26 ANIMAL EVOLUTION—THE VERTEBRATES

Interpreting and Misinterpreting the Past

In Charles Darwin's time, major groups of organisms were already identified. A big obstacle to accepting his theory of evolution by natural selection was the seeming lack of transitional forms. If new species evolve from older ones, then where were the "missing links" in the fossil record—forms with intermediate traits that bridge major groups?

Ironically, workmen at a limestone quarry in Germany had already unearthed one. The pigeon-sized fossil looked like a small meat-eating dinosaur (*Dromaeosaurus*). It had three long clawed fingers on each forelimb, a long bony tail, and short, spiky teeth. Later, diggers found another one. Later still, someone noticed the feathers. If those were birds, why did they have teeth and a bony tail? If dinosaurs, what were they doing with *feathers*? In time the specimen was named *Archaeopteryx*, meaning ancient winged one (Figure 26.1).

Between 1860 and 1988, six *Archaeopteryx* specimens and a fossilized feather were found. Anti-evolutionists tried to dismiss them as forgeries. Someone, they said, pressed modern bird bones and feathers against wet plaster and the imprints only looked like fossils. Microscopic examination confirmed the fossils are real. Further confirmation of their age came from the remains of obviously ancient jellyfishes, worms, and other species in the same limestone layers.

Radiometric dating shows that *Archaeopteryx* lived 150 million years ago. Why are its remains so well preserved? This vertebrate lived in a tropical forest near a large, warm, stagnant lagoon, and reefs kept out oxygenated water from the sea. It was not an inviting place for scavenging animals that might have eaten the remains of *Archaeopteryx* and other organisms that fell from the sky or drifted offshore.

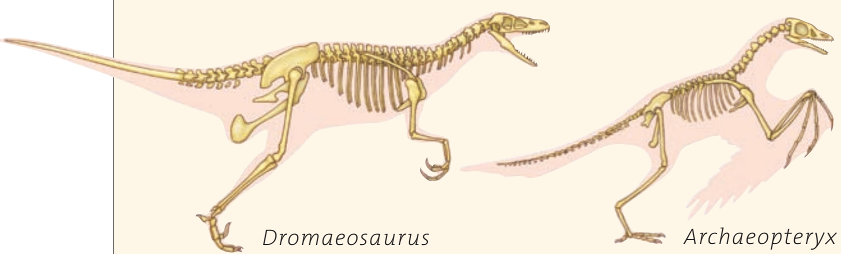


Figure 26.1 Placing *Archaeopteryx* in time. This painting is based on fossils of plants and animals that lived in a tropical forest during the Jurassic. In the center foreground, gliding *Archaeopteryx*. In the background, left to right, *Stegosaurus* and *Apatosaurus* (herbivores), *Saurophaganax* ("king of reptile eaters"), and *Camptosaurus* (a beaked herbivore). At far right, a climbing mammal. Tiny-brained *Apatosaurus* grew as long as 27 meters (90 feet) and weighed 33 to 38 tons; it was one of the largest land animals that ever lived. On the facing page, one of the *Archaeopteryx* fossils.

IMPACTS, ISSUES

Watch the video online!

With each storm surge, fine sediments driven over the reefs gently buried carcasses on the bottom of the lagoon. Over time, soft, muddy sediments were slowly compacted and hardened. They became a limestone tomb for more than 600 species, including *Archaeopteryx*.

No one was around to witness such transitions in the history of life. But fossils are real, just as the morphology, biochemistry, and molecular makeup of living organisms are real. Radiometric dating assigns fossils to their place in time. *Biological evolution is not "just a theory."* Remember, a scientific theory differs from speculation because its predictive power has been tested in nature many times, in many different ways. If a theory stands, there is a high probability that it is not wrong.

Evolutionists argue all the time among themselves. They argue over how to interpret the evidence and which mechanisms and events can explain life's history. At the same time, they do not ignore evidence—which is there for us to gather and interpret. Here is one account of vertebrate evolution, including our own origins.

