posterior to the anus, provides much of the propulsion in aquatic species. Segmentation allows each muscle block to contract independently; waves of contractions pass down one side of the animal and then down the other, sweeping the body and tail back and forth in a smooth and continuous movement.

Dorsal Hollow Nerve Cord. The central nervous system of chordates is a hollow nerve cord on the dorsal side of the animal (see Section 48.3). By contrast, most nonchordate invertebrates have solid nerve cords on the ventral side. In vertebrates, an anterior enlargement of the nerve cord forms a brain; in invertebrates, an anterior concentration of nervous system tissue is usually described as a *ganglion*.

Perforated Pharynx. The chordate pharynx, the part of the digestive system just posterior to the mouth, typically contains perforations or slits during some stage of the life cycle. These paired openings originated as exit holes for water that carried particulate food into the mouth, allowing chordates to gather large quantities of food. Invertebrate chordates also collect oxygen and release carbon dioxide across the walls of the pharynx. In fishes, **gill arches**, the supporting structures between the slits in the pharynx, are often sites of gas exchange, allowing animals to extract oxygen efficiently from the water. Invertebrate chordates and fishes retain a perforated pharynx throughout their lives. In most air-breathing vertebrates, the slits are present only during embryonic development and in larvae.

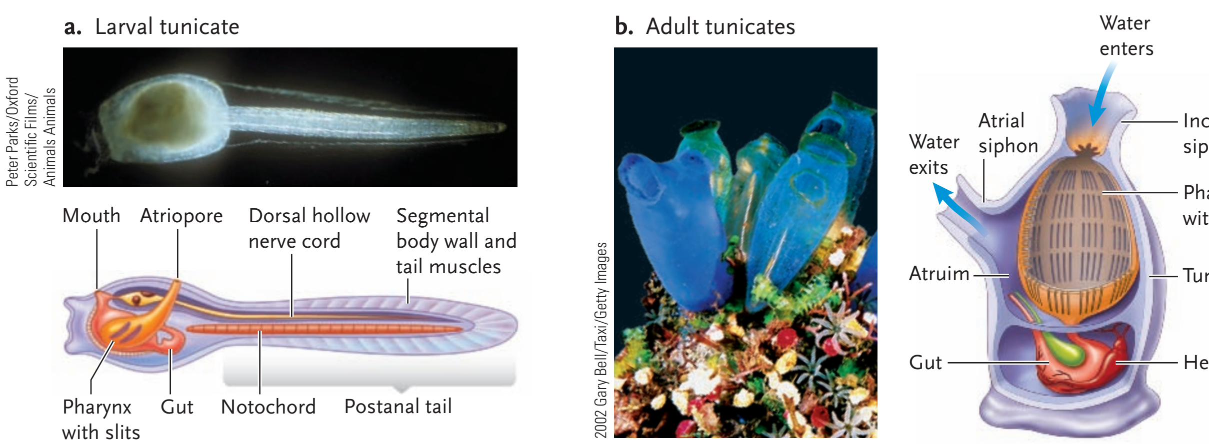


Figure 30.6
Urochordates. **(a)** A tadpolelike tunicate larva metamorphoses into **(b)** a sessile adult; shown here is *Rhopalaea crassa*. After a larva attaches to a substrate at its anterior end, the tail, notochord, and most of the nervous system are recycled to form new tissues. Slits in the pharynx multiply, the mouth becomes the incurrent siphon, and the atriopore becomes the atrial siphon.

Invertebrate Chordates Are Small, Marine Suspension Feeders

Two subphyla of invertebrate chordates exhibit the basic chordate body plan in its simplest form.

Subphylum Urochordata. The 2500 species of tunicates, sometimes called sea squirts (subphylum Urochordata, from *oura* = tail), float in surface waters or attach to substrates in shallow marine habitats. The sessile adults of many species secrete a gelatinous or leathery "tunic" around their bodies and squirt water through a siphon when disturbed; adults grow to several centimeters **(Figure 30.6).** In the most common group of sea squirts (Ascidiacea), the swimming larvae possess the defining chordate features. Larvae eventually attach to substrates and transform into sessile adults. During metamorphosis, they lose most traces of the notochord, dorsal nerve cord, and tail, and their basketlike pharynx enlarges. In adults, beating cilia pull water into the pharynx through an **incurrent siphon.** A mucous net traps particulate food, which is carried, with the mucus, to the gut. Water passes through the pharyngeal slits, enters a chamber called the **atrium,** and is expelled—along with digestive wastes and carbon dioxide—through the **atrial siphon.** Oxygen is absorbed across the walls of the pharynx.

Subphylum Cephalochordata. The 28 lancelet species (subphylum Cephalochordata, from *kephale* = head) occupy warm, shallow marine habitats where they lie mostly buried in sand **(Figure 30.7).** Although generally sedentary, they have well-developed body wall muscles and a prominent notochord. Most species are included in the genus *Branchiostoma* (formerly *Amphioxus*). Lancelet bodies, which are 5 to 10 cm long, are pointed at both ends like the double-edged surgical tools for which they are named. Adults have light receptors on the head as well as chemical sense organs on tentacles that grow from the **oral hood.** Lancelets use cilia to draw food-laden water through hundreds of pharyngeal slits; water flows into the atrium and is expelled through the **atriopore.** Most gas exchange occurs across the skin.

Vertebrates Possess Several Unique Tissues, Including Bone and Neural Crest

The most distinctive anatomical characteristic of the subphylum Vertebrata is an internal skeleton that provides structural support for muscles and protection for the nervous system and other organs. The skeleton and the muscles attached to it enable most vertebrates to move rapidly through the environment. A vertebrate's skeleton is composed of many separate, bony elements. Indeed, vertebrates are the only animals that have **bone,** a connective tissue in which living cells secrete the mineralized matrix that surrounds them (see Figure 36.5d). The **vertebral column,** made up of individual **vertebrae,** surrounds and protects the dorsal nerve cord, and a bony **cranium** surrounds the brain. The cranium, vertebral column, ribs, and sternum (breastbone) make up the **axial skeleton.** Most vertebrates also have a **pectoral girdle** anteriorly and a **pelvic girdle** posteriorly that attach bones in the fins or limbs to the axial skeleton. Bones of the two girdles and the appendages constitute the **appendicular skeleton.** One vertebrate lineage, Chondrichthyes, has lost its bone over evolutionary time; its skeleton is made of cartilage, a dense but flexible connective tissue that is often a developmental precursor of bone (see Section 36.2).

Vertebrates also possess a unique cell type, **neural crest,** which is distinct from endoderm, mesoderm, and ectoderm. Neural crest cells arise next to the developing nervous system, but later migrate throughout a vertebrate's body. They ultimately contribute to many uniquely vertebrate structures, including parts of the cranium, teeth, sensory organs, cranial nerves, and the medulla (that is, the interior part) of the adrenal glands.

Finally, the brains of vertebrates are much larger and more complex than those of invertebrate chordates.

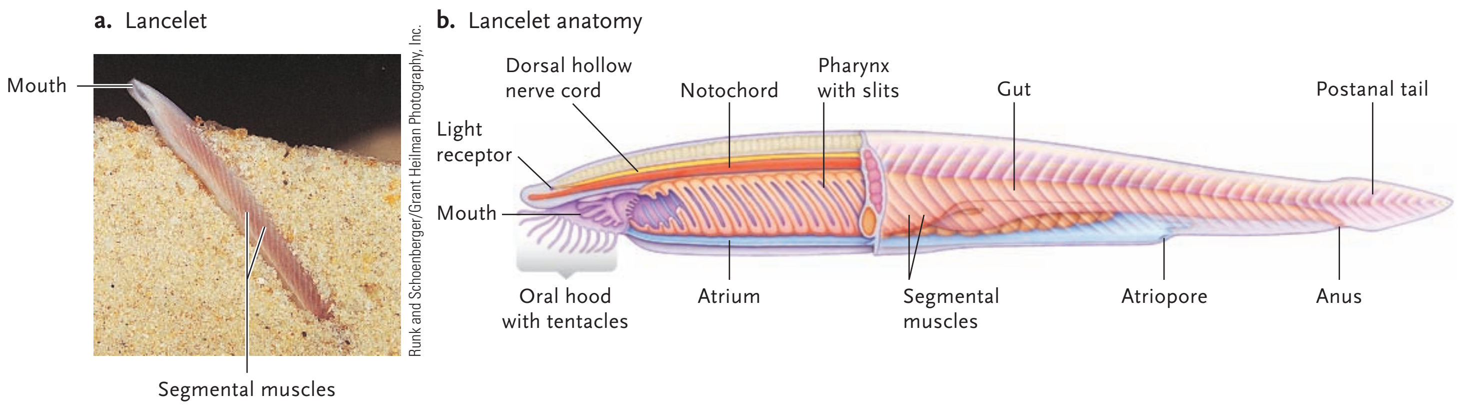


Figure 30.7 Cephalochordates. **(a)** The unpigmented skin of adult lancelets reveals their segmental body wall muscles. A cutaway view **(b)** illustrates their internal anatomy.

Moreover, the vertebrate brain is divided into three regions—the forebrain, midbrain, and hindbrain—each of which governs distinct nervous system functions (see Section 38.1).

Study Break

1. On a field trip to a lake, a college student captures a worm-shaped animal with segmental body wall muscles. While examining the specimen in laboratory the following day, she determines that the main nerve cord runs along the ventral side of the animal. Is this animal a chordate?
2. What structures distinguish vertebrates from invertebrate chordates?

30.3 The Origin and Diversification of Vertebrates

Biologists use embryological, molecular, and fossil evidence to trace the origin of vertebrates and to chronicle their evolutionary diversification.

Vertebrates Probably Arose from a Cephalochordate-Like Ancestor through the Duplication of Genes That Regulate Development

Molecular sequence studies suggest that vertebrates are more closely related to cephalochordates than to urochordates. The evolution of vertebrates from a cephalochordate-like ancestor was marked by the emergence of neural crest, bone, and other typically vertebrate traits. What genetic changes were responsible for these remarkable developments? Biologists now hypothesize that an increase in the number of homeotic—structure determining—genes may have made the development of more complex anatomy possible. (Homeotic genes are described further in Sections 22.6 and 48.6.)

In animals, one group of homeotic genes, the *Hox* genes, influences the three-dimensional shape of the animal and the locations of important structures—such as eyes, wings, and legs—particularly along the head to tail axis of the body. *Hox* genes are arranged on the chromosomes in a particular order, forming what biologists call the *Hox* gene complex (see Section 22.6). Each gene in the complex governs the development of particular structures. Animal groups with the simplest structure,

Figure 30.8
***Hox* genes and the evolution of vertebrates.** The *Hox* genes in different animals appear to be homologous, indicated here by their color and position in the complex. Vertebrates have many more individual *Hox* genes than most invertebrates do, and the entire *Hox* gene complex was duplicated in the vertebrate lineage.

such as cnidarians, have two *Hox* genes. Those with more complex anatomy, such as insects, have 10. Chordates have as many as 13 or 14. Thus, lineages with many *Hox* genes generally have more complex anatomy than do those with fewer *Hox* genes.

Molecular analyses also reveal that the entire *Hox* gene complex was duplicated several times in the evolution of vertebrates, producing multiple copies of all its genes **(Figure 30.8).** The cephalochordate *Branchiostoma* has just one *Hox* gene complex, but the most primitive living vertebrates, the jawless hagfishes described later, have two. All vertebrates that possess jaws, a derived characteristic, have at least four sets, and some fishes have as many as seven. Evolutionary developmental biologists hypothesize that the duplication of *Hox* genes and other tool-kit genes allowed the evolution of new structures: while the original copies of these genes maintained their ancestral functions, the duplicate copies assumed *new* functions, directing the development of novel structures, such as the vertebral column and jaws.

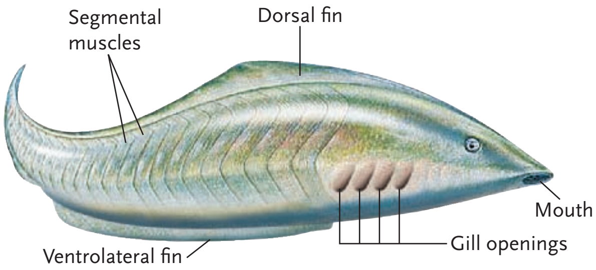


Figure 30.9 An early vertebrate. *Myllokunmingia*, one of the earliest vertebrates yet discovered, had no bones; it was about 3 cm long.

Early Vertebrates Diversified into Numerous Lineages with Distinctive Adaptations

The oldest known vertebrate fossils were discovered in the late 1990s, when scientists in China described several species from the early Cambrian period, about 550 million years ago. Both *Myllokunmingia* and *Haikouichthys* were fish-shaped animals about 3 cm long **(Figure 30.9).** In both species the brain was surrounded by a cranium, which, in these cases, was formed of fibrous connective tissue or cartilage. They also had segmental body wall muscles and fairly well-developed fins, but neither shows any evidence of bone.

The early vertebrates gave rise to numerous descendants, which varied greatly in anatomy, physiology, and ecology. New feeding mechanisms and locomotor structures were often crucial to their success. Today, vertebrates occupy nearly every habitat and feed on virtually all other organisms. Here we briefly introduce the major vertebrate lineages **(Figure 30.10).**

Although biologists use four key morphological innovations—a cranium, vertebrae, bone, and neural crest cells—to identify vertebrates, these structures did not arise all at once. Instead, they appeared somewhat independently of one another as new groups arose. Some researchers and textbooks present a phylogeny and classification that places the "vertebrates" (animals that have vertebrae) within a larger lineage called the "craniates" (animals that have a cranium). But only one small group, the hagfishes (Myxinoidea, described later), has a cranium but no vertebrae, and some recent molecular analyses do not support its separation from the other vertebrates. Thus, for the sake of simplicity, we describe organisms that possessed any of the four key innovations as "vertebrates."

Several groups of early jawless vertebrates are described as *agnathans* (*a* = not; *gnathos* = jawed), but they do not form a monophyletic group. Although most became extinct in the Paleozoic era, two ancient lineages, Myxinoidea and Petromyzontoidea, still live today. All other vertebrates possess moveable jaws; they are members of the monophyletic lineage **Gnathostomata** ("jawed mouth"). The first jawed fishes, the Acanthodii and Placodermi, are now extinct, but several other lineages of jawed fishes are still abundant in aquatic habitats: the Chondrichthyes includes fishes with cartilaginous skeletons, such as sharks and skates; the Actinopterygians and Sarcopterygians comprise the bony fishes, which have bony endoskeletons. All jawless vertebrates and jawed fishes are restricted to aquatic habitats, and they use gills to extract oxygen from the water that surrounds them.

The Gnathostomata also includes the monophyletic lineage **Tetrapoda** (*tetra* = four; *pod* = foot); most tetrapods use four limbs for locomotion. Many tetrapods are semiterrestrial or terrestrial, although some, like sea turtles and porpoises, have secondarily returned to aquatic habitats. Adult tetrapods generally use air-breathing lungs for gas exchange. Within the Tetrapoda, one lineage, the amphibians, includes animals, such as frogs and salamanders, that typically need standing water to complete their life cycles. Another lineage, the **Amniota,** comprises animals with specialized eggs that can develop on land. Shortly after their appearance, the amniotes diversified into three lineages: one is ancestral to living mammals; another to the living turtles; and a third to lizards, snakes, alligators, and birds. We consider the detailed evolutionary history of the amniotes in Section 30.7.

Study Break

1. How do the *Hox* genes of vertebrates differ from those of cephalochordates?
2. Which of the taxonomic groups Amniota, Gnathostomata, and Tetrapoda includes the largest number of species? Which includes the fewest?

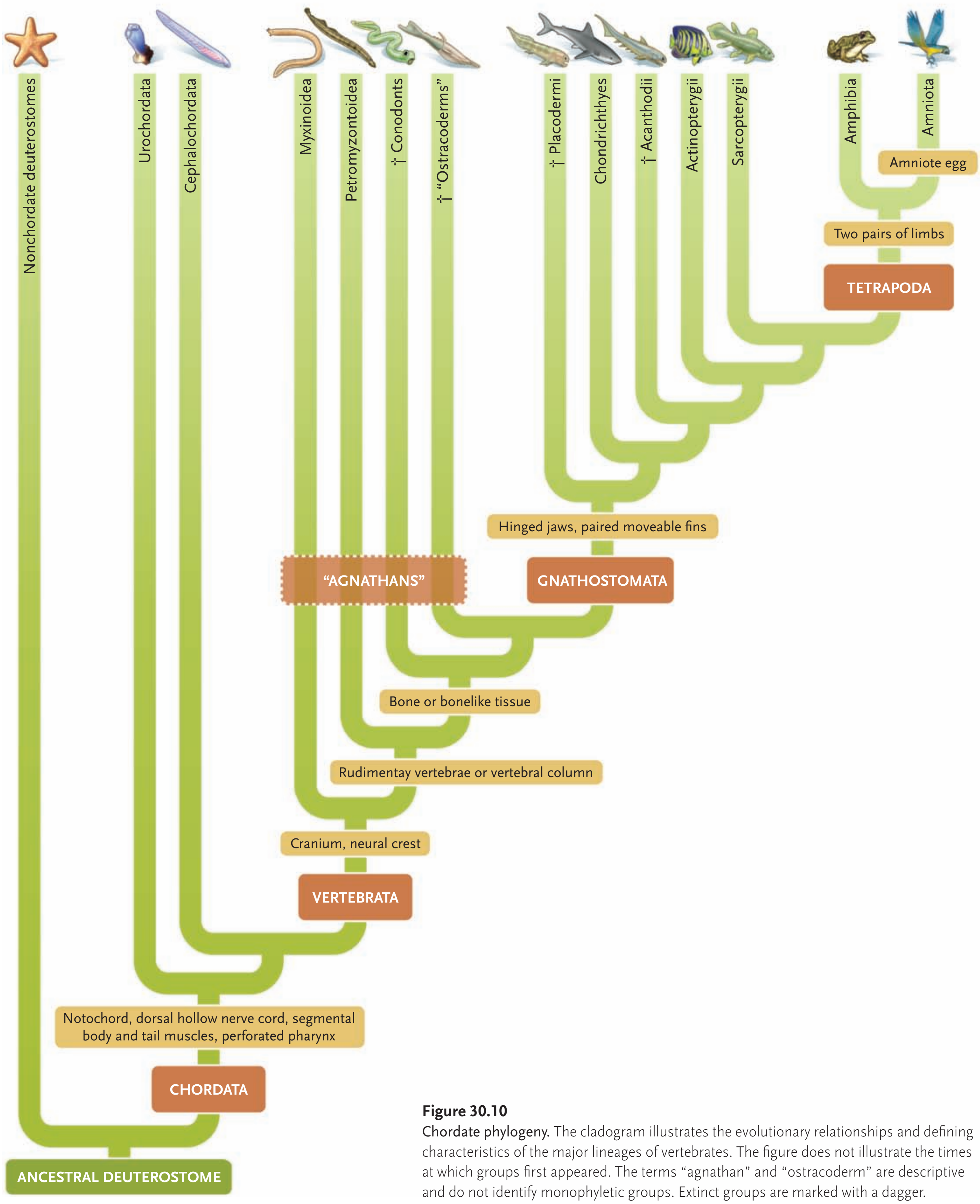
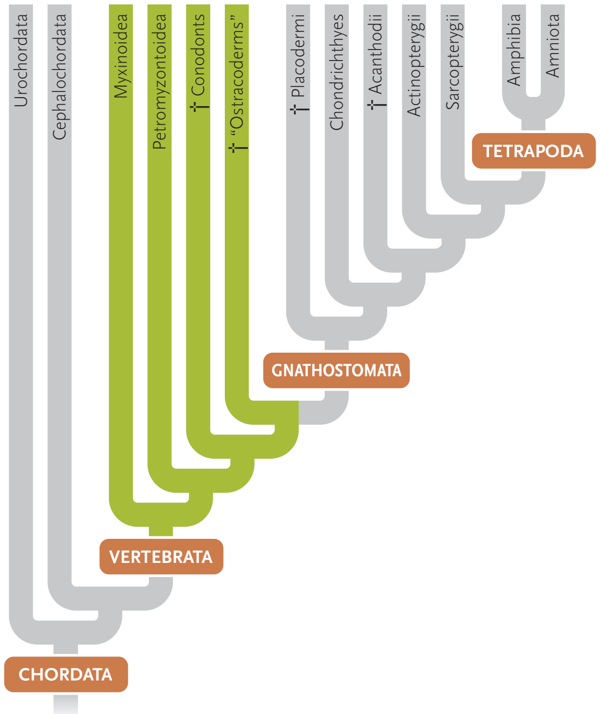


Figure 30.10
Chordate phylogeny. The cladogram illustrates the evolutionary relationships and defining characteristics of the major lineages of vertebrates. The figure does not illustrate the times at which groups first appeared. The terms "agnathan" and "ostracoderm" are descriptive and do not identify monophyletic groups. Extinct groups are marked with a dagger.