How Would You Vote?

Private collectors find and protect fossils, but a private market for rare vertebrate fossils raises the cost to museums and encourages theft from protected fossil beds. Should private collecting of vertebrate fossils be banned? See BiologyNow for details, then vote online.

Key Concepts

CHARACTERISTICS OF CHORDATES

Four features develop in chordate embryos and set them apart from other animals: a supporting rod (notochord), a dorsal nerve cord, a pharynx with gill slits in the wall, and a tail extending past the anus. Section 26.1

TRENDS AMONG VERTEBRATES

In some early vertebrate lineages, a backbone replaced the notochord as a partner of muscles used in locomotion. Jaws evolved, sparking the evolution of novel sensory organs and brain expansions. On land, lungs replaced gills, and more efficient blood circulation enhanced gas exchange. Fleshy fins with skeletal supports evolved into limbs of amphibians, reptiles, birds, and mammals. Section 26.2

TRANSITION FROM WATER TO LAND

Vertebrates evolved in the seas, and the greatest diversity still resides in lineages of cartilaginous and bony fishes. Mutations in master genes that control body plans were pivotal in the rise of aquatic tetrapods and their move onto dry land. Sections 26.3–26.11

THE AMNIOTES

Amniotes—known informally as the reptiles, birds, and mammals—are vertebrate lineages that radiated into nearly all habitats on land. Sections 26.6–26.9

EARLY HUMANS AND THEIR ANCESTORS

Primates that were ancestral to the human lineage became physically and behaviorally adapted to long-term changes in climate, geography, and resource availability. Humans have dispersed throughout the world through behavioral flexibility and the force of culture. Sections 26.12–26.15

Links to Earlier Concepts

Take a moment to assess how far you have come on life's evolutionary road by reviewing the family tree in Section 19.7. Refer to the geologic time scale (17.5) to see where you are heading. Remember an earlier point, that highly active life-styles are not possible without aerobic respiration (8.1)? Here you will see how tetrapods hit the jackpot.

You will come across more examples of how small changes in master genes changed the course of evolution (15.3, 17.8). You will draw on your understanding of speciation, adaptive radiation, and extinctions (19.4). You will revisit the dinosaurs (Chapter 17) and biochemical and molecular tools (17.9).

26.1 The Chordate Heritage

LINKS TO SECTIONS 19.7, 25.12

As you consider vertebrates and their chordate heritage, remember this: Each kind of organism is a mosaic of traits—many conserved from remote ancestors, and others unique to its branch on the family tree.

CHORDATE CHARACTERISTICS

The preceding chapter ended with echinoderms, one of the earliest lineages of deuterostomes. Dominating this branch of the animal family tree are the **chordates** (Figure 26.2). These coelomate, bilateral animals are characterized in part by four features. *First*, a rod of stiffened tissue—not bone or cartilage—helps support the body. It is a notochord. *Second*, a nerve cord runs parallel with the notochord and gut; its anterior end develops into a brain. Unlike invertebrate nerve cords, this one is dorsal. *Third*, the wall of their pharynx, a muscular tube, has **gill slits**—openings that function in feeding, respiration, or both. *Fourth*, a tail extends past the anus. These features develop in all chordate embryos, but they do not always persist in adults.

Like the sea stars and other echinoderms, about 2,100 species of chordates are "invertebrates," which have no internal backbone. Far more—about 48,000—are **vertebrates**. These animals contain a backbone of cartilage or bone. They also have a cranium, which is a chamber of cartilage or bone that encloses the brain. Appendix I has an expanded classification system for vertebrates. Unit VI explores their body plans and functions. Here we start with their closest relatives.

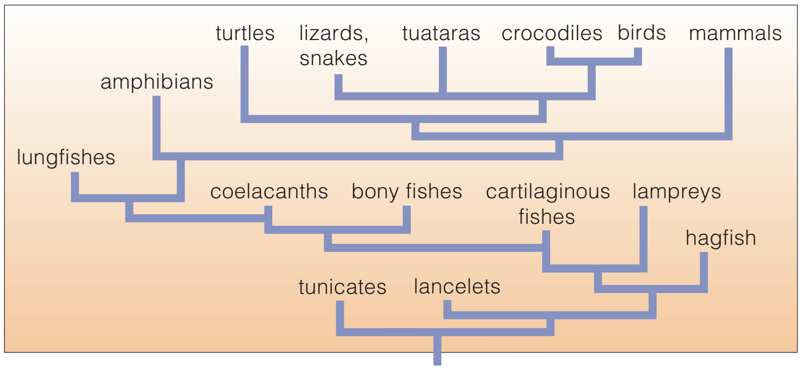


Figure 26.2 Family tree for the chordates which, together with echinoderms and some other lesser known groups, belong to the deuterostome lineage.

INVERTEBRATE CHORDATES

Urochordates Tunicates are among the bag-shaped animals called **urochordates**, which are characterized in part by larvae that have a firm, flexible notochord extending through a tail. Adults secrete a gelatinous or leathery "tunic" around a pharynx with gill slits (Figure 26.3). Most are only a few centimeters long. They range from intertidal zones to the deep ocean.

The adults are **filter feeders**. They filter food from seawater flowing through a siphon, past gill slits in a pharynx, then out through another siphon. They spurt out water when something irritates them; hence their familiar name, sea squirts. Their pharynx also acts as a respiratory organ. It takes up dissolved oxygen, which diffuses into blood vessels. Carbon dioxide wastes of aerobic respiration diffuse into water flowing out.

An intriguing point is that the sea squirt larvae are bilateral swimmers. Their notochord is like a torsion bar. It interacts with bands of muscles located under the epidermis. When muscles of one or the other side

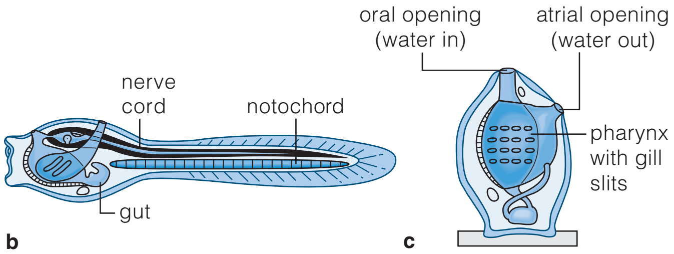


Figure 26.3 (**a**) Adult sea squirts (*Rhopalaea crassa*). (**b**) Sea squirt larva, which swims briefly and then undergoes drastic tissue remodeling and reorganization. Its metamorphosis starts when its head attaches to a substrate. Then its tail, notochord, and most of the nervous system are resorbed (recycled and used to form new tissues). Many gill slits form in the pharynx wall. Organs rotate until openings through which water flows into and out from the pharynx are pointing away from the substrate, as in (**c**).

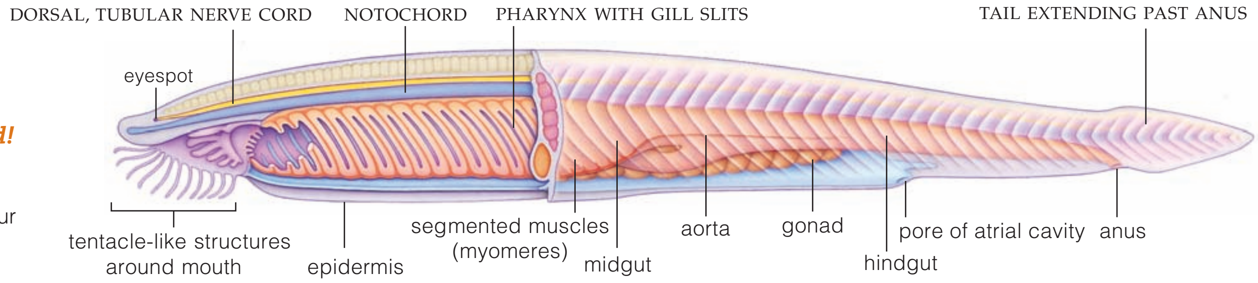


Figure 26.4 ***Animated!*** Lancelet body plan. The body plan of this small filter-feeder shows the four defining characteristics of chordates.