30.4 Agnathans: Hagfishes and Lampreys, Conodonts and Ostracoderms



Lacking jaws, most of the earliest vertebrates used a muscular pharynx to suck edible tidbits into their mouths. The two living groups of agnathans as well as species that flourished in the Paleozoic vary greatly in size and shape as well as in the number of vertebrate characters they possess.

Hagfishes and Lampreys Are the Living Descendants of Ancient Agnathan Lineages

Two apparently separate lineages of jawless vertebrates, hagfishes (Myxinoidea) and lampreys (Petromyzontoidea), still live today. Both have skeletons composed entirely of cartilage. Although scientists have found no fossilized hagfishes or lampreys from the early Paleozoic era, the absence of jaws and bone in their living descendants suggests that their lineages arose early in vertebrate history, before the evolution of bone. Hagfishes and lampreys have a well-developed notochord, but no true vertebrae or paired fins, and their skin has no scales. Individuals grow to a maximum length of about 1 m **(Figure 30.11)**.

The axial skeleton of the 60 living species of hagfishes includes only a cranium and a notochord; it has no specialized structures surrounding the dorsal nerve cord. Some biologists do not even include hagfishes among the Vertebrata, because they lack any sign of vertebrae. Hagfishes are marine scavengers that burrow in sediments on continental shelves. They feed on invertebrate prey and on dead or dying fishes. In response to predators, they secrete an immense quantity of sticky, noxious slime; when no longer threatened, a hagfish ties itself into a knot and wipes the slime from its body. Hagfish life cycles are simple and lack a larval stage.

The 40 or so living species of lampreys have traces of an axial skeleton. Their notochord is surrounded by dorsally pointing cartilages that partially cover the nerve cord; many biologists suspect that this arrangement may reflect an early stage in the evolution of the vertebral column. Most lamprey species are parasitic as adults. They have a circular mouth surrounded by a sucking disk with which they attach to a fish or other vertebrate host; they feed on a host's body fluids after rasping through its skin. In most species, sexually mature adults migrate from the ocean or a lake to the headwaters of a stream, where they lay eggs and then die. Their suspension-feeding larvae, which resemble adult cephalochordates, burrow into mud and develop for as long as seven years before undergoing metamorphosis and migrating to the sea or a lake to live as parasitic adults.

Conodonts and Ostracoderms Were Early Jawless Vertebrates with Bony Structures

Mysterious bonelike fossils, most less than 1 mm long, have long been known in oceanic rocks dating from the early Paleozoic era through the early Mesozoic era. Called **conodont** ("cone tooth") elements, these abun-

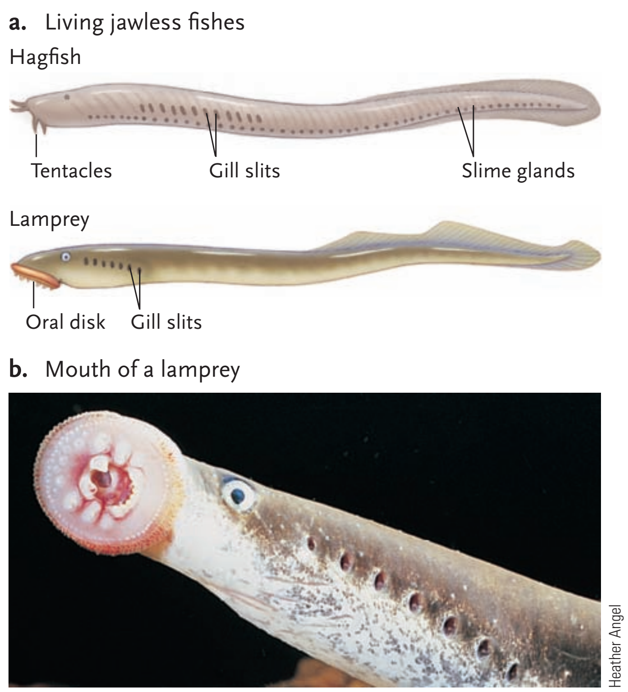


Figure 30.11
Living agnathans. **(a)** Two groups of jawless fishes, hagfishes and lampreys, survive today. **(b)** Lampreys use a toothed oral disk to attach to a host and feed on its blood and soft tissues.

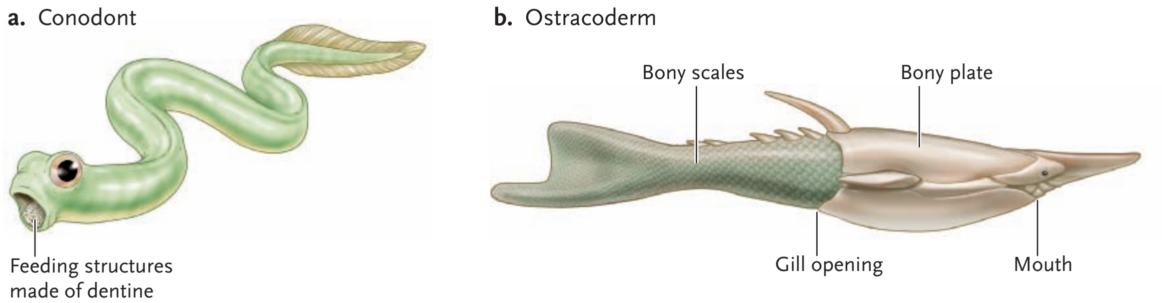


Figure 30.12

Extinct agnathans. **(a)** Conodonts were elongate, soft-bodied animals with bonelike feeding structures in the mouth and pharynx. **(b)** *Pteraspis*, an ostracoderm, had large bony plates on its head and small bony scales on the rest of its body; it was about 6 cm long.

dant fossils were once described as the support structures of marine algae or the feeding structures of ancient invertebrates. However, recent analyses of their mineral composition reveal that they were made of dentine, a bonelike component of vertebrate teeth. In the 1980s and 1990s, several research teams discovered fossils of intact conodont animals with these elements in place.

Conodonts were elongate, soft-bodied animals; most were 3 to 10 cm long. They had a notochord, cranium, segmental body wall muscles, and large, moveable eyes **(Figure 30.12a).** The conodont elements at the front of the mouth were forward pointing, hook-shaped structures that apparently functioned to collect food; those in the pharynx were stouter, suitable for crushing items that had been consumed. Paleontologists now classify conodonts as vertebrates—the earliest vertebrates with bonelike structures.

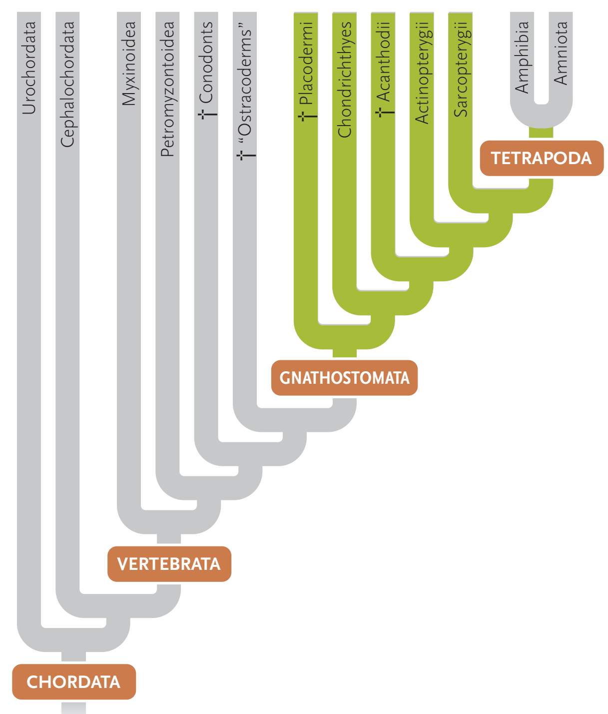
An assortment of jawless fishes, representing several evolutionary lineages and collectively called **ostracoderms** (*ostrakon* = shell), were abundant from the Ordovician through the Devonian periods **(Figure 30.12b).** Like their invertebrate chordate ancestors, ostracoderms used their pharynx to extract small food particles from mud and water. However, the ostracoderms' muscular pharynx enabled them to *suck* mud and water into their mouths, providing a much stronger flow than the cilia-driven currents of invertebrate chordates. The greater flow rate allowed ostracoderms to collect food more rapidly. It also supported a larger body size: although most were much smaller, some ostracoderms reached a length of 2 m.

The skin of ostracoderms was heavily armored with plates and scales formed of bone. Although some ostracoderms had paired lateral extensions of their bony armor, they could not move them the way living fishes move their paired fins. Ostracoderms lacked a true vertebral column, but they had rudimentary support structures surrounding the nerve cord. They also had other distinctly vertebrate-like characteristics. For example, imprints in the head shields indicate that their brains had the three regions—forebrain, midbrain, and hindbrain—typical of all later vertebrates (see Section 38.1).

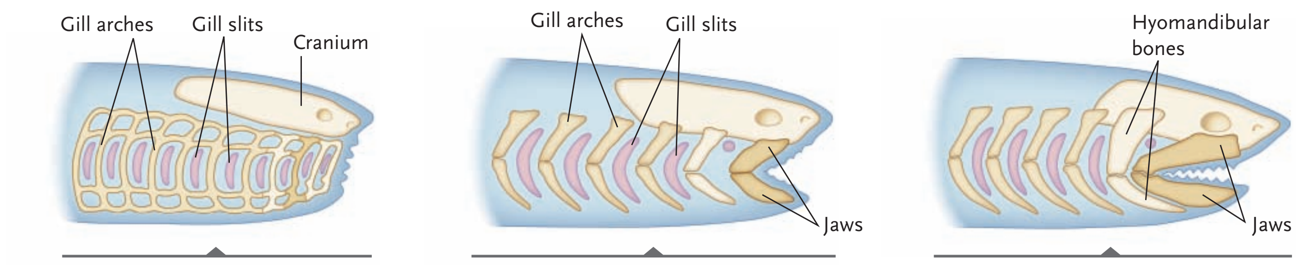
Study Break

1. What characteristics of the living hagfishes and lampreys suggest that their lineages arose very early in vertebrate evolution?
2. What traits in conodonts and ostracoderms are derived relative to those in hagfishes and lampreys?

30.5 Jawed Fishes



The first gnathostomes were jawed fishes. Key derived traits made their feeding and locomotion more efficient than those of their ancestors.



a. Jaws evolved from gill arches in the pharynx of jawless fishes.

b. In early jawed fishes, the upper jaw was firmly attached to the cranium.

c. In later jawed fishes, the jaws were supported by the hyomandibular bones, which were derived from a second pair of gill arches.

Figure 30.13
The evolution of jaws.

Jawed Fishes First Appeared in the Paleozoic Era

The renowned anatomist and paleontologist Alfred Sherwood Romer of Harvard University described the evolution of jaws as "perhaps the greatest of all advances in vertebrate history." Hinged jaws allow vertebrates to grasp, kill, shred, and crush large food items. Some species also use their jaws for defense, for grooming, to construct nests, and to transport their young.

The Origin of Jaws and Fins. Embryological evidence suggests that jaws evolved from paired gill arches in the pharynx of a jawless ancestor **(Figure 30.13).** One pair of ancestral gill arches formed bones in the upper and lower jaws, while a second pair was transformed into the hyomandibular bones that braced the jaws against the cranium. Nerves and muscles of the ancestral suspension-feeding pharynx control and move the jaws.

Innovative locomotor mechanisms have often appeared at roughly the same time as innovative feeding mechanisms in the vertebrate lineage, and many early jawed fishes also had fins. The earliest fins were folds of skin and moveable spines that stabilized locomotion and deterred predators. Moveable fins appeared independently in several lineages, and by the Devonian period, most fishes had unpaired (dorsal, anal, and caudal) and paired (pectoral and pelvic) fins **(Figure 30.14).**

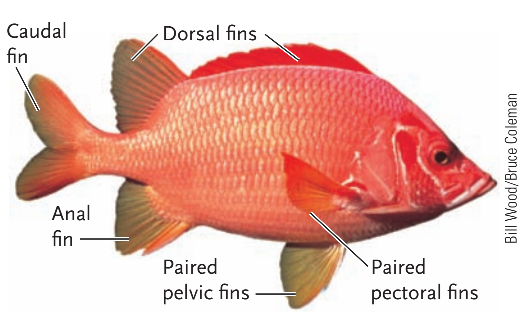


Figure 30.14
Fish fins. Most fishes have both paired and unpaired fins.

Early Jawed Fishes. In two early lineages of jawed fishes, spiny sharks and placoderms, the upper jaw was firmly attached to the cranium (see Figure 30.13b); their inflexible mouths simply snapped open and shut **(Figure 30.15).** Both groups also show evidence of an internal skeleton.

Spiny sharks (Acanthodii, from *akantha* = thorn), which persisted from the late Ordovician through the Permian periods, were less than 20 cm long. Their small, light scales; streamlined bodies; well-developed eyes; large jaws; and numerous teeth suggest that they were fast swimmers and efficient predators. Most had a row of ventral spines and fins with internal skeletal support on each side of the body. Acanthodian anatomy suggests that they are closely related to the bony fishes alive today.

Placoderms (Placodermi, from *plax* = flat surface) appeared in the Silurian and diversified in the Devonian and Carboniferous periods, but they left no direct descendants. Some, like *Dunkleosteus,* reached a length of 10 m. Their bodies were covered with large, heavy plates of bone anteriorly and smaller scales posteriorly. Their jaws had sharp cutting edges, but not separate teeth, and their paired fins had internal skeletons and powerful muscles.

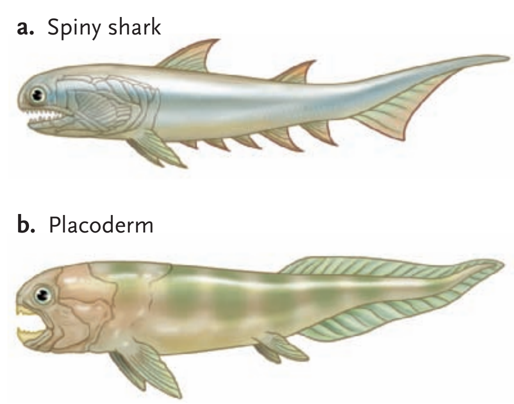


Figure 30.15
Early gnathostomes. (a) *Climatius,* an acanthodian, was small, reaching a total length of about 8 cm. **(b)** The placoderm *Dunkleosteus* was gigantic, sometimes growing to 10 m in length. Some acanthodians had teeth on their jaws, but placoderms had only sharp, cutting edges.

Chondrichthyes Includes Fishes with Cartilaginous Endoskeletons

The 850 living species in the Chondrichthyes (*chondros* = cartilage; *ichthys* = fish) have skeletons composed entirely of cartilage, which is much lighter than bone. The absence of bone in Chondrichthyes is a derived trait, however, because all earlier fishes had bony armor or bony endoskeletons.

Most living chondrichthyans are grouped in the Elasmobranchii, which includes the skates, rays, and sharks; nearly all are marine predators **(Figure 30.16).** Skates and rays are dorsoventrally flattened (see Figure 30.16a). They swim by undulating their enlarged pectoral fins. Most are bottom dwellers that often lie partly buried in sand. They feed on hard-shelled invertebrates, which they crush with massive, flattened teeth. The largest species, the manta ray *(Manta birostris),* which measures 6 m across, feeds on plankton in the open ocean. Some rays have electric organs that stun prey with as much as 200 volts.

Sharks (see Figure 30.16b) are among the ocean's dominant predators. Flexible fins, lightweight skeletons, streamlined bodies, and the absence of heavy body armor allow most sharks to pursue prey rapidly. Their livers often contain **squalene,** an oil that is lighter than water, which increases their buoyancy. The great white shark *(Carcharodon carcharias)* is the largest predatory species, attaining a length of 10 m. The whale shark *(Rhincodon typus),* which grows to 18 m, is the largest fish; it feeds on plankton.

Elasmobranchs—including sharks, skates, and rays—exhibit remarkable adaptations for acquiring and processing food. Their teeth develop in whorls under the fleshy parts of the mouth. New teeth migrate forward as old, worn teeth break free. In many sharks, the upper jaw is loosely attached to the cranium, and it swings down during feeding. As the jaws open, the mouth spreads widely, sucking in large, hard-to-digest chunks of prey, which are swallowed intact. Although the elasmobranch digestive system is short, it includes a corkscrew-shaped **spiral valve,** which slows the passage of material and increases the surface area available for digestion and absorption.

Elasmobranchs also have well-developed sensory systems. In addition to vision and olfaction, they use **electroreceptors** to detect weak electric currents produced by other animals. And their **lateral-line system,** a row of tiny sensors in canals along both sides of the body, detects vibrations in water (see Figure 39.4).

Chondrichthyans exhibit numerous reproductive specializations. Males have a pair of organs, the **claspers,** on the pelvic fins, which help transfer sperm into the female's reproductive tract. Fertilization occurs internally. In many species, females produce yolky eggs with tough leathery shells (see Figure 30.16c).

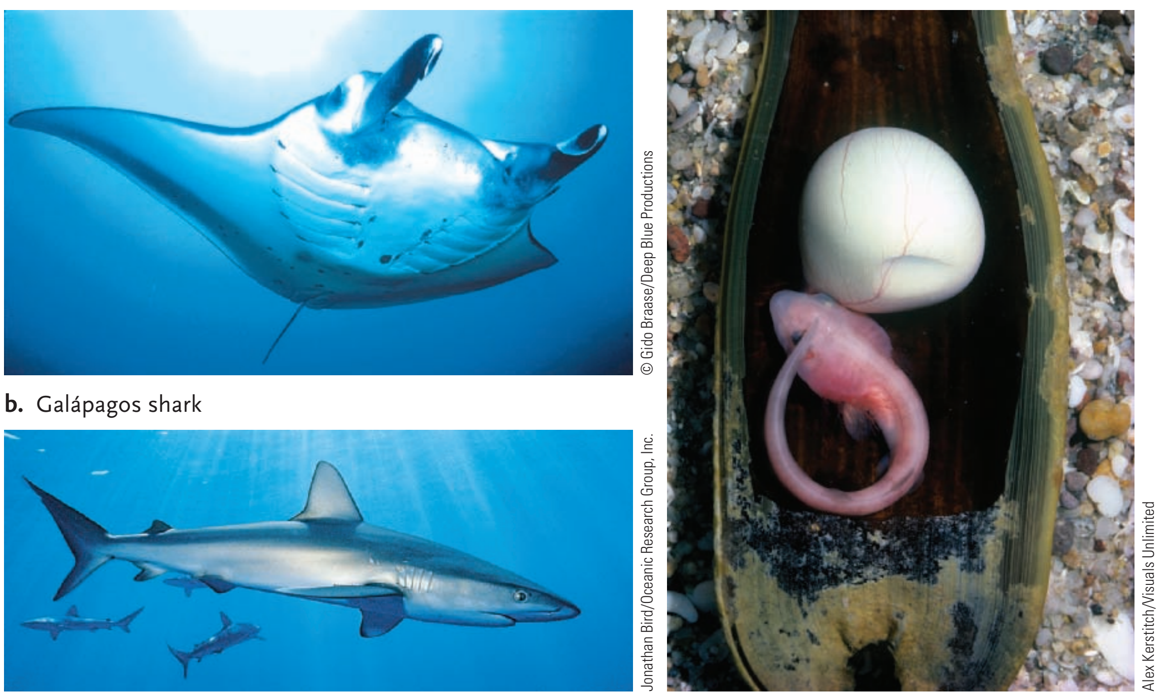


Figure 30.16

Chondrichthyes. **(a)** Skates and rays, like the manta ray *(Manta birostris)*, as well as **(b)** sharks, like the Galápagos shark *(Carcharhinus galapagensis)*, are grouped in the Elasmobranchii. **(c)** Many shark egg cases, like that of the swell shark *(Cephaloscylium ventricosum)*, include a large yolk that nourishes the developing embryo.

Others retain the eggs within the oviduct until the young hatch. A few species nourish young within a uterus.

The Actinopterygii and Sarcopterygii Are Fishes with Bony Endoskeletons

In terms of diversity and sheer numbers, the fishes with bony endoskeletons—a cranium, vertebral column with ribs, and bones supporting their moveable fins—are the most successful of all vertebrates. The endoskeleton provides lightweight support, particularly compared with the heavy bony armor of ostracoderms and placoderms, and enhances their locomotor efficiency. Bony fishes first appeared in the Silurian period and rapidly diversified into two lineages. The ray-finned fishes (Actinopterygii, from *aktis* = ray and *pteron* = wing) have fins that are supported by thin and flexible bony rays. The fleshy-finned fishes (Sarcopterygii, from *sarco* = flesh) have fins that are supported by muscles and an internal bony skeleton. Ray-finned fishes have always been more diverse, and they vastly outnumber the fleshy-finned fishes today. The 21,000 living species of bony fishes occupy nearly every aquatic habitat and represent more than 95% of living fish species. Adults range from 1 cm to more than 6 m in length.