of the tail contract, the notochord bends, then springs back when muscles relax. Strong, side-to-side motion propels the larva forward. In most fishes, muscles and a backbone bring about the same kind of motion.

Cephalochordates At one end of their nerve cord, the fish-shaped **cephalochordates**, or lancelets, have a simple brain in a head that develops as it does in the vertebrates (*cephalo*–, head). Nerve cells (neurons) in the brain control reflex responses to light and other stimuli. The body is three to seven centimeters long and tapers at both ends. It clearly displays chordate features (Figure 26.4).

Also like vertebrates, the lancelets have segmented muscles. Contractile units in muscle cells run parallel with the body's long axis. Contractile force directed against the notochord allows side-to-side swimming motions. Even so, lancelets spend most of the time burrowing into shallow sediments and filter-feeding. Coordinated beating of cilia that line numerous gill slits move water into their pharynx, where food gets caught in mucus before moving through the gut.

A gill-slitted pharynx, a simple brain, a nerve cord, and bands of muscles that parallel the body's long axis—as you will see, these features turned out to have amazing evolutionary possibilities for vertebrates.

A WORD OF CAUTION

We are describing chordate features that will help give you insight into the evolution of vertebrates, but don't assume tunicates and lancelets are missing links between vertebrates and the earliest chordates. These groups do share some traits that preceded the origin of vertebrates, but each also has unique traits that put it on a separate branch of the animal family tree.

Similarly, hagfishes are jawless fishes that resemble lancelets in some respects and vertebrates in others, but certain traits set them apart. A few cartilage plates do help protect their brain, but their endoskeleton is not hardened with mineral deposits as it is in vertebrates.

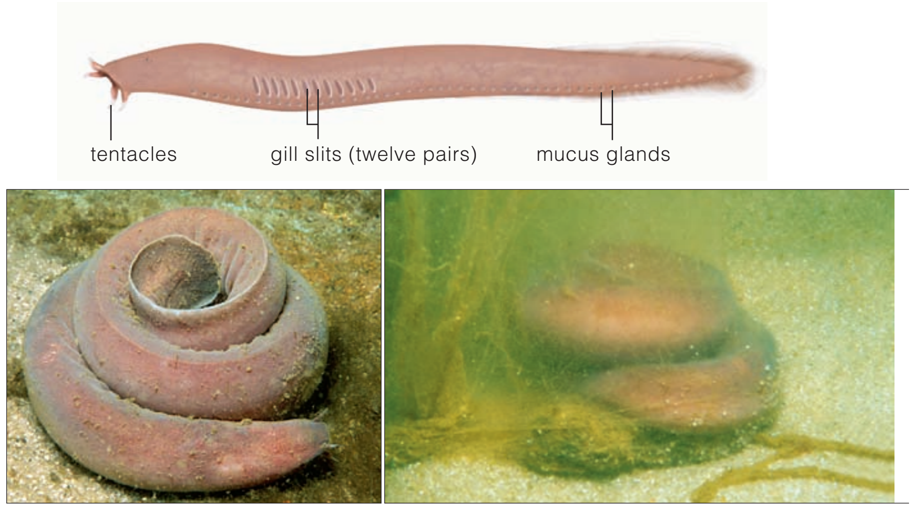


Figure 26.5 Hagfish body plan. The two photographs show a hagfish before and after it had coated its body with slimy mucous secretions.

The hagfish is less than a meter long and nearly blind, but it easily finds food with sensory tentacles (Figure 26.5). Its rasping, tonguelike structure draws small invertebrates and tissues of a dead or dying fish into its mouth. Hagfishes are burrowers, not highy active animals. But low metabolic rates work for them. They can get along without food for more than half a year.

If a hagfish is threatened, it secretes up to a gallon of sticky mucus. Fishermen who snag hagfishes view the behavior as disgusting. Even so, sliming potential predators has been a fine defense for this lineage of otherwise vulnerable, soft-bodied chordates.

All chordate embryos have a notochord, a tubular dorsal nerve cord, a pharynx with gill slits in its wall, and a tail that extends past the anus. These traits are legacies from a shared ancestor, an early invertebrate chordate.

Existing filter-feeding lancelets and tunicates are among the groups closest to the most ancient chordate lineages.

Hagfishes are at the next level in chordate complexity. Some cartilage protects a portion of their brain.

26.2 Evolutionary Trends Among the Vertebrates

LINKS TO SECTIONS 17.4, 17.5

The first vertebrates—jawless fishes—arose in Cambrian times. Before the Cambrian ended, an adaptive radiation had given rise to all modern groups of vertebrates.

EARLY CRANIATES

All fishes, amphibians, reptiles, birds, and mammals alive today are **craniates**, with a cartilaginous or bony chamber enclosing their brain. The first craniates had evolved by at least 530 million years ago, and they were active swimmers. Like the lancelets, they had a notochord and segmented muscles. Unlike lancelets, they had fins. Adults resembled the larvae of modern jawless fishes called lampreys (Figure 26.6).

Jawless fishes originated from craniate ancestors 500 million years ago. They included **ostracoderms**, which had armorlike plates of bony tissue and dentin, the same hard tissue in your teeth. Armor may have worked against pincers of the giant sea scorpions that hunted on the seafloor. It did not work against **jaws**—hinged, bony feeding structures. Jawed craniates had evolved, and when they began an adaptive radiation, most jawless fishes disappeared.

Placoderms were among the earliest fishes having a mineral-hardened backbone and jaws. Armor plates protected their head, but not much else. Their jaws were expansions of the first in a series of hard parts that structurally supported the gill slits (Figure 26.7). In certain species, the jaws had sharp bony plates.

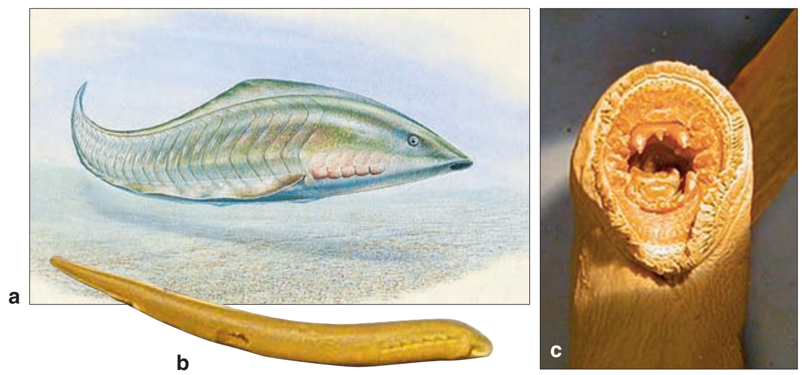


Figure 26.6 (**a**) Painting of an early craniate (*Myllokunmingia*). (**b**) Larva of a lamprey, an existing jawless fish. Most lampreys are parasitic. They attach to prey with a suckerlike oral disk and rasp at it with horny mouthparts (**c**). In the 1800s, sea lampreys probably entered the Hudson River, then canals built for commerce. By 1946, they were established in all of the Great Lakes of North America. Trout, salmon, and other natives have no defenses against them.