Bony fishes have numerous adaptations that increase their swimming efficiency. In many modern ray-finned fishes, a gas-filled **swim bladder** serves as a hydrostatic organ that increases buoyancy (see Figure 30.18a). The swim bladder is derived from an ancestral air-breathing lung that allowed early actinopterygians to gulp air, supplementing their gill respiration in aquatic habitats where dissolved oxygen concentration was low. The scales of most bony fishes are small, smooth, and lightweight. And their bodies are covered with a protective coat of mucus, which retards bacterial growth and smoothes the flow of water.

Actinopterygii. The most primitive living actinopterygians, sturgeons and paddlefishes, have mostly cartilaginous skeletons **(Figure 30.17a).** These large fishes live in rivers and lakes of the northern hemisphere. Sturgeons feed on detritus and invertebrates; paddlefish consume plankton. Gars and bowfins are remnants of a more recent radiation **(Figure 30.17b).** They occur only in the eastern half of North America, where they feed on fishes and other prey. Gars are protected from predators by a heavy coat of bony scales.

Teleosts, the latest radiation of Actinopterygii, are the most diverse, successful, and familiar bony fishes. Evolution has produced a wide range of body forms **(Figure 30.18).** Teleosts have an internal skeleton made almost entirely of bone. On either side of the head, a flap of the body wall, the **operculum,** covers a chamber that houses the gills. Sensory systems generally include large eyes, a lateral-line system, sound receptors, chemoreceptive nostrils, and taste buds. Variations in jaw structure allow different teleosts to consume plankton, seaweed, invertebrates, or other vertebrates.

Teleosts exhibit remarkable feeding and locomotor adaptations. When some teleosts open their mouths, bones at the front of the jaws swing forward to create a circular opening. Folds of skin extend backward, forming a tube through which they suck food (see Figure 30.18f). Many also have symmetrical caudal fins, posterior to the vertebral column, which provide power for locomotion. And their pectoral fins lie high on the sides of the body, providing fine control over swimming. Some species use their pectoral fins for acquiring food, for courtship, and for care of eggs and young. Some teleosts even use them for crawling on land or gliding in air.

Most marine species produce small eggs that hatch into planktonic larvae. Eggs of freshwater teleosts are generally larger and hatch into tiny versions of the adults. Parents often care for their eggs and young, fanning oxygen-rich water over them, removing fungal growths, and protecting them from predators. Some freshwater species, such as guppies, give birth to live young.

Sarcopterygii. Two groups of fleshy-finned fishes (Sarcopterygii), lobe-finned fishes and lungfishes, are now represented by only eight living species **(Figure 30.19).**

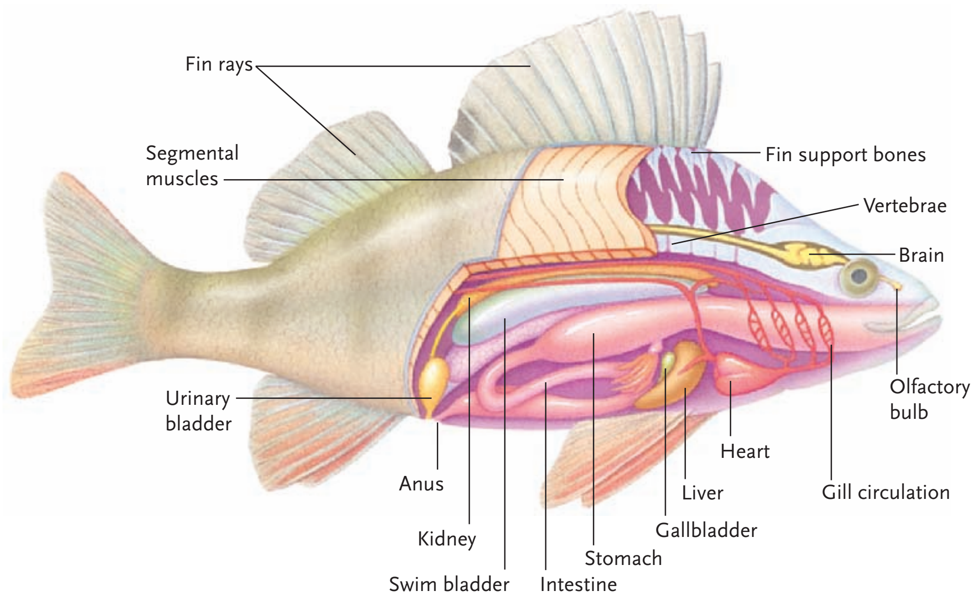
a. Lake sturgeon

b. Long-nosed gar

Ken Lucas/Visuals Unlimited

Patrice Ceisel/© 1986 John G. Shedd Aquarium

Figure 30.17
Primitive actinopterygians. **(a)** A lake sturgeon *(Accipenser fulvescens)* and **(b)** a long-nosed gar *(Lepisosteus osseus)* are living representatives of early actinopterygian radiations.



a. Teleost internal anatomy

Digital Vision/Getty Images, Inc.

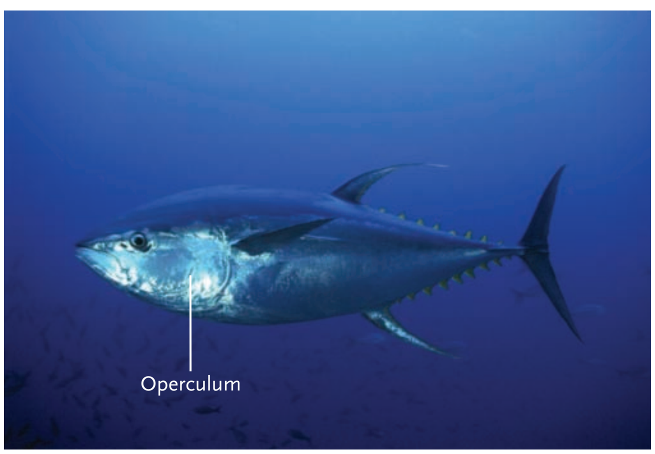
b. Sea horses, like the northern sea horse *(Hippocampus hudsonius)*, use a prehensile tail to hold on to substrates; they are weak swimmers.

Kit Kittle/Corbis

c. The long, flexible body of a spotted moray eel *(Gymnothorax moringa)* can wiggle through the nooks and crannies of a reef.

F. Graner/Peter Arnold, Inc.

d. Flatfishes, like this European flounder *(Platichthys flesus)*, lie on one side and leap at passing prey.



Brandon Cole/Visuals Unlimited

e. Open ocean predators, like the yellowfin tuna *(Thunnus albacares)*, have strong, torpedo-shaped bodies and powerful caudal fins.

Arthur W. Ambler/Photo Researchers, Inc.

f. Kissing Gouramis *(Helostoma temmincki)* extend their jaws into a tube that sucks food into the mouth.

Figure 30.18
Teleost diversity. Although all teleosts share similar internal features, their diverse shapes adapt them to different diets and types of swimming.

a. Coelacanth

b. Australian lungfish

Figure 30.19
Sarcopterygians. **(a)** The coelacanth *(Latimeria chalumnae)* is one of two living species of lobe-finned fishes. **(b)** The Australian lungfish *(Neoceratodus forsteri)* is one of only six living lungfish species.

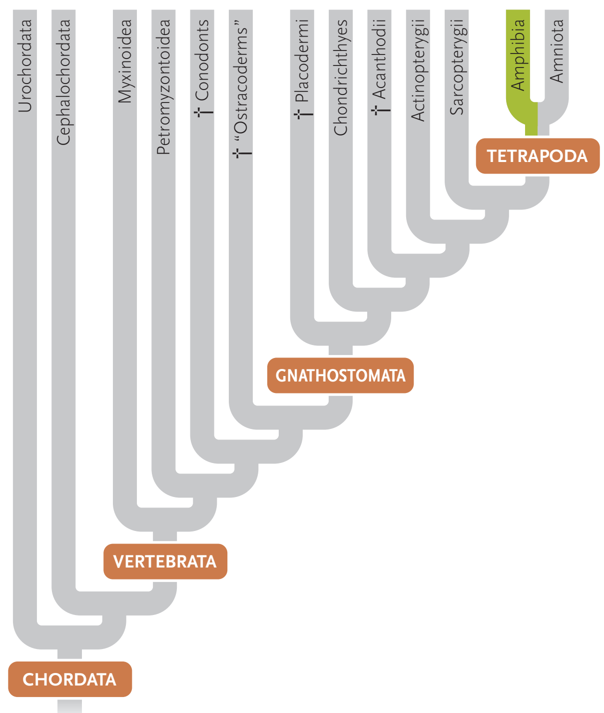
Although lobe-finned fishes were once thought to have been extinct for 65 million years, a living coelacanth *(Latimeria chalumnae)* was discovered in 1938 near the Comoros Islands, off the southeastern coast of Africa. We now know that a population of this meter-long fish lives at depths of 70 to 600 m, feeding on fishes and squid. Remarkably, a second population of coelacanths was discovered in 1998, when a specimen was found in an Indonesian fish market, 10,000 km east of the Comoros population. Based on analyses of its DNA, it is a distinct species *(Latimeria menadoensis)*.

Lungfishes have changed relatively little over the last 200 million years. Six living species are distributed on southern continents. The Australian lungfishes, which live in rivers and pools, use their lungs to supplement gill respiration when dissolved oxygen concentration is low. The South American and African species, which live in swamps, use their lungs to collect oxygen during the annual dry season, which they spend encased in a mucus-lined burrow in the dry mud. When the rains begin, water fills the burrow and the fishes awaken from dormancy.

Study Break

1. What characteristics of sharks and rays make them more efficient predators than the acanthodians or placoderms?
2. How do the air bladder and fins of ray-finned bony fishes increase their locomotor abilities?
3. How do the lungs of lungfishes allow them to survive in stressful environments?

30.6 Early Tetrapods and Modern Amphibians



The fossil record suggests that tetrapods arose from a group of fleshy-finned fishes, the *osteolepiforms*, in the late Devonian period. Osteolepiforms and early tetrapods shared several derived characteristics: both had curious infoldings of their tooth surfaces, a trait with unknown function; and the shapes and positions of bones on the dorsal side of their crania and in their appendages were similar **(Figure 30.20)**.

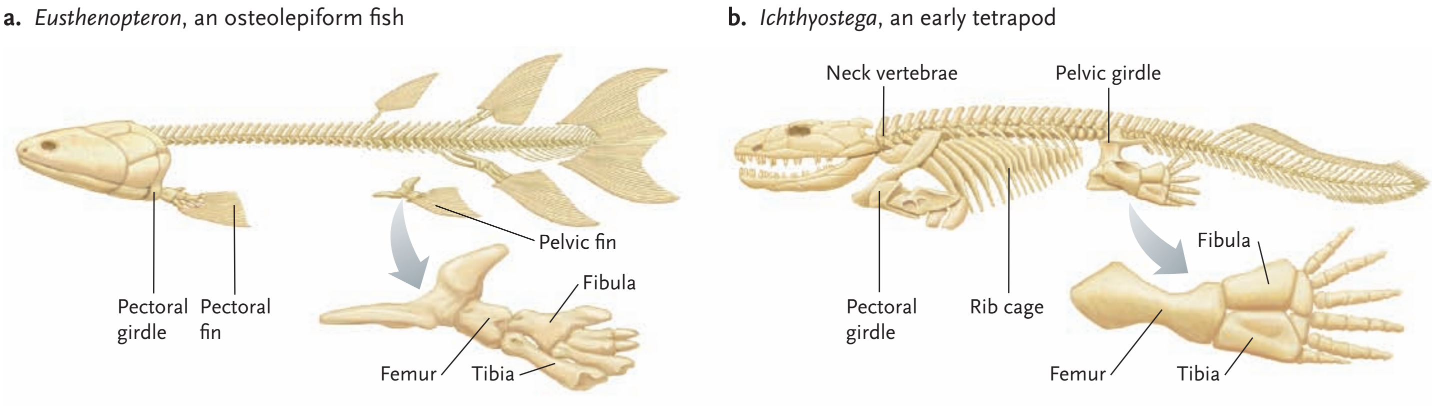


Figure 30.20
Evolution of tetrapod limbs. The limb skeleton of osteolepiform fishes, such as **(a)** *Eusthenopteron,* is homologous to that of early tetrapods, such as **(b)** *Ichthyostega.* Although *Ichthyostega* retained many fishlike characteristics, its pectoral girdle was completely freed from the cranium and it had a heavy rib cage. Fossils of its forefoot have not yet been discovered.

Key Adaptations Facilitated the Transition to Land

Fishes are not adapted to live on land, and the first tetrapods faced serious environmental challenges. First, because air is less dense than water, it provides less support for an animal's body. Second, animals exposed to air inevitably lose body water by evaporation. Third, the sensory systems of fishes, which work well under water, do not function well on land. However, swampy late Devonian habitats also offered distinct advantages. Land plants, worms, and arthropods provided abundant food; oxygen was more readily available in air than in water; and no predators lived in these new habitats.

In some ways, osteolepiforms were preadapted for terrestrial life (see Figure 30.20a). Most had strong, stout fins that enabled them to crawl on the muddy bottom of shallow pools, and their vertebral column included crescent-shaped bones that provided good support. They had nostrils leading to sensory pits that housed olfactory (smell) receptors. And they almost certainly had lungs to augment gill respiration in the swampy, oxygen-poor waters where they lived.

The earliest tetrapod for which we have nearly complete skeletal data is the semiterrestrial, meter-long *Ichthyostega* (see Figure 30.20b). Compared with its fleshy-finned ancestors, *Ichthyostega* had a stronger vertebral column, sturdier girdles and appendages, a rib cage that protected its internal organs (including lungs), and a neck. Fishes have no neck: the pectoral girdle is fused to the cranium. But several vertebrae separated these structures in *Ichthyostega,* allowing it to move its head to scan the environment and to capture food. However, *Ichthyostega* retained a fishlike lateral-line system, caudal fin, and scaly covering on its body.

Life on land also required changes in sensory systems. In fishes, for example, the body wall picks up sound vibrations and transfers them to sensory receptors directly. But sound waves are harder to detect in air. Early tetrapods developed a **tympanum,** a specialized membrane on either side of the head that is vibrated by airborne sounds. The tympanum connects to the **stapes,** a bone that is homologous to the hyomandibula, which had supported the jaws of fishes (see Figure 23.4). The stapes, in turn, transfers vibrations to the sensory cells of an inner ear.

Modern Amphibians Are Very Different from Their Paleozoic Ancestors

Most of the more than 6000 species of living amphibians—including frogs, salamanders, and caecelians—are small, and their skeletons contain fewer bones than those of Paleozoic tetrapods like *Ichthyostega*. All living amphibians are carnivorous as adults, but the aquatic larvae of some species are herbivores.

Most living amphibians have a thin, scaleless skin, well supplied with blood vessels, that is a major site of gas exchange. Because gases must enter the body across a thin layer of water, the skin of most amphibians must remain moist, restricting them to aquatic or wet terrestrial habitats. Adults of some species also acquire oxygen through saclike lungs. The evolution of lungs was accompanied by modifications of the heart and circulatory system that increase the efficiency with which oxygen is delivered to body tissues (see Section 42.1).

The life cycles of many amphibians (*amphi* = both; *bios* = life) include both larval and adult stages. Eggs are laid and fertilized in water, where they hatch into larvae, such as the tadpoles of frogs, that eventu-

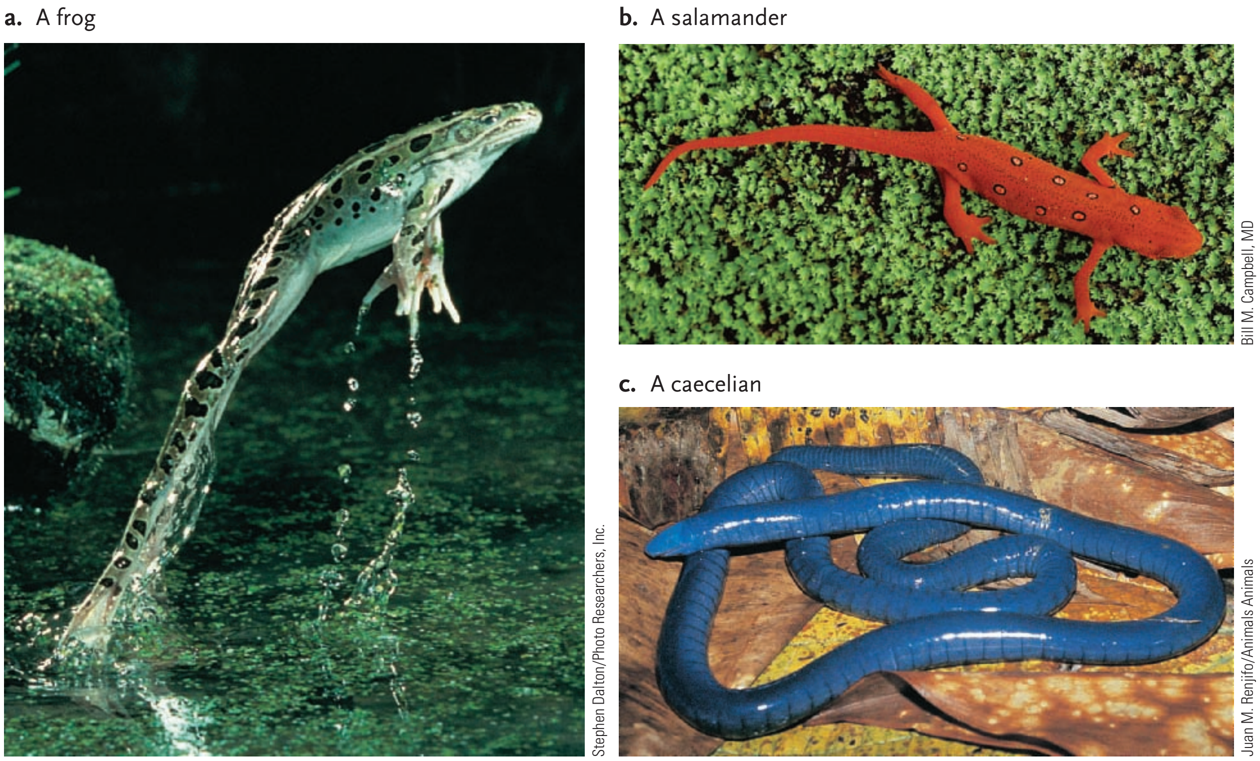


Figure 30.21
Living amphibians. **(a)** Anurans, like the northern leopard frog *(Rana pipiens)*, have compact bodies and long hind legs. **(b)** Urodeles, such as the red-spotted newt *(Notophthalmus viridescens)*, have an elongate body and four legs. **(c)** Caecelians, like *Caecelia nigricans* from Colombia, are legless burrowing animals.

ally metamorphose into adults (see Figure 40.9). Although the larvae of most species are aquatic, adults may be aquatic, amphibious, or terrestrial. Some salamanders are paedomorphic: the larval stage attains sexual maturity without changing its form or moving to land. By contrast, some frogs and salamanders reproduce on land, skipping the larval stage altogether. But even though they are terrestrial breeders, their eggs dry out quickly unless they are laid in moist places.

Modern amphibians are represented by three lineages **(Figure 30.21)**. Populations of practically all amphibians have declined rapidly in recent years, probably because of exposure to acid rain, high levels of ultraviolet B radiation, or parasitic infections.

Anura. The 3700 species of frogs and toads (Anura, from *an* = without; *oura* = tail) have short, compact bodies, and adults lack tails. Their elongate hind legs and webbed feet allow them to hop on land or swim. A few species are adapted to dry habitats, withstanding periods of drought by encasing themselves in mucous cocoons.