KEY INNOVATIONS

The appearance of jawed fishes profoundly changed the course of animal evolution. Unlike their nearly brainless, filter-feeding relatives, jawed fishes had cells that could form **bone tissue** with mineral-hardened secretions. They formed a linear series of cartilaginous or bony segments—**vertebrae** (singular, vertebra)—which replaced the notochord. That vertebral column was part of an inner skeleton, and it was more flexible and less clunky than armor plates. The hard segments

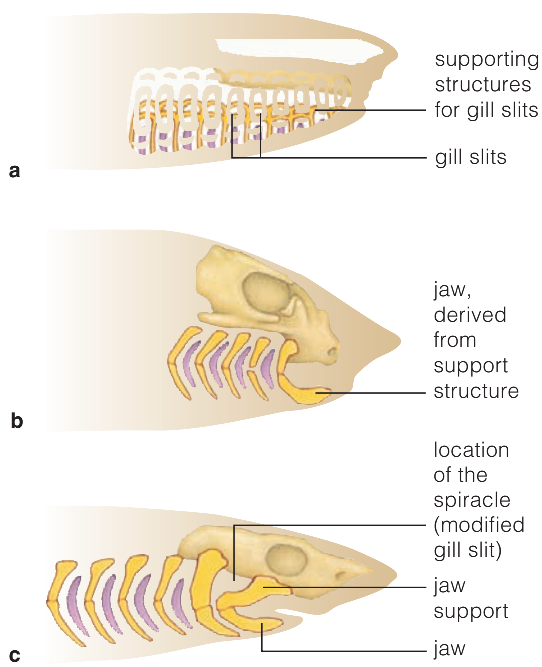
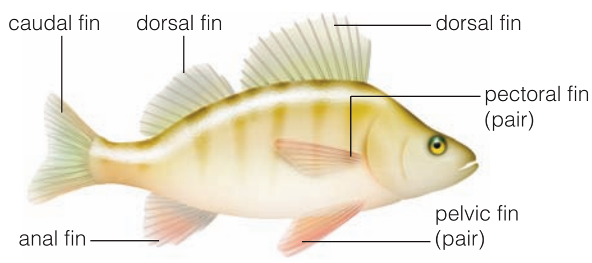


Figure 26.7 ***Animated!*** Comparison of gill-supporting structures. (**a**) In early jawless fishes, supporting elements reinforced a series of gill slits on both sides of the body. (**b**) In placoderms and other early jawed fishes, the first elements in the series were modified, and they functioned as jaws. Cartilage reinforced the mouth's rim. (**c**) Sharks and other modern jawed fishes have strong jaw supports. *Above*, the size of a human compared with an extinct jawed fish, the placoderm *Dunkleosteus*.

were paired with muscle segments, which permitted more flexibility and more forceful contractions. *The vertebral column was a starting point for the evolution of fast-moving, agile predators and prey in the seas.*

Jaws sparked another trend. Early chordate feeding modes were limited to filtering, sucking, and rasping food. When placoderms started biting and ripping off chunks of prey, better defenses evolved, as did ways to overcome them. For instance, fishes with better eyes for detecting predators or bigger brains that could plan pursuit or escape now had a competitive edge. *A trend toward more complex sensory organs and nervous systems started among ancient lineages of fishes, and much later in time, it continued among vertebrates on land.*

Another trend started when pairs of fins evolved. **Fins** are appendages that help propel, stabilize, and guide a body through water. They go by these names:



Some Devonion fishes had fleshy pelvic and anal fins with internal skeletal supports. *Paired, fleshy fins were a starting point for all legs, arms, and wings that evolved among amphibians, reptiles, birds, and mammals.*

A shift in respiration set another trend in motion. In lancelets, oxygen and carbon dioxide diffuse across skin. In most early vertebrates, paired gills evolved. **Gills** are respiratory organs having moist, thin folds serviced by blood vessels. They have a large surface area that exchanges gases between the environment and the body. Oxygen diffuses *from* water inside the mouth into blood vessels within each gill, *and* carbon dioxide diffuses *into* the surrounding water.