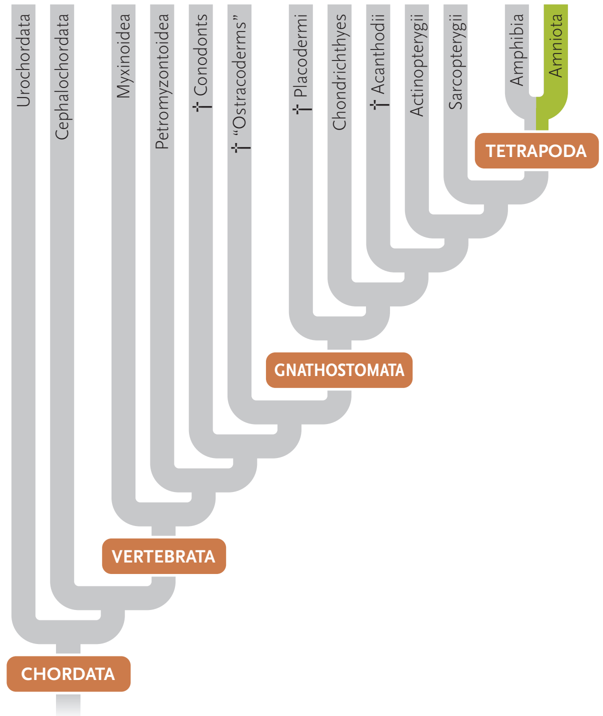
Urodela. Most of the 400 species of salamanders (Urodela, from *oura* = tail; *delos* = visible) have an elongate, tailed body and four legs. They walk by alternately contracting muscles on either side of the body much the way fishes swim. Species in the most diverse group, the lungless salamanders, are fully terrestrial throughout their lives, using their skin and the lining of the throat for gas exchange.

Gymnophiona. The 200 species of caecelians (Gymnophiona, from *gymnos* = naked; *ophioneos* = snakelike) are legless burrowing animals with wormlike bodies. They occupy tropical habitats throughout the world. Unlike other modern amphibians, caecelians have small bony scales embedded in their skin. Fertilization is internal, and females give birth to live young.

Study Break

1. For the first tetrapods, what were the advantages and disadvantages of moving onto the land?
2. What parts of the life cycle in most modern amphibians are dependent on water or very moist habitats?

30.7 The Origin and Mesozoic Radiations of Amniotes



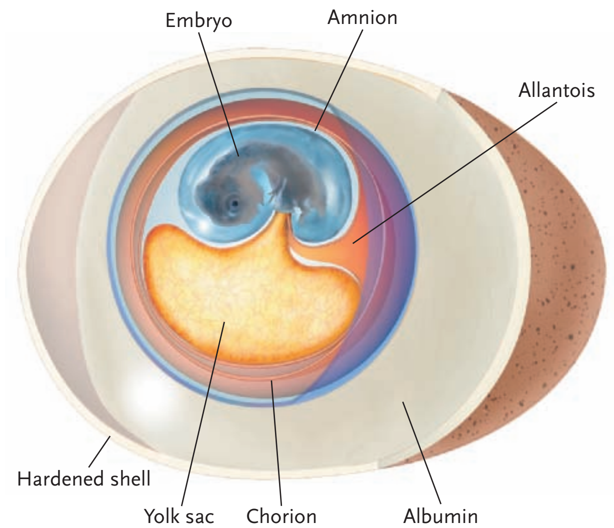


Figure 30.22
The amniote egg. A water-retaining egg with four specialized membranes (the amnion, allantois, chorion, and yolk sac) and a hard or leathery shell allowed amniotes and their descendants to reproduce in dry environments.

The amniote lineage arose during the Carboniferous period, when seed plants and insects, which served as excellent food resources, began to occupy higher ground. The lineage is named for the amnion, a fluid-filled sac that surrounds the embryo during development.

Key Adaptations Allow Amniotes to Live a Fully Terrestrial Life

Although the fossil record includes abundant skeletons of early amniotes, it provides little direct information about their soft body parts and physiology. For amniotes living today, three key adaptations allow them to live in dry habitats, freeing them from a dependency on moist surroundings and standing water. First, they have a tough, dry skin. Its cells are filled with keratin and lipids, which are relatively impermeable to water. Thus, amniotes do not dehydrate in air as quickly as amphibians do.

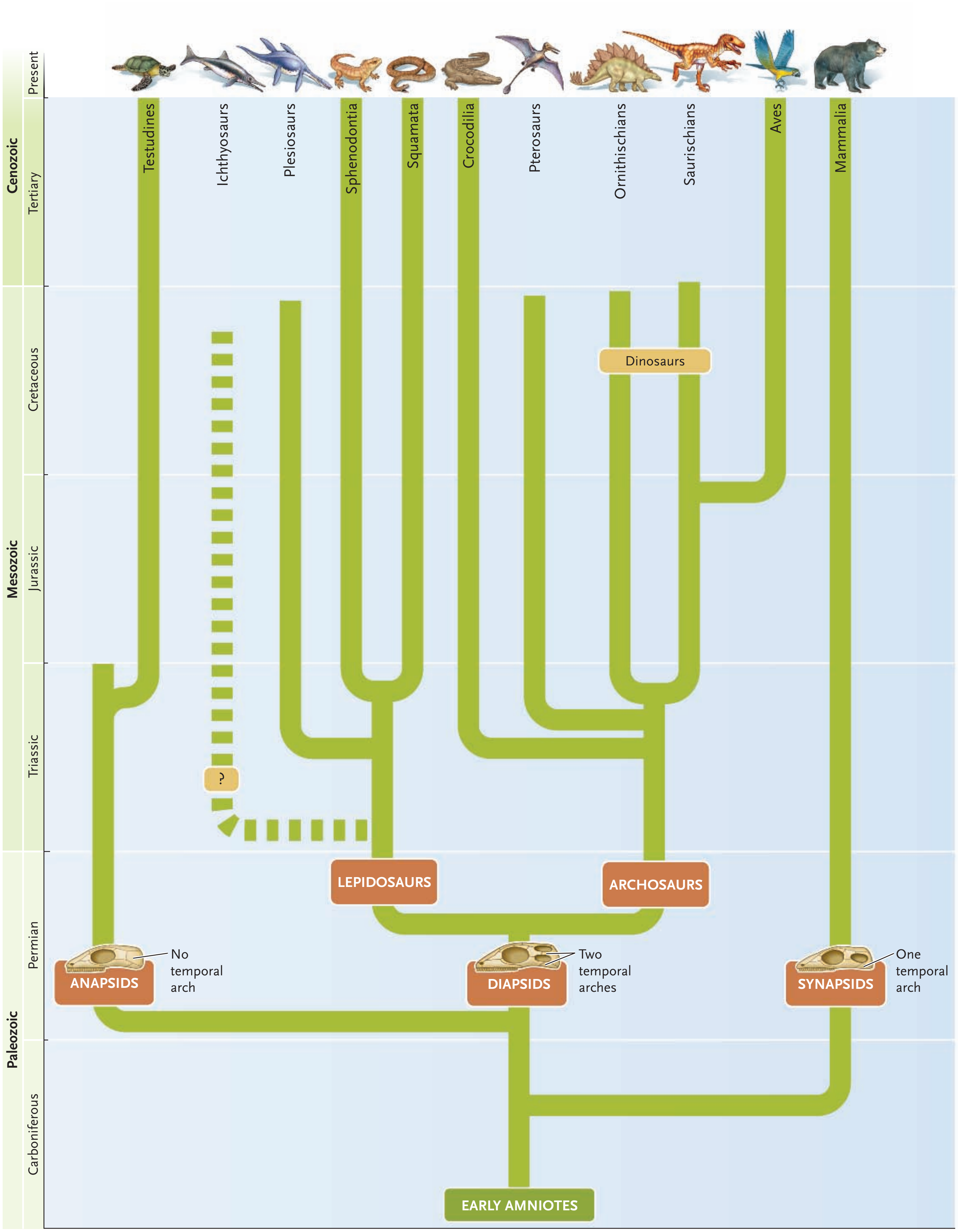
Second, many amniotes produce an **amniote egg**, which can survive and develop on dry land. The eggs of modern reptiles and birds have four specialized membranes and a hard or leathery shell perforated by microscopic pores **(Figure 30.22).** The membranes protect the developing embryo and facilitate gas exchange and excretion; the shell mediates the exchange of air and water between the egg and its environment. The egg also includes generous supplies of **yolk**, the embryo's main energy source, and **albumin**, a source of nutrients and water. Compared with those of amphibians, amniote eggs are large; and lacking a larval stage, the young hatch as miniature versions of the adult. By contrast to reptiles and birds, the eggs of virtually all mammals lack a shell; embryos, with the same four membranes, implant in the wall of the mother's uterus and receive nutrients and oxygen directly from her.

Third, some amniotes produce uric acid as a waste product of nitrogen metabolism (see Chapter 46). By contrast, fishes and amphibians produce ammonium ions or urea, toxic materials that require lots of water to flush them from body tissues. Because uric acid is less toxic than these other compounds, it can be excreted as a semisolid paste, conserving body water.

Amniotes Diversified into Three Main Lineages

Based on the abundance and diversity of their fossils, amniotes were extremely successful; they quickly replaced many nonamniote species in terrestrial habitats. During the Carboniferous and Permian periods, amniotes produced three radiations: synapsids, anapsids, and diapsids **(Figure 30.23).** Differences in skull structure—specifically, the number of bony arches in the temporal region of the skull—distinguish the three groups. In those animals that have temporal arches, the openings between the arches provide space for

Figure 30.23
Amniote ancestry. The early amniotes gave rise to three lineages (anapsids, synapsids, and diapsids) and numerous descendants. The lineages are distinguished by the number of bony arches in the temporal region of the skull (indicated on the small icons).



Cenozoic
Mesozoic
Paleozoic
Present
Tertiary
Cretaceous
Jurassic
Triassic
Permian
Carboniferous
Testudines
Ichthyosaurs
Plesiosaurs
Sphenodontia
Squamata
Crocodilia
Pterosaurs
Ornithischians
Saurischians
Aves
Mammalia
Dinosaurs
?
LEPIDOSAURS
ARCHOSAURS
ANAPSIDS
No temporal arch
DIAPSIDS
Two temporal arches
SYNAPSIDS
One temporal arch
EARLY AMNIOTES

large and powerful jaw muscles to bunch up when they contract.

Synapsida. The first offshoot from the ancestral amniotes was a group of small terrestrial predators, the **synapsids** (*syn* = with; *apsis* = arch), which had one temporal arch on each side of the head. Synapsids emerged late in the Permian period; mammals are their living descendants.

Anapsida. A second lineage to emerge was the **anapsids** ("no arch"), which had no temporal arches and no spaces on the sides of the skull. Many biologists believe that turtles are living representatives of this group.

Diapsida. Most Mesozoic amniotes belong to the third lineage, **diapsids** ("two arches"), which had two temporal arches. Their living descendants include lizards and snakes, crocodilians, and birds.

Diapsids Diversified Wildly during the Mesozoic Era

The early diapsids differentiated into two lineages, the **Archosauromorpha** (*archos* = ruler; *saurus* = lizard; *morphe* = form) and the **Lepidosauromorpha** (*lepis* = scale), which differed in many skeletal characteristics. The archosauromorphs (commonly called archosaurs), or "ruling reptiles," include crocodilians, pterosaurs, and dinosaurs. Crocodilians, which first appeared during the Triassic period, have bony armor and a laterally flattened tail that propels them through water. Pterosaurs, now extinct, were flying predators of the Jurassic and Cretaceous periods. Their wings, which spanned as much as 13 m, were composed of thin sheets of skin attached to the sides of the body and supported by an elongate finger. Small pterosaurs may have been active fliers, but large ones probably soared on air currents as vultures do today.

Two lineages of dinosaurs, "lizard-hipped" saurischians and "bird-hipped" ornithischians proliferated in the Triassic and Jurassic periods. As their names imply, they differed in the anatomy of their pelvic girdles. The saurischian lineage included bipedal carnivores and quadrupedal herbivores. Most carnivorous saurischians were swift runners. Their forelimbs, however, were often ridiculously short. *Tyrannosaurus,* which was 15 m long and stood 6 m high, is the most familiar, but most species were much smaller. One group of small carnivorous saurischians was ancestral to birds. By the Cretaceous period, some herbivorous saurischians had also attained gigantic size, and many had long, flexible necks. For example, *Apatosaurus* (previously known as *Brontosaurus*) was 25 m long and may have weighed 50,000 kg.

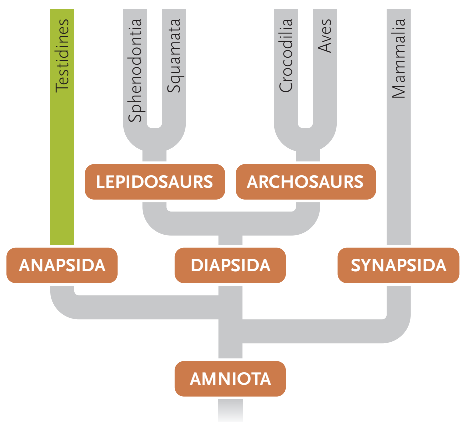
The largely herbivorous ornithischian dinosaurs had enormous, chunky bodies. This lineage included the armored or plated dinosaurs (*Ankylosaurus* and *Stegosaurus*), the duck-billed dinosaurs *(Hadrosaurus)*, horned dinosaurs *(Styracosaurus)*, and some with remarkably thick skulls *(Pachycephalosaurus)*. The ornithischians were most abundant in the Jurassic and Cretaceous periods.

The second major lineage of diapsids was the lepidosauromorphs (commonly called lepidosaurs), a diverse group that included both marine and terrestrial animals. Plesiosaurs were marine, fish-eating creatures that used long, paddlelike limbs to row through the water. Ichthyosaurs were porpoiselike animals with laterally flattened tails. They were so highly specialized for marine life that they could not venture onto land, even to reproduce. Instead, they gave birth to live young, as porpoises and whales do today. A third important group within this lineage is the squamates, which includes the living lizards and snakes.

Study Break

1. How did the evolution of the amniote egg free amniotes from a dependence on standing water?
2. What groups of animals are included in each of the three amniote lineages?
3. Based upon the evolutionary history of the diapsid amniotes, are crocodilians more closely related to lizards or to birds?

30.8 Testudines: Turtles



Turtles Have Bodies Encased in a Bony Shell

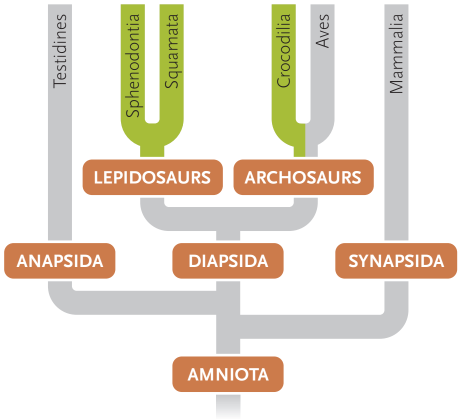
The turtle body plan, largely defined by a bony, boxlike shell, has changed little since the group first appeared during the Triassic period **(Figure 30.24).** The shell includes a dorsal **carapace** and a ventral **plastron.** A turtle's ribs are fused to the inside of the carapace, and, in contrast to other tetrapods, the pectoral and pelvic girdles lie within the ribcage. Large keratinized scales cover the bony plates that form the shell.

The 250 living species of turtles occupy terrestrial, freshwater, and marine habitats. They range from 8 cm to 2 m in length. All species lack teeth, but they use a keratinized beak and powerful jaw muscles to feed on plants or animal prey. When threatened, most species retract into their shells. Many species are now highly endangered because adults are hunted for meat, their eggs are consumed by humans and other predators, and their young are collected for the pet trade.

Study Break

How does the overall structure of turtles distinguish them from other amniotes?

30.9 Living Nonfeathered Diapsids: Sphenodontids, Squamates, and Crocodilians

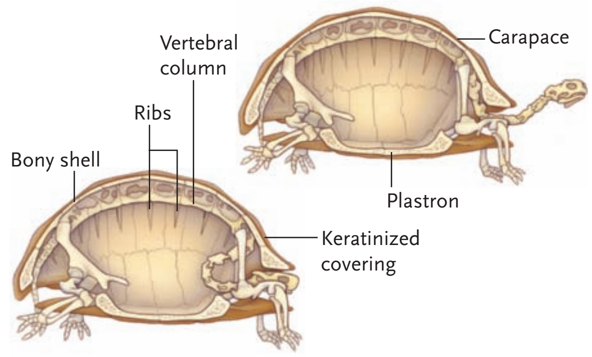


Biologists once grouped living turtles, lizards and snakes, and crocodilians in the class Reptilia, because they all have a dry, scaly skin, produce amniote eggs, and have low metabolic rates and variable body temperatures. But as you read in Section 23.5, these animals do not represent a monophyletic lineage. Turtles are probably not closely related to the other groups. Moreover, the "class Reptilia" excludes birds, which, like crocodilians, are part of the archosaur lineage. In this section, we describe all of the living diapsids except birds, which we consider separately in Section 30.10 because of their unique derived traits and their conspicuous evolutionary success.

Living Sphenodontids Are Remnants of a Diverse Mesozoic Lineage

The tuatara *(Sphenodon punctatus)* is one of two living representatives of the sphenodontids (*sphen* = wedge; *odont* = tooth), a diverse Mesozoic lineage **(Figure 30.25a).** These lizardlike animals survive on a few islands off the coast of New Zealand. Adults are about 60 cm long. They live in dense colonies, where males and females defend small territories using vocal and visual displays. They often share underground burrows with seabirds, feeding mainly on invertebrates and small vertebrates. They are primarily nocturnal and maintain low body temperatures during periods of activity.

a. The turtle skeleton



b. An aquatic turtle

Figure 30.24
Testudines. **(a)** Most turtles can withdraw their heads and legs into a bony shell. **(b)** Aquatic turtles, like the Eastern painted turtle *(Chrysemys picta)*, often bask in the sun to warm up. The sunlight may also help eliminate parasites that cling to the turtle's skin.

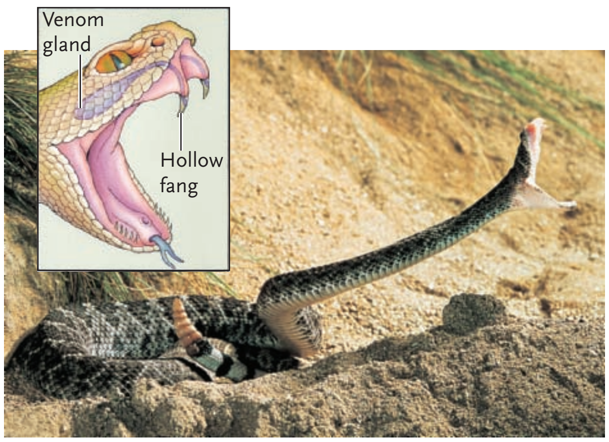
Squamates—Lizards and Snakes—Are Covered by Overlapping, Keratinized Scales

The skin of lizards and snakes (Squamata, from *squama* = scale) is composed of overlapping, keratinized scales that protect against dehydration. Squamates periodically shed their skin as they grow, much the way arthropods shed their old exoskeletons (see Section 29.7). Most squamates regulate their body temperature behaviorally: they are active only when weather conditions are favorable, and they shuttle between sunny and shady places when they need to warm up or cool down (see Section 46.7).

Most of the 3700 lizard species are less than 15 cm long **(Figure 30.25b).** However, the Komodo dragon *(Varanus komodoensis)* grows to nearly 3 m. Lizards occupy a wide range of habitats, but they are especially

a. Sphenodontia includes the tuatara *(Sphenodon punctatus)* and one other species.

b. Basilisk lizards *(Basiliscus basiliscus)* escape from predators by running across the surface of streams.



c. A western diamondback rattlesnake *(Crotalus atrox)* of the American southwest bares its fangs with which it injects a powerful toxin into prey.

d. Crocodilia includes semiaquatic predators, like this resting African Nile crocodile *(Crocodylus niloticus)*, that frequently bask in the sun.

Figure 30.25
Living nonfeathered diapsids.

common in deserts and the tropics; one species *(Zootoca vivipara)* occurs within the Arctic Circle. Most lizards feed on insects, although some eat leaves or meat. The diverse tropical genus *Anolis* has become a frequent subject of research, as described in *Focus on Research.*

The 2300 species of snakes evolved from a lineage of lizards that lost their legs over evolutionary time **(Figure 30.25c).** Streamlined bodies make snakes efficient burrowers or climbers. Many subterranean species are only 10 or 15 cm long, but the giant constrictors may grow to 10 m. Unlike lizards, all snakes are predators that swallow prey whole. Snakes have smaller skull bones than their lizard ancestors did, and the bones are connected to each other by elastic ligaments that stretch remarkably, allowing some snakes to swallow food that is larger than their head. Snakes also have well-developed sensory systems for detecting prey. The flicking tongue carries airborne molecules to sensory receptors in the roof of the mouth. Most snakes can detect vibrations on the ground, and some, like rattlesnakes, have heat-sensing organs (see Figure 39.22). Many snakes kill by constriction, which suffocates prey, and several groups produce toxins that immobilize, kill, and partially digest it.

Crocodilians Are Semiaquatic, Predatory Archosaurs

The 21 species of alligators and crocodiles (Crocodilia, from *crocodilus* = crocodile), along with the birds, are the remnants of the once-diverse archosaur lineage **(Figure 30.25d).** The largest species, the Australian saltwater crocodile *(Crocodylus porosus)*, grows to 7 m. Crocodilians are aquatic predators that consume other vertebrates. Striking anatomical adaptations distinguish them from living lepidosaurs, including a four-chambered heart that is homologous to the heart in birds.

American alligators *(Alligator mississippiensis)* exhibit strong maternal behavior, which also reflects their relationship to birds. Females guard their nests ferociously and free their offspring from the nest after they hatch. Young stay close to the mother for about a year, feeding on scraps that fall from her mouth and

Focus on Research

Model Research Organisms: *Anolis* Lizards of the Caribbean

The lizard genus *Anolis* has been a model system for studies in ecology and evolutionary biology since the 1960s, when Ernest E. Williams of Harvard University's Museum of Comparative Zoology first began studying it. With more than 400 known species—and new ones being described all the time—*Anolis* is one of the most diverse vertebrate genera. Most anoles are less than 10 cm long, not including the tail, and many occur at high densities, making it easy to collect lots of data in a relatively short time. Male anoles defend territories, and their displays make them conspicuous even in dense forests.

Anolis species are widely distributed in South America and Central America, but nearly 40% occupy Caribbean islands. The number of species on an island is generally proportional to the island's size. Cuba, the largest island, has more than 50 species, whereas small islands have just one or two.

Studies by Williams and others suggest that the anoles on some large islands are the products of independent adaptive radiations. Eight of the 10 *Anolis* species now found on Puerto Rico probably evolved on that island from a common ancestor. Similarly, the seven *Anolis* species on Jamaica shared a common ancestor, which was different from the ancestor of the Puerto Rican species. The anole faunas on Cuba and Hispaniola are the products of several independent radiations on each island.

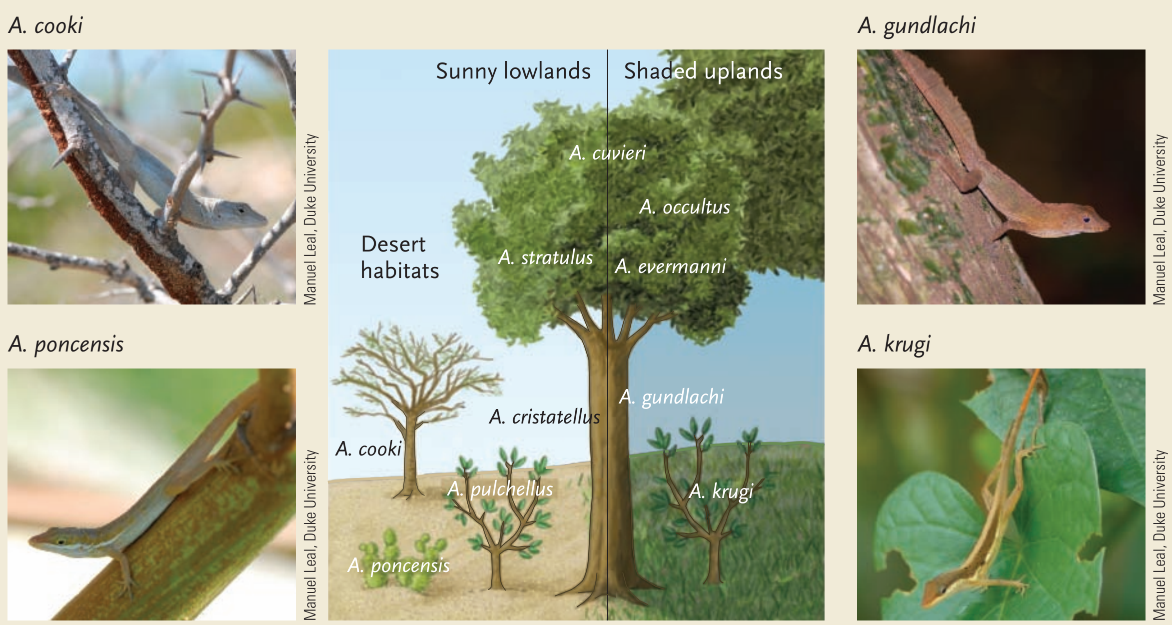
Williams discovered that these independent radiations had produced similar-looking species on different islands. He developed the concept of the *ecomorph,* a group of species that have similar morphological, behavioral, and ecological characteristics even though they are not closely related within the genus. Williams named the ecomorphs after the vegetation that they commonly used (see **figure**). For example, grass anoles are small, slender species that usually perch on low, thin vegetation. Trunk-ground anoles have chunky bodies and large heads, and they perch low on tree trunks, frequently jumping to the ground to feed. Although the grass anoles or the trunk-ground anoles on different islands are similar in many ways, they are not closely related to each other. Their resemblances are the products of convergent evolution.

Ecomorphs exist because evolutionary processes have accentuated the morphological differences among species that occupy different types of vegetation. Jon Losos of Harvard University has demonstrated that trunk-ground anoles, which have relatively long legs and tails, can run faster on wide surfaces and jump farther than species with relatively short legs. And in nature the trunk-ground anoles run and jump more frequently than the other ecomorphs do.

Different ecomorphs on an island use different parts of their habitats by choosing different perch sites (grass, tree trunks, rocks). When two or more species of the same ecomorph inhabit the same island, they occupy habitats with different temperature and shade conditions (see the figure). For example, in Puerto Rico, one species of trunk-ground anole *(Anolis gundlachi)* occupies cool, shady uplands; another *(Anolis cristatellus)* lives in warm, fairly open lowland habitats; and a third species *(Anolis cooki)* lives in desert habitats. Other species in Puerto Rico exhibit similar differences in their distributions. These differences in geographical distribution and habitat use presumably allow the different species to avoid competition with each other and gain access to the resources they need to survive and reproduce.

Evolutionary processes have also fostered physiological differences that reinforce the ecological separation established by the lizards' use of different habitats. For example, *A. cristatellus* maintains higher body temperatures than *A. gundlachi,* and neither is physiologically adapted to the environment of the other: *A. cristatellus* dies in the high altitude forests where *A. gundlachi* thrives, while *A. gundlachi* suffers heat stress at body temperatures that are typical for *A. cristatellus.*

Researchers throughout the Americas continue to explore the ecology and evolution of anoles. Some unravel their biogeography and systematic relationships; others focus on the ecology of populations and communities; still others study their social behavior or sensory physiology. With so many species distributed across hundreds of Caribbean islands, the lizard genus *Anolis* provides fertile ground for testing hypotheses about nearly every aspect of vertebrate biology.

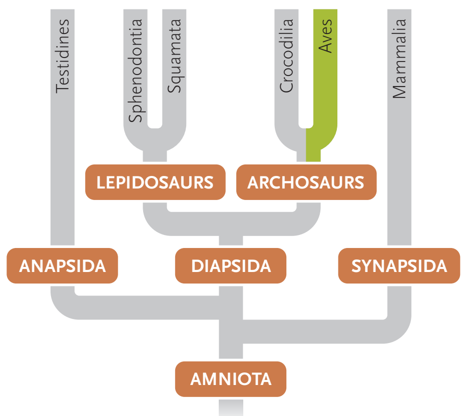


living under her watchful protection. Most alligator and crocodile species are highly endangered. Their habitats have been disrupted by human activities, and they have been hunted for meat and leather. Protection efforts have been extremely successful, however. American alligators, for example, recently recovered from the brink of extinction.

Study Break

1. In addition to losing their legs over evolutionary time, how do snakes differ from their lizard ancestors?
2. What anatomical and behavioral characteristics of crocodilians demonstrate their relatively close relationship to birds?

30.10 Aves: Birds



Birds (Aves) appeared in the Jurassic period as descendants of carnivorous, bipedal dinosaurs. Thus, they are full-fledged members of the archosaur lineage. Their evolutionary relationship to dinosaurs is evident in their skeletal anatomy, the scales on their legs and feet, and their posture when walking. However, powered flight gave birds access to new adaptive zones, setting the stage for their astounding evolutionary success **(Figure 30.26a).**

Key Adaptations Reduce Body Weight and Provide Power for Flight

The skeletons of birds are both lightweight and strong **(Figure 30.26b).** For example, the endoskeleton of the frigate bird, which has a 1.5 m wingspan, weighs little more than 100 g, far less than its feathers. Most birds have hollow limb bones with small supporting struts that crisscross the internal cavities. Evolution has also reduced the number of separate bony elements in the wings, skull, and vertebral column (especially the tail), making the skeleton light and rigid. And all modern birds lack teeth, which are dense and heavy; they acquire food with a lightweight, keratinized bill. Many species have a long, flexible neck, which allows them to use their bills for feeding, grooming, nest-building, and social interactions.

The bones associated with flight are generally large. The forelimb and forefoot are elongate, forming the structural support for the wing. And most modern birds possess a **keeled sternum** (breastbone) to which massive flight muscles attach **(Figure 30.26c).** Not all birds are strong fliers, however; ostriches and other bipedal runners have strong, muscular legs but small wings and flight muscles (see Figure 19.2).

Like the skeleton, soft internal organs are modified in ways that reduce weight. Most birds lack a urinary bladder; uric acid paste is eliminated with digestive wastes. Females have only one ovary and never carry more than one mature egg; eggs are laid as soon as they are shelled.

All birds also possess **feathers (Figure 30.26d),** sturdy, lightweight structures derived from scales in the skin of their ancestors. Each feather has numerous barbs and barbules with tiny hooks and grooves that maintain the feathers' structure, even during vigorous activity. Flight feathers on the wings provide lift; contour feathers streamline the surface of the body; and down feathers form an insulating cover close to the skin. Worn feathers are replaced once or twice each year.

Other adaptations for flight allow birds to harness the energy needed to power their flight muscles. Their metabolic rates are eight to ten times higher than those of other comparably sized diapsids, and they process energy-rich food rapidly. A complex and efficient respiratory system (see Figure 44.7) and four-chambered heart (see Figure 42.5d) enable them to consume and distribute oxygen efficiently. As a consequence of high rates of metabolic heat production, birds maintain a high and constant body temperature (see Section 46.8).

Flying Birds Were Abundant by the Cretaceous Period

Although the earliest known bird, the pigeon-sized *Archaeopteryx,* had feathers, its skeleton was essentially that of a small dinosaur (see Figure 19.12). It had digits and claws on the forelimbs, teeth on its jaws, many bones in its wings and vertebral column, and only a poorly developed sternum. How could flight evolve in so unbirdlike an animal? Biologists hypothesize that *Archaeopteryx* ran after prey, using its feathered wings like fly swatters. Larger wings would have provided extra lift when they jumped at prey, and gradual evolutionary modifications of the wing bones and muscles could have led to powered flight.

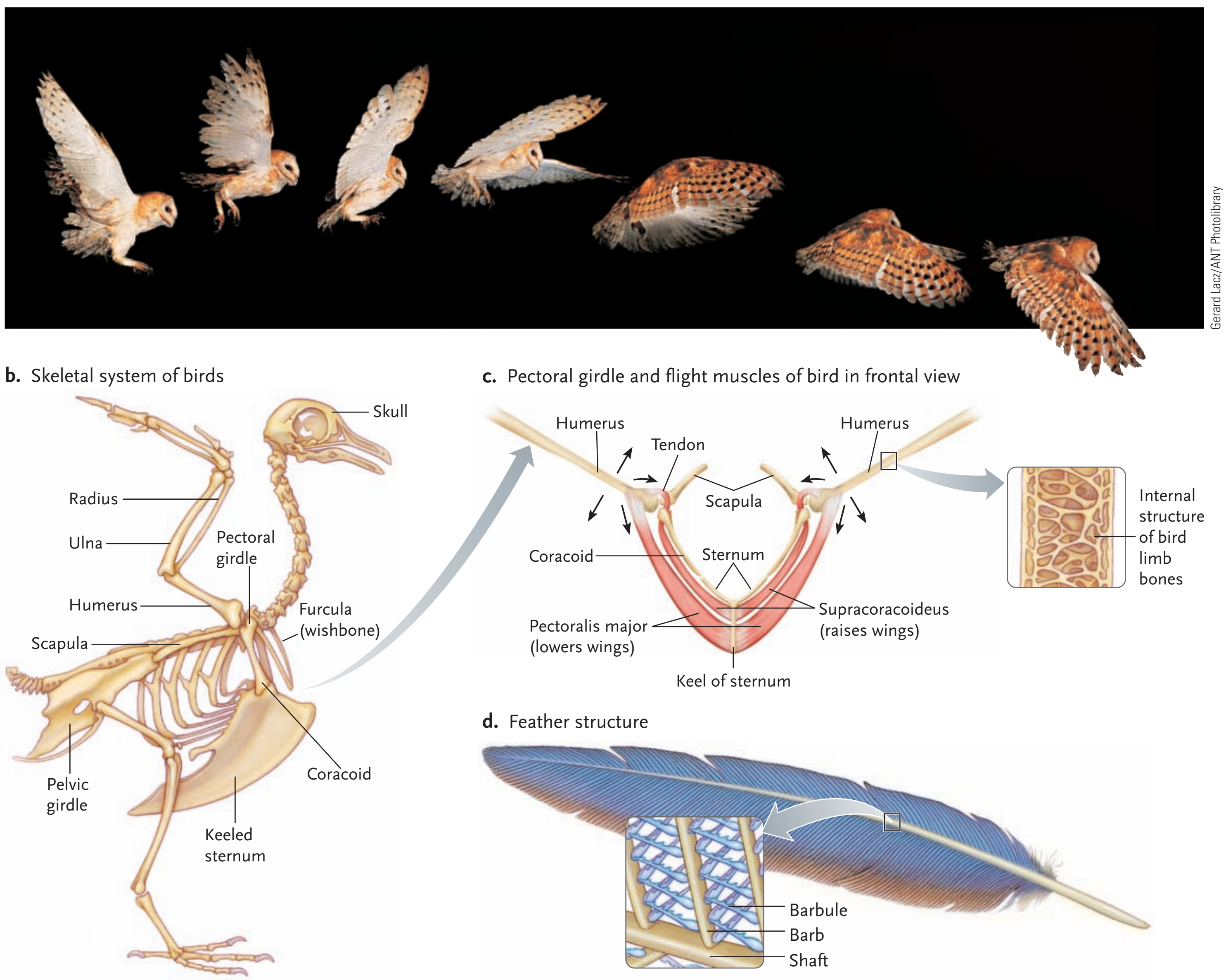
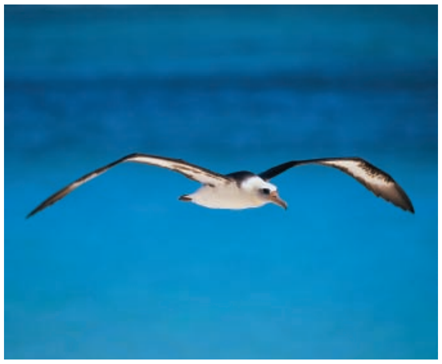


Figure 30.26
Adaptations for flight in birds. **(a)** The flapping movements of a bird's wing provide *thrust* for forward movement and *lift* to counteract gravity. **(b)** The bird skeleton includes a boxlike trunk, short tail, long neck, lightweight skull and beak, and well-developed limbs. In large birds, limb bones are hollow. **(c)** Two sets of flight muscles attach to a keeled sternum; one set raises the wings, and the other lowers it. **(d)** Flexible feathers form an airfoil on the wing surface.

Crow-sized birds with full flight capability appeared by the early Cretaceous period. They had a keeled sternum and other modern skeletal features. The modern groups of wading birds and seabirds first appear in late Cretaceous rocks; fossils of other modern groups are found in slightly later deposits. Woodpeckers, perching birds, birds of prey, pigeons, swifts, the flightless ratites, penguins, and some other groups were all present by the end of the Oligocene; birds continued to diversify through the Miocene (see Table 22.1).

Modern Birds Vary in Morphology, Diet, Habits, and Patterns of Flight

The 9000 living bird species show extraordinary ecological specializations, but they share the same overall body plan. Living birds are traditionally classified into nearly 30 groups **(Figure 30.27).** They vary in size from the bee hummingbird *(Mellisuga helenae)* of Cuba, which weighs little more than 1 g, to the ostrich *(Struthio camelus),* which can weigh as much as 150 kg.



Devin Schafer/Corbis

a. The Laysan albatross (Procellariiformes, *Phoebastria immutabilis*) has the long thin wings typical of birds that fly great distances.

Arthur Morris/Visuals Unlimited

b. The roseate spoonbill (Ciconiformes, *Ajaia ajaja*) uses its bill to strain food particles from water.

Ron Sanford/Corbis

c. The bald eagle (Falconiformes, *Haliaeetus leucocephalus*) uses its sharp bill and talons to capture and tear apart prey.

Wim Klomp/Foto Natura/Minden Pictures

d. A European nightjar (Caprimulgiformes, *Caprimulgus europaeus*) uses its wide mouth to capture flying insects.

Robert A. Tyrrell

e. A Bahama woodstar hummingbird (Apodiformes, *Calliphlox evelynae*) hovers before a hibiscus blossom to drink nectar from the base of the flower.

Tim Zurowski/Corbis

f. The chestnut-backed chickadee (Passeriformes, *Parus rufescens*) uses its thin bill to probe for insects in dense vegetation.

Figure 30.27
Bird diversity.

The structure of the bill usually reflects a bird's diet. Seed and nut eaters, such as finches and parrots, have deep, stout bills that crack hard shells. Carnivorous hawks and carrion-eating vultures have sharp beaks to rip flesh, and nectar-feeding hummingbirds have slender bills to reach into flowers. The bills of ducks are modified to extract particulate matter from water, and many perching birds have slender bills to feed on insects.

Birds also differ in the structure of their feet and wings. Predators have large, strong talons (claws), whereas ducks and other swimming birds have webbed feet that serve as paddles. Long-distance fliers like albatrosses have narrow wings; those that hover at flowers, such as hummingbirds, have wide ones. The wings of some species, like penguins, are so specialized for swimming that they are incapable of aerial flight.

All birds have well-developed sensory and nervous systems, and their brains are proportionately larger than those of other diapsids of comparable size. Large eyes provide sharp vision, and most species also have good hearing, which nocturnal hunters like owls use to locate prey. Some vultures and other species have a good sense of smell, which they use to find food. Migrating birds use polarized light, changes in air pressure, and Earth's magnetic field for orientation.

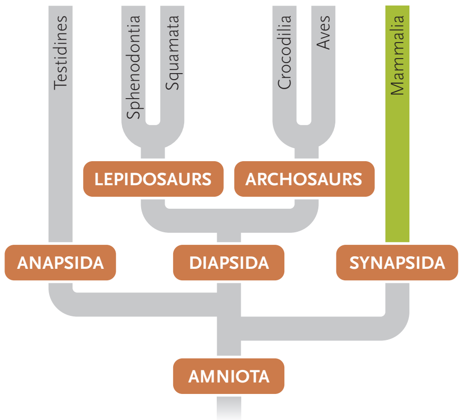
Most birds exhibit complex social behavior, including courtship, territoriality, and parental care. Many species communicate with vocalizations and visual displays to challenge other individuals or attract mates. Most raise their young in a nest, using body heat to incubate eggs. The nest may be a simple depression on a gravely beach, a cup woven from twigs and grasses, or a feather-lined hole in a tree.

Many bird species embark on a semiannual long-distance migration (see Section 55.1). The golden plover *(Pluvialis dominica)*, for example, migrates 20,000 km twice each year. Migrations are a response to seasonal changes in climate. Birds travel toward the tropics as winter approaches; in spring, they return to high latitudes using seasonally available food sources.

Study Break

1. What specific adaptations allow birds to fly?
2. How do the structures of a bird's bill, wings, and feet reflect its dietary and habitat specializations?

30.11 Mammalia: Monotremes, Marsupials, and Placentals



The synapsid lineage, which includes the living mammals, was the first group of amniotes to diversify broadly on land. Indeed, during the late Paleozoic era, medium- to large-sized synapsids were the most abundant predators in terrestrial habitats. One particularly successful and persistent branch of the synapsid lineage, the *therapsids,* exhibited many mammal-like characteristics in their legs, skulls, jaws, and teeth. And by the end of the Triassic period, the earliest mammals—most of them no bigger than a rat—had emerged from therapsid ancestors. Several mammalian lineages coexisted with dinosaurs and other diapsids throughout the Mesozoic, but paleontologists hypothesize that most Mesozoic mammals were active only at night to avoid predatory dinosaurs, which were active during the day. Two mammalian lineages, the egg-laying Prototheria (or monotremes) and the live-bearing Theria (marsupials and placentals), survived the mass extinction that eliminated most dinosaurs at the end of the Mesozoic. The Theria diversified into the mammalian groups that are most familiar today.

Mammals Exhibit Key Adaptations in Anatomy, Physiology, and Behavior

Four sets of key adaptations fostered the success of mammals.