Gills became more efficient in larger, more active fishes. But gills do not function out of water; their thin surfaces stick together unless flowing water moistens them. In fishes ancestral to land vertebrates, two tiny outpouchings developed on the gut wall and evolved into **lungs**: internally moistened sacs for gas exchange. Lungs supplemented and then replaced gills during the invasion of land. In a related trend, modifications to the heart enhanced the uptake of oxygen and removal of carbon dioxide. *The earliest vertebrates on land relied more on a pair of lungs than on gills. Increased efficiency of circulatory systems accompanied the evolution of lungs.*

In the Carboniferous, the heavy-plated placoderms and other jawed fishes died out as faster, more agile, brainier predators replaced them. By adaptation, key innovations, and plain luck, the descendants of some jawless and jawed groups made it to the present.

MAJOR VERTEBRATE GROUPS

Figure 26.8 shows how different vertebrate groups are related to one another. Besides lampreys, the major groups are known as cartilaginous fishes, bony fishes, amphibians, reptiles, birds, and mammals. The rest of this chapter considers their characteristics, using the evolutionary trends as the conceptual framework.

Vertebrates arose in the Cambrian. All of the major modern groups evolved during an adaptive radiation of jawed fishes.

Jaws, a vertebral column, paired fins, and lungs were pivotal developments in the evolution of lineages that gave rise to amphibians, reptiles, birds, and mammals.

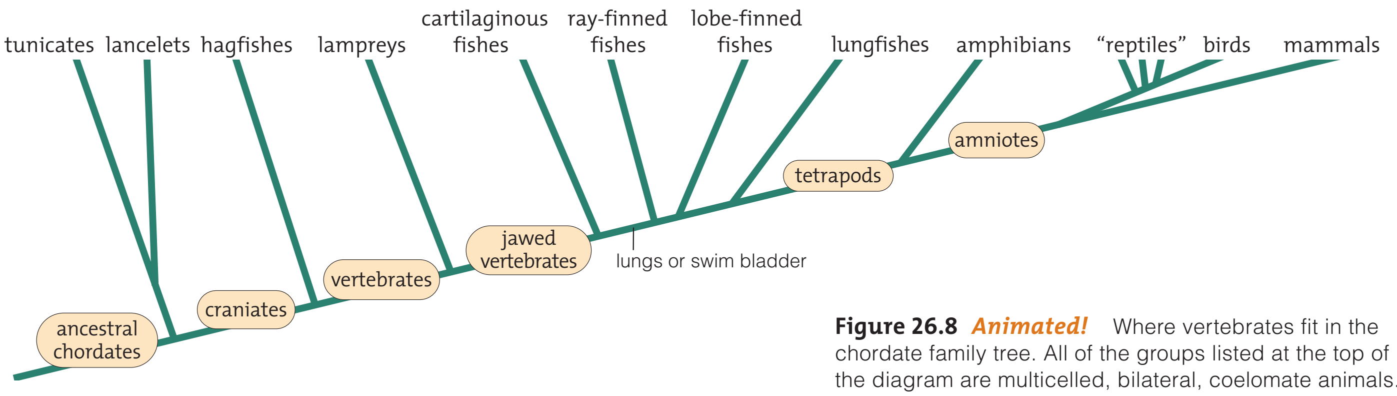


Figure 26.8 ***Animated!*** Where vertebrates fit in the chordate family tree. All of the groups listed at the top of the diagram are multicelled, bilateral, coelomate animals.

26.3 Jawed Fishes and the Rise of Tetrapods

Unless you study underwater life, you may not know that the number and diversity of fishes exceed those of all other vertebrate groups combined.