High Metabolic Rate and Body Temperature. Like birds, mammals have high metabolic rates that release enough energy to maintain high activity levels and enough heat to maintain high body temperatures (see Section 46.8). An outer covering of fur and a layer of subcutaneous fat help retain body heat. Using metabolic heat to stay warm requires lots of oxygen, and mammals have a muscular organ, the diaphragm, that fills their lungs with air (see Figure 44.8). Four-chambered hearts and complex circulatory systems deliver oxygen to active tissues (see Figure 42.5d).

Specializations of the Teeth and Jaws. Mammals also have anatomical features that allow them to feed efficiently. Ancestrally, mammals have four types of teeth (see Figure 45.17): flattened **incisors** nip and cut food; pointed **canines** pierce and kill prey; and two sets of cheek teeth, **premolars** and **molars**, grind and crush food. Moreover, teeth in the upper and lower jaws occlude (that is, fit together) tightly as the mouth is closed; thus, mammals can use their large jaw muscles to chew food thoroughly.

Parental Care. Mammals provide more parental care to their young than any other animals. In most species, young complete development within a female's uterus, deriving nourishment through the **placenta**, a specialized organ that mediates the delivery of oxygen and nutrients (see Section 47.2). Females also have **mammary glands**, specialized structures that produce energy-rich milk, a watery mixture of fats, sugars, proteins, vitamins, and minerals. This perfectly balanced diet is the sole source of nutrients for newborn offspring.

Complex Brains. Finally, mammals have larger brains than other tetrapods of equivalent body size; the difference lies primarily in the **cortex**, the part of the forebrain responsible for information processing and learning (see Figure 38.6). Extensive postnatal care provides opportunities for offspring to learn from older individuals. Thus, mammalian behavior is strongly influenced by past experience as well as by genetically programmed instincts.

The Major Groups of Modern Mammals Differ in Their Reproductive Adaptations

Biologists recognize a primary distinction between two lineages of modern mammals: the egg-laying Prototheria (*protos* = first; *therion* = wild beast), or monotremes, and the live-bearing Theria. The Theria, in turn, diversified into two sublineages, the Metatheria (*meta* = between), or marsupials, and the Eutheria (*eu* = true), or placentals, which also differ in their reproductive adaptations.

Monotremes. The three living species of monotremes (Prototheria), which are limited to the Australian region, reproduce with a leathery-shelled egg **(Figure 30.28).** Newly hatched young lap up milk secreted by modified sweat glands on the mother's belly. The duck-billed platypus *(Ornithorhynchus anatinus)* lives in burrows along riverbanks and feeds on aquatic invertebrates. The two species of echidnas, or spiny anteaters (*Tachyglossus aculeatus* and *Zaglossus bruijni*), feed on ants or termites.

Marsupials. The 240 species of marsupials (Metatheria) have short gestation: the young are nourished through a placenta very briefly—sometimes only for

a. Short-nosed echidna

D. & V. Blagden/ANT Photo Library

b. Duck-billed platypus

Jean Phillipe Varin/Jacana/Photo Researchers, Inc.

Figure 30.28
Monotremes. **(a)** The short-nosed echidna *(Tachyglossus aculeatus)* is terrestrial. **(b)** The duck-billed platypus *(Ornithorhynchus anatinus)* raises its young in a streamside burrow.

Milse, T./Arco Images/Peter Arnold, Inc.

Figure 30.29
Marsupials. An Eastern gray kangaroo *(Macropus giganteus)* carries her "joey" in her pouch.

8 to 10 days—before birth. Newborns use their forelimbs to drag themselves across the mother's belly fur and enter her abdominal pouch, the **marsupium**, where they complete development attached to a teat. Marsupials are the dominant native mammals of Australia and a minor component of the South American fauna **(Figure 30.29);** only one species, the opossum *(Didelphis virginiana)*, occurs in North America. South America once had a diverse marsupial fauna, but it declined after the Isthmus of Panama bridged the seaway between North and South America (see *Focus on Research* in Chapter 22).

Placentals. The 4000 species of placental mammals (Eutheria) are the dominant mammals today. They complete embryonic development in the mother's uterus, nourished through a placenta until they reach a fairly advanced stage of development. Some species, like humans, are helpless at birth, but others, such as horses, are quickly mobile.

Biologists divide eutherians into about 18 groups, only eight of which contain more than 50 living species **(Figure 30.30).** Rodents (Rodentia) make up about 45% of eutherian species, and bats (Chiroptera) comprise another 22%. Our own group, Primates, is represented by fewer than 170 living species (less than 5% of all mammalian species), many of which are highly endangered. Researchers still do not agree on the details of eutherian evolution. *Insights from the Molecular Revolution* describes the use of molecular techniques to resolve one question about their relationships.

Some eutherians have highly specialized locomotor structures. Whales and dolphins (Cetacea) and manatees and dugongs (Sirenia) are descended from terrestrial ancestors, but their appendages do not function on land, and they are now restricted to aquatic habitats. By contrast, seals and walruses (Carnivora) feed under water but rest and breed on land. Bats (Chiroptera) use wings for powered flight.

Although early mammals appear to have been insectivorous, the diets of modern eutherians are diverse. Odd-toed ungulates (*ungula* = hoof) like horses and rhinoceroses (Perissodactyla), even-toed ungulates like cows and camels (Artiodactyla), and rabbits and hares (Lagomorpha) feed on vegetation. Carnivores (Carnivora) consume other animals. Most insectivores (Insectivora) and bats eat insects, but some feed on flowers,

Theo Allofs/Photonica/Getty Images, Inc.

a. The capybara (Rodentia, *Hydrochoerus hydrochaeris*), the largest rodent, feeds on vegetation in South American wetlands.

J. Scott Altenbach, University of New Mexico

b. Most bats, like the Yuma Myotis (Chiroptera, *Myotis yumanensis*), are nocturnal predators on insects.

Leonard Lee Rue III/FPG/Getty Images, Inc.

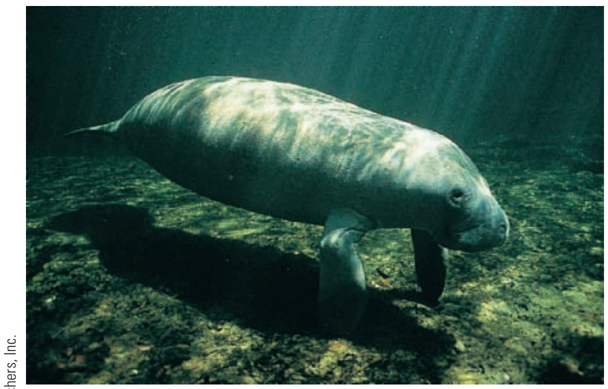
c. Walruses (Carnivora, *Obodenus rosmarus*) feed primarily on marine invertebrates in frigid arctic waters.

Martin Harvey/Peter Arnold, Inc.

d. The black rhinoceros (Perissodactyla, *Diceros bicornis*) feeds on grass in sub-Saharan Africa.

David Parker/SPL/Photo Researchers, Inc.

e. Arabian camels (Artiodactyla, *Camelus dromedarius*) use enlarged foot pads to cross hot desert sands.



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f. Antillean manatees (Sirenia, *Trichechus manatus*) are herbivores that live in warm coastal marshes and rivers from Florida to northern South America.

Figure 30.30
Eutherian diversity.

fruit, and nectar. Many whales and dolphins prey on fishes and other animals, but some eat plankton. And some groups, including rodents and primates, feed opportunistically on both plant and animal matter.

Study Break

1. During the Mesozoic era, why were most mammals active only at night?
2. Which key adaptations in mammals allow them to be active under many types of environmental conditions?
3. On what basis are the major groups of living mammals distinguished?

30.12 Nonhuman Primates

We now focus our attention on Primates, the mammalian lineage that includes humans, apes, monkeys, and their close relatives. The first Primates appeared early in the Eocene epoch, about 55 million years ago, in forested habitats in North America, Europe, Asia, and North Africa.

Key Derived Traits Enabled Primates to Become Arboreal, Diurnal, and Highly Social

Several derived traits allow primates to be arboreal (to live in trees rather than on the ground). For example, most primates have a more erect posture than

Insights from the Molecular Revolution

The Guinea Pig Is Not a Rat

Using the Linnaean system of taxonomy, the Rodentia has traditionally included more than 1800 species distributed among 29 families, including squirrels, rats and mice, guinea pigs, and porcupines. Their placement in the same order implies that they have a common evolutionary ancestor not shared by any other groups within the mammals. Biologists commonly accepted this interpretation until a molecular study compared the amino acid sequences of 15 proteins encoded in the nuclear DNA of various rodents. The comparisons revealed differences suggesting that guinea pigs should be placed in a separate order. Since then, further molecular evaluations of nuclear genes have produced contradictory results, with some studies supporting the traditional classification of guinea pigs as rodents and others placing them outside the Rodentia.

A cooperative study by Anna Maria D'Erchia and her colleagues at universities and institutes in Italy and Sweden now adds molecular weight to the conclusion that guinea pigs belong in an order of their own. The research team used mitochondrial DNA (mtDNA) sequences because they are easy to isolate and purify, and typically undergo many random mutations and rearrangements that have no apparent effect on gene function. Thus the changes observed in mtDNA are expected to reflect more faithfully the ticking of the molecular clock that tracks the time course of evolutionary events.

For their study, the researchers sequenced mtDNA of the guinea pig and another mammal considered by some biologists to be closely related to rodents, rabbits (Lagomorpha). Other workers had previously sequenced the mtDNAs of 14 other mammals in eight orders, including primates (Primates), seals (Carnivora), cows (Artiodactyla), whales (Cetacea), horses (Perissodactyla), mice and rats (Rodentia), hedgehogs (Insectivora), and opossums (Marsupialia).

The researchers evaluated these sequences with three different statistical programs that use similarities and differences in mtDNA sequences to construct evolutionary trees. They also conducted analyses using nuclear DNA, including separate evaluations of the entire nuclear genome, the protein-encoding sequences, and the DNA encoding ribosomal RNA. Significantly, all the methods produced essentially the same family tree (shown in **Figure a**).

The tree places guinea pigs in a group of their own, sharing a more recent common ancestor with all of the mammalian orders examined except those represented by rodents, hedgehogs, and opossums. The lineage that includes guinea pigs and most other mammals shared a common ancestor with the lineage leading to rodents at a point further back in evolutionary time. And the lineage that includes rodents, guinea pigs, and most other mammals split off from the ancestors of hedgehogs and opossums even earlier. Thus, guinea pigs merit placement in a separate group from rodents. The results for rabbits also indicate that they are more closely related to other mammals than they are to mice and rats. Incidentally, the tree also supports the conclusion from other molecular studies that cows and whales are more closely related to each other than to other mammals (see *Insights from the Molecular Revolution* in Chapter 23).

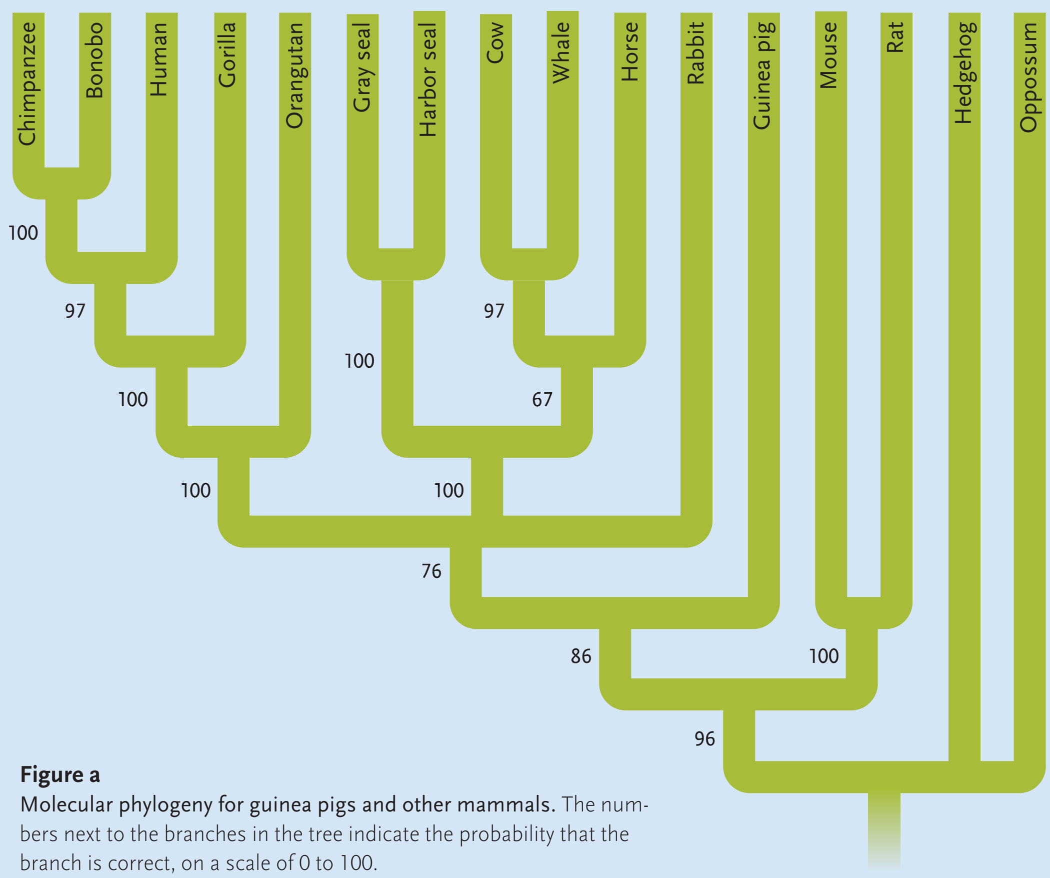


Figure a
Molecular phylogeny for guinea pigs and other mammals. The numbers next to the branches in the tree indicate the probability that the branch is correct, on a scale of 0 to 100.

other mammals, and they have flexible hip and shoulder joints, which allow a variety of locomotor activities. They can grasp objects with their hands and feet, because they have nails, not claws, on their fingers and toes; their fingertips are well endowed with sensory nerves that enhance the sense of touch. Unlike other mammals, most primates have an opposable big toe, which can touch the tips of other digits and the sole of the foot; many species also have an opposable thumb.

Most primates are diurnal (active during daylight hours), and, unlike most mammals, they rely more on vision than on their sense of smell. Thus, they generally have short snouts and small olfactory lobes of the brain. Most species have forward-facing eyes with overlapping fields of vision, providing excellent depth perception, which comes in handy when moving through trees. Many species have color vision.

Primate brains—especially the regions that integrate information—are large and complex. As a result, they have an exceptional capacity to learn. Most species live in social groups; thus, young primates, which mature slowly, can interact with and learn from their elders and peers during an extended period of parental care. Females give birth to only one or two young at a time, allowing them to devote substantial attention to each offspring.

Living Primates Include Two Major Lineages

Primatologists recognize two lineages within the Primates **(Figure 30.31),** the Strepsirhini (*streptos* = twisted or turned, *rhin* = nose) and the Haplorhini (*haploos* = single or simple).

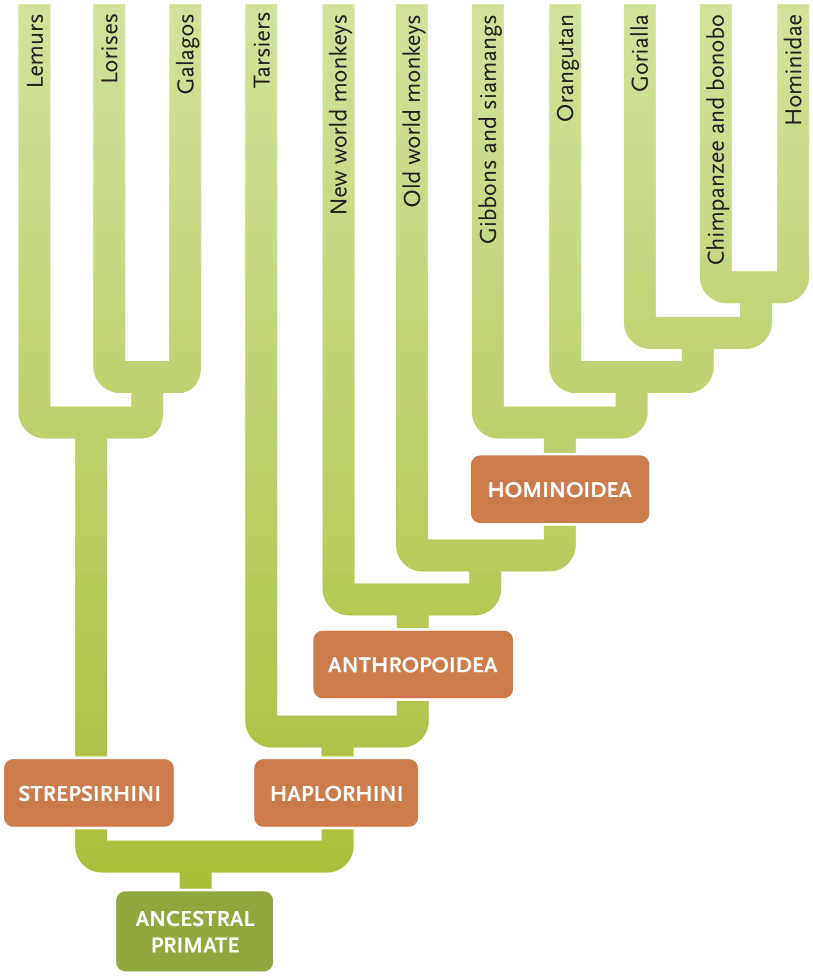


Figure 30.31
Primate phylogeny. A phylogenetic tree for the Primates illustrates the two main lineages: Strepsirhini and Haplorhini. Note that chimpanzees are the closest living relatives of humans.

Strepsirhini. The 36 living species of Strepsirhini—lemurs, lorises, and galagos—possess many ancestral morphological traits, including moist, fleshy noses and eyes that are positioned somewhat laterally on their heads **(Figure 30.32).** Strepsirhines generally have short gestation periods and rapid maturation. Today, 22 lemur species survive on Madagascar, a large island off the east coast of Africa; they are ecologically diverse and range in size from 40 g to 7 kg; some lemurs are arboreal, whereas others spend substantial time on the ground. The 12 species of lorises and galagos occupy tropical forest and subtropical woodlands in Africa, India, and Southeast Asia; they are all arboreal and nocturnal.

Haplorhini. Most species in the Haplorhini—the familiar monkeys and apes—have many derived primate characteristics, including compact, dry noses, and forward-facing eyes.

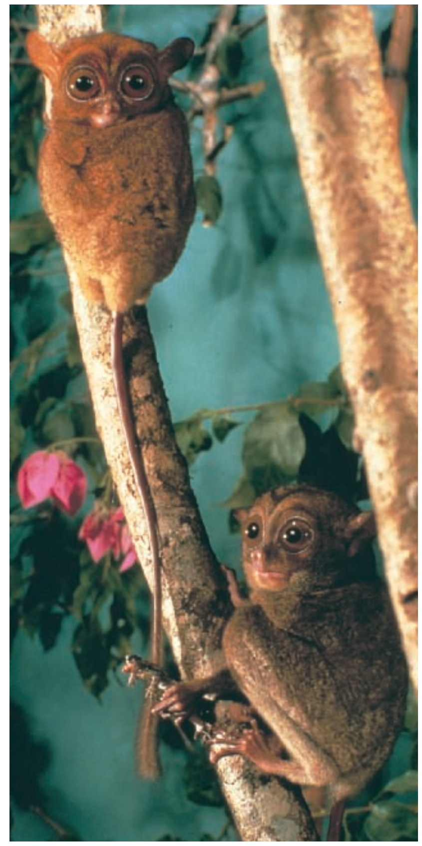
However, five species of tarsiers, which are restricted to tropical forests on the islands of Southeast Asia, exhibit several ancestral traits: small body size (about 100 g), large eyes and ears, and two grooming claws on each foot **(Figure 30.33).** But they share the derived characteristics of dry noses and forward-facing eyes with the other haplorhines; and DNA sequence data link them to the monkeys and apes and not to the strepsirhines described earlier.

The 130 or so species of monkeys, 13 species of apes, and humans constitute the monophyletic haplorhine lineage **Anthropoidea,** which probably arose in Africa; fossils of a diverse and abundant radiation of forest-dwelling anthropoids, dating from the late Eocene epoch, have been discovered in northern Egypt. Continental drift then established long-term geographical and evolutionary separation of anthropoids in the New World and Old World **(Figure 30.34).**

By the middle of the Oligocene epoch, about 30 million years ago, the ancestors of the New World monkeys had arrived in South America and begun to diversify there. They probably rafted across the

Cagan Sekercioglu/Visuals Unlimited

Figure 30.32
Strepsirhines. The ring-tailed lemur *(Lemur catta)* of Madagascar has ancestral primate characteristics, such as a long snout and wet nose.



Larry Burrows/Aspect Photolibrary

Figure 30.33
Tarsiers. Tarsiers *(Tarsius bancanus)* are classified as haplorhines, but they retain many ancestral characteristics.

a. Spider monkey **b.** Hamadryas baboon

Joseph Van Os/Getty Images, Inc.

Figure 30.34
New World and Old World monkeys. (a) Many New World monkeys, such as the spider monkey *(Ateles geoffroyi)*, have prehensile tails, which they use as a fifth limb. Old World monkeys lack prehensile tails, and many, such as **(b)** the Hamadryas baboon *(Papio hamadryas)*, are largely terrestrial.

Atlantic, which was narrower at that time, on trees or other storm debris. New World monkeys now live in Central and South America (see Figure 30.34a). They range in size from tiny marmosets and tamarins (350 g) to hefty howler monkeys (10 kg). Most are exclusively arboreal and diurnal. The larger species may hang below branches by their arms, and some use a prehensile (grasping) tail as a fifth limb.

Anthropoids diversified most spectacularly in the Old World, however, eventually giving rise to two lineages—one ancestral to Old World monkeys and the other to apes and humans. Although many people assume that the apes are descended from Old World monkeys, the fossil record contradicts that impression. The earliest hominoid (ape) fossils date to the early Miocene, roughly 23 million years ago, but the oldest known Old World monkeys appeared several million years later.

Old World monkeys, which occupy habitats ranging from tropical rain forests to deserts in Africa and Asia, may grow as large as 35 kg (see Figure 30.34b). Many species are sexually dimorphic; in other words, males and females attain different adult sizes (see Section 20.3). Arboreal species use all four limbs for locomotion, but none has a prehensile tail. Some species, such as baboons, often walk or run on the ground.

Within the anthropoid lineage, the **Hominoidea** ("humanlike") is a monophyletic group that includes apes and humans. The climate of the early Miocene was wetter than it is today, and eastern Africa, where many early hominoid fossils are found, was covered with extensive forests. A climate shift in the middle Miocene, around 14 million years ago, converted dense forests into woodlands and grasslands. Hominoids probably adopted a more terrestrial existence and shifted their diets. Miocene hominoids ranged in size from 4 kg to 80 kg. They occupied both forest and open woodland habitats; some were probably ground dwelling.

Although hominoids are closely related to Old World monkeys, several characteristics distinguish them. Apes lack a tail, and great apes (orangutans, gorillas, chimpanzees, and bonobos) are much larger than monkeys. Moreover, the posterior region of the vertebral column is shorter and more stable in apes. Apes also show more complex behavior.

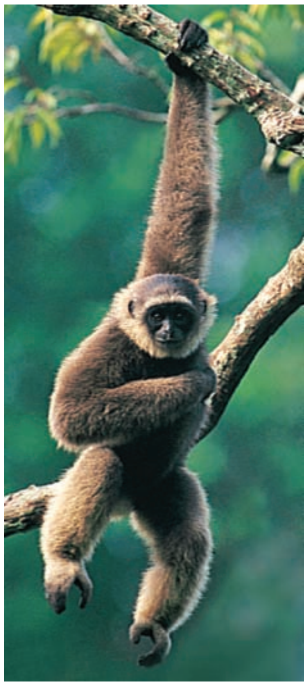
The gibbons and siamangs, which live in tropical forests in Southeast Asia, are the smallest of the apes, ranging in weight from 6 to 11 kg. With extremely long arms and strong shoulders, they hang below branches by their arms and swing themselves forward, a pattern of locomotion called **brachiation** **(Figure 30.35a).** The much larger orangutan *(Pongo pygmaeus),* now restricted to forested areas on the islands of Borneo and Sumatra, can grow to 90 kg. Orangutans use both hands and feet to climb trees; they sometimes venture onto the ground on all fours.

Gorillas *(Gorilla gorilla),* which are currently restricted to two large central African forests, are the largest of the living primates. Males can weigh 180 kg; females are about half that size. Because of their size, gorillas spend most of their time on the ground. They often use "knuckle-walking" locomotion, leaning forward and supporting part of their weight on the backs of their hands. Gorillas are almost exclusively vegetarian.

Chimpanzees *(Pan troglodytes)* are also forest dwellers, weighing up to 45 kg **(Figure 30.35b).** Like gorillas, they spend most of their waking hours on the ground; they often knuckle-walk, but sometimes adopt a **bipedal** (two-legged) stance and swagger short distances. Groups of related males form loosely defined communities of up to 50 individuals, which may cooperate in hunts and foraging. Bonobos *(Pan paniscus),* sometimes called pygmy chimpanzees, are restricted to a small area in central Africa. Somewhat smaller than chimps, they have longer legs and smaller heads.

The Primates also includes humans *(Homo sapiens),* which occupy virtually all terrestrial habitats. Humans have adaptations that allow an upright posture and bipedal locomotion. They are ground-dwelling animals with extremely broad diets and complex social behavior.

a. Black-handed gibbon



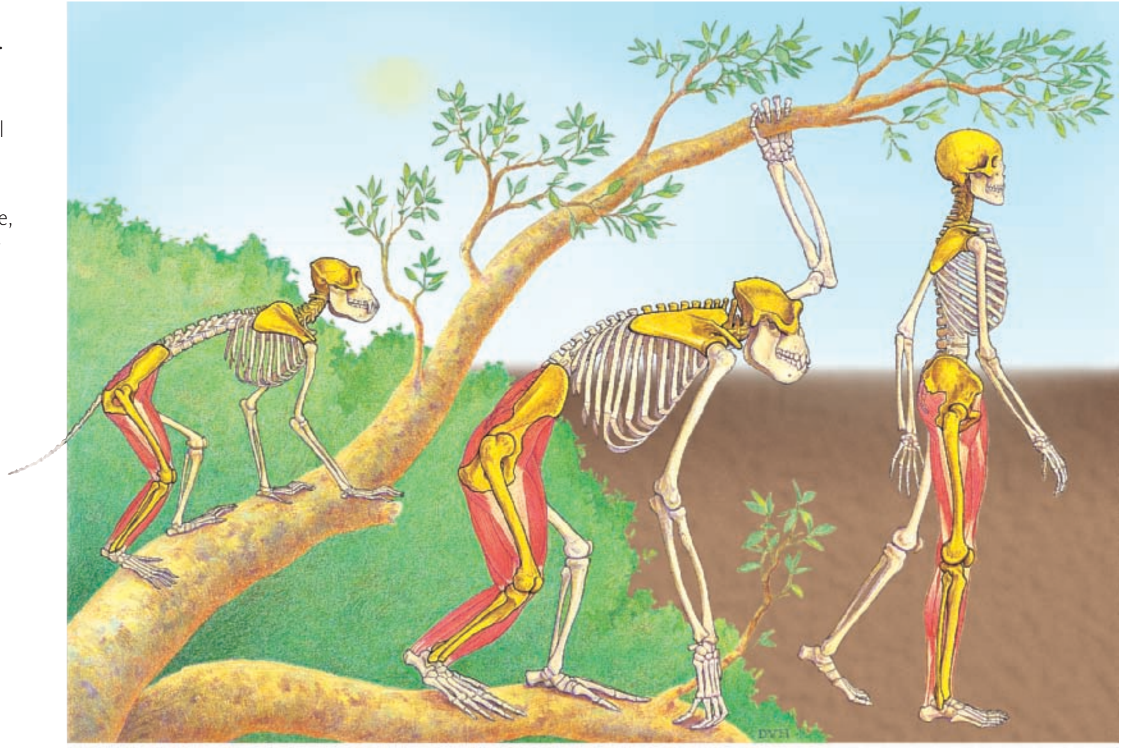
Art Wolfe/Photo Researchers, Inc.

b. Chimpanzee

Kenneth Garrett/National Geographic Image Collection

Figure 30.35
Apes. **(a)** Small-bodied apes, such as the black-handed gibbon *(Hylobates agilis)* are agile brachiators that swing through the trees with ease. **(b)** Among the large-bodied apes, chimpanzees *(Pan troglodytes)* have opposable thumbs and big toes.

Figure 30.36
Adaptations for bipedal locomotion. Differences in the posture, skeleton, and muscles of monkeys, great apes, and humans illustrate the anatomical changes that accompanied upright, bipedal locomotion. Evolutionary changes in the spine, pelvis, hip, knee, ankle, and foot were accompanied by changes in the sizes of leg muscles and their points of attachment to the bones they move.



Study Break

1. What characteristics of primates allow them to spend a great deal of time in trees?
2. What is the lowest taxonomic group that includes monkeys, apes, and humans? What is the lowest taxonomic group that includes only apes and human?
3. Which species of ape spend most of the time on the ground?

30.13 The Evolution of Humans

Genetic analyses of living hominoid species indicate that African hominoids diverged into several lineages between 10 million and 5 million years ago; one lineage, the **hominids,** includes modern humans and our bipedal ancestors.

Hominids First Walked Upright in East Africa about 6 Million Years Ago

Upright posture and bipedal locomotion are key adaptations that distinguish hominids from apes. Researchers identify early hominid fossils from features of the skull, spine, pelvis, knees, ankles, and feet that make bipedal locomotion possible **(Figure 30.36).** As a consequence of bipedal locomotion, the hands were no longer used for locomotor functions, allowing them to become specialized for other activities, such as tool use. Evolutionary refinements in grasping ability allow hominids to hold objects tightly with a *power grip* or manipulate them precisely with a *precision grip* **(Figure 30.37).** Hominids also developed larger brains.

Paleontologists have uncovered fossil of numerous hominids that lived in East Africa and South Africa from roughly 6 million to 1 million years ago **(Figure 30.38).** In 2000, researchers found 13 fossils of *Orrorin tugenensis* ("first man" in a local African language), a species that lived about 6 million years ago in East Af-

Figure 30.37
Power grip versus precision grip. Hominids grasp objects in two distinct ways. **(a)** The power grip allows us to grasp an object firmly. **(b)** The precision grip allows us to manipulate objects with fine movements.

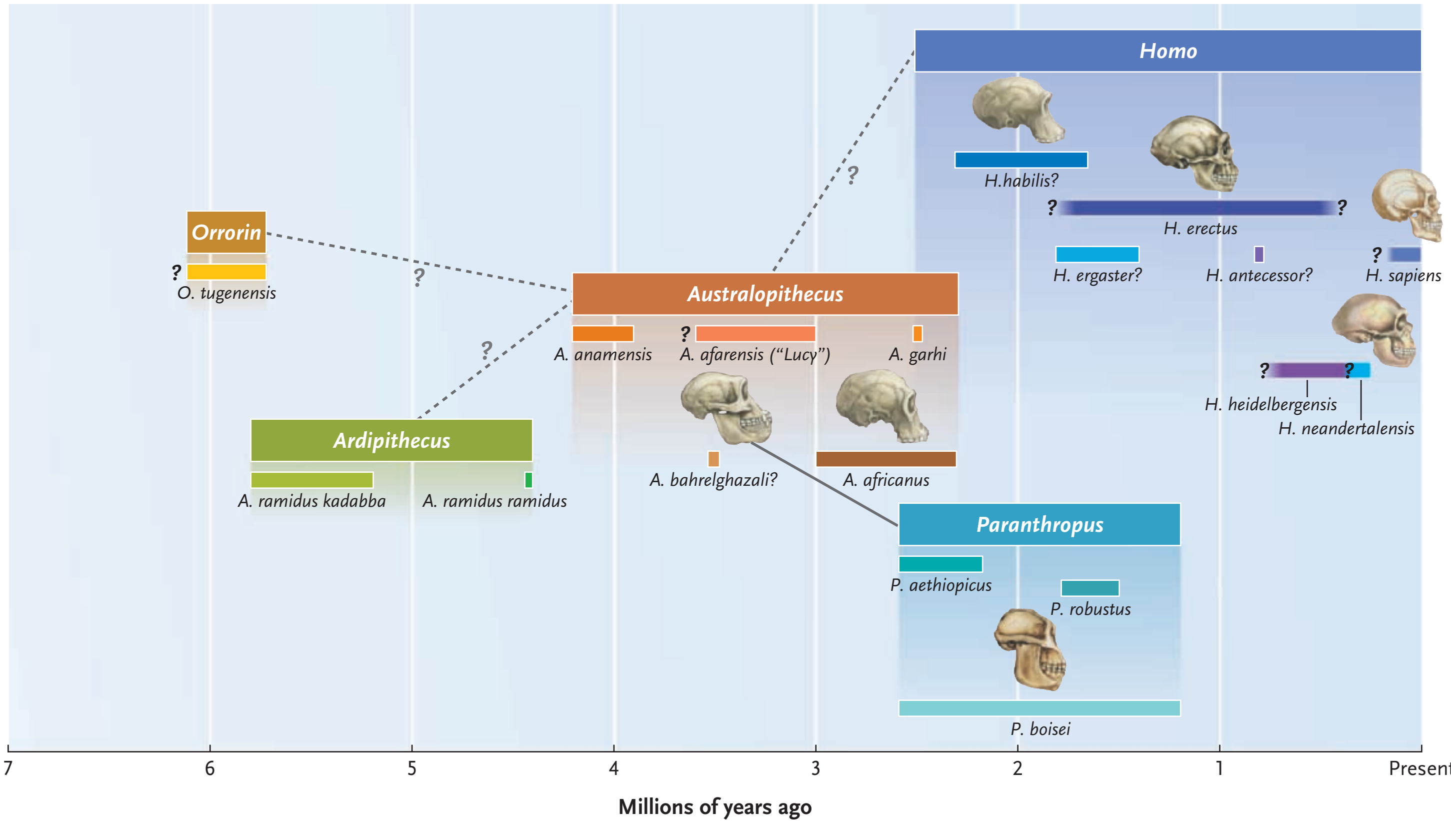


Figure 30.38
Hominid time line. Several species of hominids lived simultaneously at sites in eastern and southern Africa. The time line for each species and genus reflects the ages of known fossils. The numerous question marks indicate researchers' uncertainty about the classification, the ages of fossils, and the evolutionary relationships among the species. Some of the skulls pictured are reconstructed from fragmentary fossils.

rican forests. However, these remains are fragmentary, and experts are still evaluating them. The best-studied early hominid fossils, the remains of 50 individuals discovered in the East African Rift Valley, date from about 5 million years ago. Named *Ardipithecus ramidus,* these hominids stood 120 cm tall and had apelike teeth. Other *Ardipithecus* fossils, recently discovered at a different site, appear to be much older (5.8 million years) and show evidence of bipedal locomotion.

Hominid fossils from 4.2 million to 1.2 million years ago are known from many sites in East, Central, and South Africa. They are currently assigned to the genera *Australopithecus* (*australis* = southern; *pithekos* = ape) and *Paranthropus* (*para* = beside; and *anthropos* = human being). With their large faces, protruding jaws, and small skulls and brains, most of these hominids had an apelike appearance (see Figure 30.38). *Australopithecus anamensis,* which lived in East Africa around 4 million years ago, is the oldest known species. It had thick enamel covering on its teeth, a derived hominid characteristic; the structure of a fossilized leg bone suggests that it was bipedal.

Specimens of more than 60 individuals of *Australopithecus afarensis* have been found in northern Ethiopia, including about 40% of a female's skeleton, named "Lucy" by its discoverers **(Figure 30.39).** *A. afarensis* lived 3.5 million to 3 million years ago, but it retained several ancestral characteristics. For example, it had moderately large and pointed canine teeth, and a relatively small brain. Males and females were 150 cm and 120 cm tall, respectively. Skeletal analyses suggest that *A. afarensis* was fully bipedal, a conclusion supported by fossilized footprints preserved in a layer of volcanic ash.

Other species of *Australopithecus* and *Paranthropus* lived in East Africa or South Africa between 3.7 million and 1 million years ago. Adult males ranged from 40 to 50 kg in weight and from 130 to 150 cm in height; females were smaller. Most species had deep jaws and large molars. Several species had a crest of bone along the midline of the skull, providing a large surface for the attachment of jaw muscles. These anatomical features suggest that they fed on hard food, such as nuts, seeds, and other vegetable products. One species,

Figure 30.39
Australopithecines. **(a)** Researchers named the most complete fossil of *Australopithecus afarensis* "Lucy." **(b)** Mary Leakey discovered australopithecine footprints, made in soft, damp volcanic ash about 3.7 million years ago. The footprints indicate that australopithecines were fully bipedal.

Australopithecus africanus, known only from South Africa, had small jaws and teeth, indicating that it probably consumed a softer diet. The phylogenetic relationships of the species classified as *Australopithecus* and *Paranthropus*—and their exact relationships to later hominids—are not yet fully understood. But most scientists agree that *Australopithecus* was ancestral to humans, which are classified in the genus *Homo*.

Homo habilis Was Probably the First Hominid to Manufacture Stone Tools

Pliocene fossils of the earliest humans, which may have included several species, are fragmentary. They are also widely distributed in space and time, complicating analyses of their relationships. For the sake of simplicity, we describe them as belonging to one species, *Homo habilis* ("handy man").

From 2.3 million to 1.7 million years ago, *H. habilis* occupied the woodlands and savannas of eastern and southern Africa, sharing these habitats with various species of *Paranthropus*. The two genera are easy to tell apart because the brains of *H. habilis* were at least 20% larger, and they had larger incisors and smaller molars than their hominid cousins. Their diet included hard-shelled nuts and seeds as well as soft fruits, tubers, leaves, and insects. They may also have hunted small prey or scavenged carcasses left by large predators.

Researchers have found numerous tools dating to the time of *H. habilis,* but they are not sure which species used them. Many of the hominid species alive at the time probably cracked marrowbones with rocks or scraped flesh from bones with sharp stones. Paleoanthropologist Louis Leakey was the first to discover evidence of tool *making* at East Africa's Olduvai Gorge, which cuts through a great sequence of sedimentary rock layers. The oldest tools at this site are crudely chipped pebbles, which were probably manufactured by *H. habilis*.

Homo erectus Dispersed from Africa to Other Continents

Early in the Pleistocene epoch, about 1.8 million years ago, new species of humans appeared in East Africa. Most fossils are fragmentary. For convenience, we describe them all as *Homo erectus* ("upright man"), recognizing that they probably represent several species. One nearly complete skeleton suggests that *H. erectus* was taller than its ancestors, had a much larger brain, a thicker skull, and protruding brow ridges **(Figure 30.40).**

H. erectus made fairly sophisticated tools, including the hand axe (see Figure 30.40b), which they apparently used to cut food and other materials, to scrape meat from bones, and to dig for roots. *H. erectus* probably fed on both plants and animals; they may have hunted and scavenged

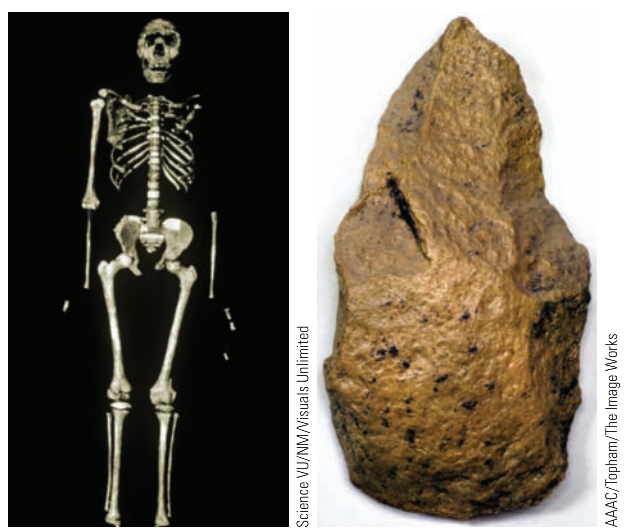


Figure 30.40
Homo erectus. **(a)** A nearly complete skeleton of *Homo erectus* was discovered in Kenya. **(b)** Hand axes are frequently found at *H. erectus* sites.

animal prey. Archaeological data points to their use of fire to process food and to keep themselves warm.

The pressure of growing populations apparently forced groups of *H. erectus* out of Africa about 1.5 million years ago. They dispersed northward from East Africa into both northwestern Africa and Eurasia. Some moved eastward through Asia as far as the island of Java. Recent discoveries in Spain indicate that *H. erectus* also occupied parts of Western Europe.

Modern Humans Are the Only Surviving Descendants of *Homo erectus*

Judging from its geographical distribution, *Homo erectus* was successful in many environments. It produced several descendant species, of which modern humans (*Homo sapiens,* "wise man") are the only survivors.

Fossils from Africa, Asia, and Europe indicate that archaic humans, the now-extinct descendants of *H. erectus,* first appeared at least 400,000 years ago. They generally had a larger brain, rounder skull, and smaller molars than *H. erectus.*

Neanderthals. The Neanderthals *(Homo neanderthalensis),* who occupied Europe and western Asia from 150,000 to 28,000 years ago, are the best-known archaic humans. Compared with modern humans, they had a heavier build, more-pronounced brow ridges, and slightly larger brains (see Figure 30.38). Neanderthals were culturally and technologically sophisticated. They made complex tools, including wooden spears, stone axes, and flint scrapers and knives. At some sites they built shelters of stones, branches, and animal hides, and they routinely used fire. They were successful hunters and probably consumed nuts, berries, fishes, and bird eggs. Some groups buried their dead, and they may have had rudimentary speech.

Researchers once classified Neanderthals as a subspecies of *H. sapiens,* but most scientists now believe that they were a separate species. In 1997 two teams of researchers, Matthias Kring and Svante Pääbo of the University of Munich and Anne Stone and Mark Stoneking of Pennsylvania State University, independently analyzed short segments of mitochondrial DNA (mtDNA) extracted from the fossilized arm bone of a Neanderthal. Unlike nuclear DNA, which individuals inherit from both parents, only mothers pass mtDNA to offspring. It does not undergo genetic recombination (see Section 13.5), and it has a high mutation rate, making it useful for phylogenetic analyses. Many scientists believe that mutation rates in mtDNA are fairly constant, allowing this molecule to serve as a molecular clock (see Section 23.6). Comparing the Neanderthal sequence with mtDNA from 986 living humans, the researchers discovered three times more differences between the Neanderthals and modern humans than between pairs of modern humans in their sample. These results suggest that Neanderthals and modern humans are different species that diverged from a common ancestor 690,000 to 550,000 years ago—hundreds of thousands of years before modern humans appeared.

Modern Humans. Modern humans *(Homo sapiens)* differ from Neanderthals and other archaic humans in having a slighter build, less-protruding brow ridges, and a more prominent chin. The earliest fossils of modern humans found in Africa and Asia are 150,000 years old; those from the Middle East are 100,000 years old. Fossils from about 20,000 years ago are known from Western Europe, the most famous being those of the Cro-Magnon deposits in southern France. The widespread appearance of modern humans roughly coincided with the demise of Neanderthals in Western Europe and the Middle East 40,000 to 28,000 years ago. Although the two species apparently coexisted in some regions for thousands of years, we have little concrete evidence that they interacted.

One Origin or Many? *Homo erectus* apparently left Africa in waves between 1.5 million and 500,000 years ago. But when and where did modern humans first arise? Researchers use fossils and genetic data from contemporary human populations to address two competing hypotheses about this question.

According to the **African Emergence Hypothesis,** a population of *H. erectus* gave rise to several descendant species between 1.5 million and 0.5 million years ago. The early descendants, archaic humans, left Africa and established populations in the Middle East, Asia, and Europe. Some time later, 200,000 to 100,000 years ago, *H. sapiens* arose in Africa. These modern humans also migrated into Europe and Asia, and eventually drove the archaic humans to extinction. Thus, the African Emergence Hypothesis suggests that all modern humans are descended from a fairly recent African ancestor.

According to the **Multiregional Hypothesis,** populations of *H. erectus* and archaic humans had spread through much of Europe and Asia by 0.5 million years ago. Modern humans then evolved from archaic humans in many regions simultaneously. Although these geographically separated populations may have experienced some evolutionary differentiation (see Section 21.3), gene flow between them prevented reproductive isolation and maintained them as a single, but variable, species, *H. sapiens.*

Paleontological data do not clearly support either hypothesis. Some scientists argue that human remains with a mixture of archaic and modern characteristics confirm the Multiregional Hypothesis. In late 1998, for example, researchers in Portugal discovered a fossilized child that had been buried only 24,000 years ago, when only modern humans are thought to have occupied Europe. This fossil shows a surprising mix of Neanderthal and modern human traits, possibly indicating that the two groups interbred. On the other hand, recent finds in the Mideast indicate that Neanderthals and modern humans coexisted without interbreeding for 50,000 years. Thus, Neanderthals could not have been the ancestors of those modern humans.

Scientists also use DNA sequences from modern humans to evaluate the two hypotheses. In 1987, Rebecca Cann, Mark Stoneking, and Allan Wilson of the University of California at Berkeley and their colleagues published an analysis of mtDNA sequences from more than 100 ethnically diverse humans on four continents. They found that contemporary African populations contain the greatest variation in mtDNA. One explanation for this observation is that neutral mutations have been accumulating in African

Unanswered Questions

What causes the evolution of diversity?

In this chapter, you have read about the extensive diversity—in size, shape, color, structure, lifestyle, and habitats—of the vertebrate animals. Their mechanisms for maintaining themselves—including behaviors such as moving, feeding, reproducing, hiding, fighting, and sleeping—are equally varied. But nearly all vertebrates share some fundamental features of life. Recent research shows us that this generality is especially true of early development, but it is also apparent in many of the basic homeostatic mechanisms that vertebrates share—features of digestion and metabolism, respiration, and other characteristics regulated by the products of genetic networks and cascades. Biologists had long thought that once we understood the genetics of a variety of species, we would also understand the basis for their evolution and the maintenance of diversity. But now that a number of animal genomes have been sequenced completely, we have actually learned more about the genetic information that is shared by all animal species than we have about the genes that promote diversification. One of the great unanswered questions in biology, therefore, is how diversity arises and how it is maintained, given that so much genetic information is shared among even distantly related species. Equally important is why the same kinds of features evolved almost identically time after time in many unrelated lineages.

The ever-increasing body of genetic information is opening the "black box" of why there are so many species, and how they came to be. For example, we've long known that limbs evolved from fins, based on fossil evidence (which continues to accumulate, providing additional supportive evidence). But we haven't known what the *mechanisms* for forming a fin or a limb are, and how selection works to modify such structures. Now, with our knowledge of *Hox* and other tool-kit genes that control embryonic development, we understand how fins and limbs are formed. We can also experimentally manipulate development and perform selection experiments to test possible pathways of evolution—the "how they came to be."

Why do we see the recurrent, independent evolution of common themes?

A phenomenon that we often see, but don't yet fully understand, is why certain themes—such as body elongation, limblessness, and tooth modification—recur among distantly related vertebrates. The evolution of viviparity, live-bearing reproduction, is one such theme. In the vast majority of animals, reproduction occurs when a female lays her eggs in water and a male sprays sperm over them; typically both parents then abandon the fertilized eggs. But some species in many separate vertebrate lineages have evolved forms of viviparity. Cartilaginous and bony fishes exhibit diverse modes of embryonic nutrition, and in one group, the sea horses, it is the males that become pregnant. Amphibians also exhibit diverse patterns of viviparity: some have pregnant fathers and others have mothers that brood embryos in the skin of their backs, in their stomachs, or in their oviducts. And many squamate reptiles grow placentas similar to those of mammals. All mammals except monotremes are live-bearers with maternal nutrition. In fact, among the living vertebrate groups, birds are the only group that has not evolved the live-bearing habit. Can you think of some reasons why?

In some fishes, amphibians, and squamates, the mother supplies all the nutrition for the developing young through her investment in the egg; but in other species, females resorb their yolks and provide nutrients directly to offspring that are born as fully metamorphosed juveniles. Given that viviparity has evolved independently in approximately 200 vertebrate groups, it is not surprising that we see such a variety of reproductive patterns. Biologists are just beginning to understand the evolution of viviparity and to determine which patterns are shared among different evolutionary lineages and which are not. It appears that the hormonal basis for viviparity is similar in many groups, although the timing, the receptors involved, and the physiological responses vary. Researchers are now identifying candidate genes in the hope of unraveling the genetic networks that have fostered the different modes of viviparity. Ecological studies are revealing the interactions of potential selection regimes that influence reproductive modes. However, we still have much to learn about how genetics, development, physiology, and ecology interact in the evolution of diversity and common recurring themes.

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populations longer than in others, marking the African populations as the oldest on Earth. They also found that all human populations contain at least one mtDNA sequence of African origin, suggesting an African ancestry for all modern humans. Cann and her colleagues named the ancestral population, which lived approximately 200,000 years ago, the "mitochondrial Eve."

Proponents of the Multiregional Hypothesis criticized the statistical techniques used by Cann and her colleagues. Some also noted that if ancient populations in Africa were larger than those in other parts of the world, population size, rather than age, could account for high genetic variability (see Section 20.4). Moreover, recent research suggests that mutation rates in mtDNA might not be constant and that natural selection can influence mtDNA sequences, calling into question mtDNA's usefulness as a molecular clock.

Other researchers have examined genetic material that males inherit only from their fathers. In 1995, L. Simon Whitfield and his colleagues at Cambridge University published a study on an 18,000-base-pair sequence from the Y chromosome, which does not undergo recombination with the X chromosome. Because the sequence contains no genes, it should not be subject to natural selection. Thus, sequence variations should result only from random mutations, which can serve as a molecular clock. The researchers discovered only three sequence mutations among the five subjects examined—a surprising result, given that the sample included a European, a Melanesian, a South American, and two Africans. By contrast, a chimpanzee exhibited 207 differences from the human version of the sequence. Using a sophisticated statistical analysis, the Whitfield team calculated that the common ancestor of these five diverse humans, dubbed the "African Adam," lived between 37,000 and 49,000 years ago. The limited genetic diversity and relatively recent origin of a common ancestor clearly support the African Emergence Hypothesis. Follow-up studies on the Y chromosomes of thousands of men from Africa, Europe, Asia, Australia, and the Americas have confirmed that all modern humans are the descendants of a single migration out of Africa.

Some controversies about human evolution arise because researchers who use genetic data must make assumptions about the sizes and geographical ranges of ancient populations, the amount of gene flow they experienced, and how natural selection may have affected them. And one of a scientist's important responsibilities is to question the assumptions made by other workers. Controversies also surround the particular statistical tests that researchers use to analyze these data. But intellectual disputes are routine in science, and they challenge researchers to refine their hypotheses and to test them in new ways. Questions about the details of human origins are at the center of one of the liveliest debates in evolutionary biology today; additional research will surely clarify the evolutionary history of our species.

Study Break

1. What trait allows researchers to distinguish between apes and humans?
2. What evidence suggests that Neanderthals and modern humans represent two distinct species?
3. How do the African Emergence Hypothesis and the Multiregional Hypothesis differ in what they say about the origin of modern humans?

Review

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30.1 Invertebrate Deuterostomes

- Echinoderms have secondary radial symmetry, a five-part body plan, and a unique water vascular system that is used in locomotion and feeding (Figures 30.2 and 30.3).
- Hemichordates collect oxygen and particulate food from seawater that enters the mouth and exits the pharynx through the gill slits (Figure 30.4).

30.2 Overview of the Phylum Chordata

- Chordates share several derived characteristics: a notochord; postanal tail; segmentation of body wall and tail muscles; a dorsal, hollow nerve cord; and a perforated pharynx at some stage of the life cycle (Figure 30.5).
- Two subphyla of invertebrate chordates use their perforated pharynx to collect particulate food (Figures 30.6 and 30.7).
- The subphylum Vertebrata includes animals with a bony endoskeleton, structures derived from neural crest cells, and a brain divided into three regions.

Animation: Tunicate body plan

Animation: Lancelet body plan

30.3 The Origin and Diversification of Vertebrates

- Vertebrates evolved from an invertebrate chordate ancestor, probably through duplication of the *Hox* gene complex (Figure 30.8).

- Vertebrates diversified into numerous lineages (Figure 30.10). Gnathostomata includes all jawed vertebrates. Tetrapoda includes all lineages that ancestrally had four legs. Amniota includes groups descended from animals that produced an amniote egg.

  Animation: Vertebrate evolution

30.4 Agnathans: Hagfishes and Lampreys, Conodonts and Ostracoderms

- Living agnathans—hagfishes and lampreys—are jawless fishes that lack vertebrae and paired fins (Figure 30.11).
- Conodonts had bonelike elements in the pharynx. Ostracoderms were heavily armored, jawless fishes that sucked particulate food into their mouths (Figure 30.12).

  Animation: Jawless fishes

30.5 Jawed Fishes

- Jaws arose through the evolutionary modification of gill arches, which supported the pharynx of ostracoderms (Figure 30.13). Fins arose at the same time (Figure 30.14).
- The first jawed fishes, Acanthodii and Placodermi, are now extinct (Figure 30.15). Chondrichthyans have a skeleton composed of cartilage (Figure 30.16). Actinopterygians and Sarcopterygians have a skeleton composed of bone. Actinopterygians have fins supported by bony rays (Figures 30.17 and 30.18). Sarcopterygians have fins supported by muscles and a bony endoskeleton (Figure 30.19).

  Animation: Evolution of jaws

  Animation: Cartilaginous fishes

  Animation: Bony fish body plan

30.6 Early Tetrapods and Modern Amphibians

- Tetrapods arose in the late Devonian (Figure 30.20). Key tetrapod adaptations include a strong vertebral column, girdles, limbs, and modified sensory systems.
- Modern amphibians are generally restricted to moist habitats. Their life cycles often include larval and adult stages. Urodeles (salamanders) are elongate, tailed amphibians. Anurans (frogs) have compact bodies, long legs, and no tails. Caecelians are legless burrowers (Figure 30.21).

  Animation: Evolution of limb bones

  Animation: Salamander locomotion

30.7 The Origin and Mesozoic Radiations of Amniotes

- Key adaptations in amniotes, the first fully terrestrial vertebrates, included a water-resistant skin, amniote eggs (Figure 30.22), and the excretion of nitrogen wastes as uric acid.
- Early amniotes diversified into anapsids, synapsids, and diapsids, distinguished by the number of temporal arches on the skull (Figure 30.23).
- Diapsids split into two lineages, archosaurs and lepidosaurs.

  Animation: Amniote egg

30.8 Testudines: Turtles

- The turtle body plan includes a bony shell, with a dorsal carapace and ventral plastron (Figure 30.24).

  Animation: Tortoise shell and skeleton

30.9 Living Nonfeathered Diapsids: Sphenodontids, Squamates, and Crocodilians

- Sphenodontids are remnants of a once-diverse lineage (Figure 30.25a).
- Squamates have skin composed of overlapping, keratinized scales (Figure 30.25b and c).
- Crocodilians are semiaquatic predators (Figure 30.25d).

  Animation: Crocodile body plan

30.10 Aves: Birds

- Birds have adaptations that reduce their weight and generate power for flight (Figure 30.26).
- Modern birds exhibit adaptations of their bills, feet, wings, and behavior (Figure 30.27).

  Animation: Feather development

  Animation: Avian bone and muscle structure

30.11 Mammalia: Monotremes, Marsupials, and Placentals

- Key adaptations of mammals include endothermy, which allows high levels of activity; modification of the teeth and jaws; extensive parental care of offspring; and large and complex brains.
- Three major groups of mammals, Prototheria, the monotremes; and two lineages of Theria, the marsupials and the placentals, differ in their reproductive patterns.
- Monotremes are restricted to Australia and New Guinea (Figure 30.28). Marsupials are abundant in Australia and occur in South America and North America (Figure 30.29). Most living mammals are placentals, occupying nearly all terrestrial and aquatic habitats (Figure 30.30).

  Animation: Mammalian dentition

  Animation: Mammalian radiations

  Animation: Structure of the placenta

30.12 Nonhuman Primates

- Key adaptations allow Primates to be arboreal and diurnal: upright posture and flexible limbs; good depth perception; and a large and complex brain.
- The Strepsirhini have many ancestral primate characteristics (Figure 30.32). The Haplorhini have many derived primate characteristics (Figures 30.33 and 30.34).
- Primates arose in forests about 55 mya. The hominoid lineage, which includes apes and humans, arose in Africa about 23 mya (Figure 30.35).

  Animation: Primate skeletons

  Animation: Skulls of extinct primates

30.13 The Evolution of Humans

- Hominids, the lineage that includes humans, arose in Africa between 10 mya and 5 mya. Hominid anatomy permits bipedal locomotion (Figure 30.36). Over time, hominids developed larger brains, improved grasping ability in the hands (Figure 30.37), and tool-making behavior. Several genera of hominids occupied sub-Saharan Africa for several million years (Figures 30.38 and 30.39).
- *Homo habilis* was the first hominid species to make stone tools. *Homo erectus,* which arose in East Africa about 1.8 mya, made sophisticated stone tools (Figure 30.40).

- The early descendants of *H. erectus* left Africa in waves, populating Asia and Europe. Neanderthals, the best known of these groups, became extinct about 30,000 years ago.
- Modern humans, *Homo sapiens,* arose approximately 150,000 years ago and migrated out of Africa, eventually replacing archaic humans in Europe and Asia.

Animation: Fossils of australopiths

Animation: *Homo* skulls

Animation: Primate phylogenetic tree

Animation: Genetic distance between human groups

Questions

Self-Test Questions

1. Which phylum includes animals that have a water vascular system?
   a. Echinodermata
   b. Hemichordata
   c. Chordata
   d. Tetrapoda
   e. Amniota
2. Which of the following is *not* a characteristic of all chordates?
   a. notochord with postanal tail
   b. segmental body wall and tail muscles
   c. segmented nervous system
   d. dorsal hollow nerve cord
   e. perforated pharynx
3. Which group of vertebrates has adaptations that allow it to reproduce on land?
   a. agnathans
   b. tetrapods
   c. gnathostomes
   d. amniotes
   e. ichthyosaurs
4. Which group of fishes has the most living species today?
   a. sarcopterygians
   b. actinopterygians
   c. chondrichthyans
   d. acanthodians
   e. ostracoderms
5. Modern amphibians:
   a. closely resemble their Paleozoic ancestors.
   b. always occupy terrestrial habitats as adults.
   c. never occupy terrestrial habitats as adults.
   d. are generally larger than their Paleozoic ancestors.
   e. are generally smaller than their Paleozoic ancestors.
6. Which of the following key adaptations allows amniotes to occupy terrestrial habitats?
   a. the production of carbon dioxide as a metabolic waste product
   b. an unshelled egg that is protected by jellylike material
   c. a dry skin that is largely impermeable to water
   d. a lightweight skeleton with hollow bones
   e. feathers or fur that provide insulation against cold weather
7. Which of the following characteristics does *not* contribute to powered flight in birds?
   a. a lightweight skeleton
   b. efficient respiratory and circulatory systems
   c. enlarged forelimbs and a keeled sternum
   d. a high metabolic rate that releases energy from food rapidly
   e. scaly skin on the legs and feet
8. Which of the following characteristics did *not* contribute to the evolutionary success of mammals?
   a. extended parental care of young
   b. an erect posture and flexible hip and shoulder joints
   c. specializations of the teeth and jaws
   d. enlargement of the brain
   e. high metabolic rate and high body temperature
9. The Hominoidea is a monophyletic group that includes:
   a. apes and monkeys
   b. apes only
   c. humans and human ancestors
   d. apes and humans
   e. monkeys, apes, and humans
10. Which of the following hominid species was the earliest?
    a. *Ardipithecus ramidus*
    b. *Australopithecus afarensis*
    c. *Homo habilis*
    d. *Homo erectus*
    e. *Homo neanderthalensis*

Questions for Discussion

1. Most sharks and rays are predatory, but the largest species feed on plankton. Construct a hypothesis to explain this observation. How would you test your hypothesis?
2. When tetrapods first ventured onto the land, what new selection pressures did they face? What characteristics might have fostered the success of these animals as they made the transition from aquatic to terrestrial habitats?
3. Use a pair of binoculars to observe several species of birds that live in different types of environments, such as lakes and forests. How are their beaks and feet adapted to their habitats and food habits?
4. Imagine that you unearthed the complete fossilized remains of a mammal. How would you determine the food habits of this now extinct animal?
5. Many myths about human evolution are embraced by popular culture. Using the information you have learned about human evolution, argue against each of the following myths.
   a. Humans evolved from chimpanzees.
   b. Evolution occurred in a steady linear progression from primitive primate to anatomically modern humans.
   c. All human characteristics, such as bipedal locomotion and an enlarged brain, evolved simultaneously and at the same rate.

Experimental Analysis

Walking along a rocky coast one day, you discover two small creatures—one lumpy and the other worm-shaped. What anatomical studies would you conduct to determine whether or not they are chordates? What genetic studies might provide supplementary evidence?

Evolution Link

Birds and crocodiles are both descended from an ancestral archosaur. What shared anatomical and behavioral characteristics reflect this common ancestry? Explain why dinosaurs, which were also members of the archosaur lineage, may have shared these traits as well. Review Figure 30.23 before formulating your answer.

How Would You Vote?

Private collectors find and protect fossils, but a private market for rare vertebrate fossils raises the cost of museums and encourages theft from protected fossil beds. Should private collecting of vertebrate fossils be banned? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.