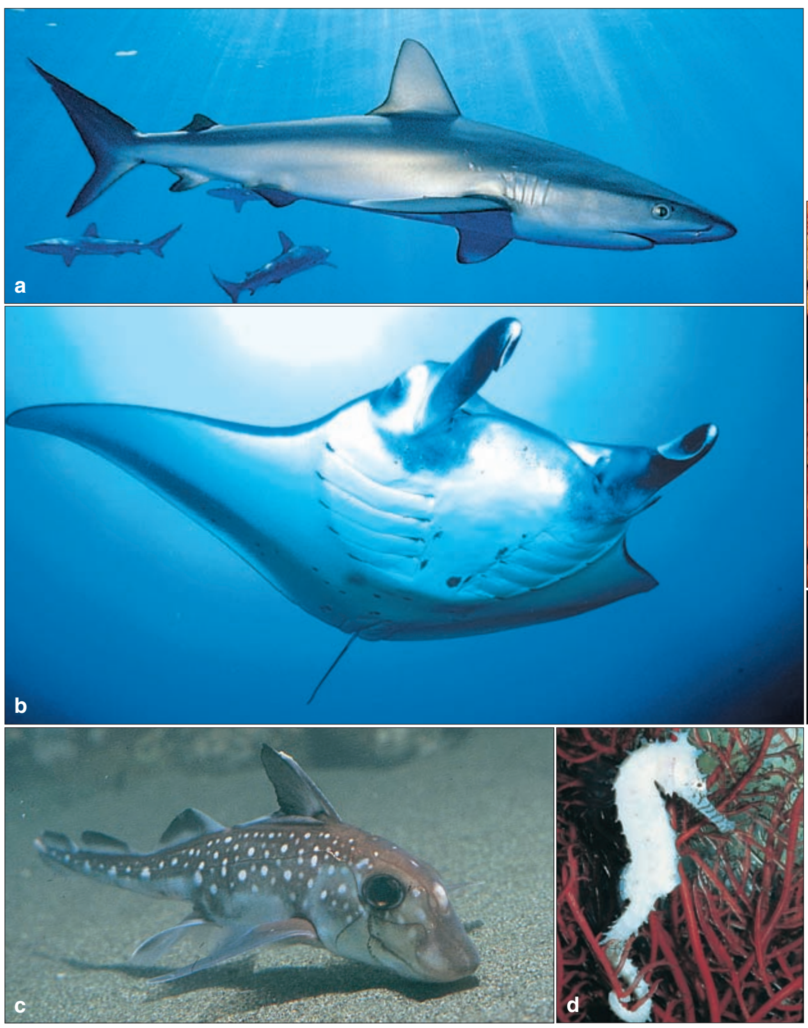
The body form and behavior of fishes offer clues to the challenges of life in water. Water is 800 times more dense than air and resists movements through it. One response to this physical constraint is a streamlined body that reduces friction during chases. Sharks and other predators of the open ocean have such a body, with strong muscles for forward propulsion (Figure 26.9*a*). Species that do not make high-speed runs tend to have small-finned, flattened bodies that easily slip through crevices, as in reefs. Fish scales also assist in motion. Collectively, these small and usually thin bony plates protect the body without weighing it down.

A trout suspended in shallow water is an example of adaptation to the density of water. Like many other fishes, it maintains neutral buoyancy by adjusting the volume of its **swim bladder**, a flotation device that exchanges gases with blood. It adjusts the volume of its swim bladder as it gulps air at the water's surface.

CARTILAGINOUS FISHES

Cartilaginous fishes (Chondrichthyes) include about 850 species of skates, sharks, and chimaeras (Figure 26.9). These marine predators have prominent fins, a skeleton of cartilage, and five to seven gill slits on both sides. At fifteen meters in length, some sharks are among the largest living vertebrates. They all shed and replace their teeth on an ongoing basis. The teeth are modified scales having a dentin core and an outer enamel layer. Many strong-jawed sharks grab and rip chunks off prey. They have been ocean predators for hundreds of millions of years, but the rare attacks on humans give the whole group a bad reputation.

Most skates and rays have flattened teeth that crush shelled prey on the seafloor. Manta rays are up to six meters across. Stingrays have a venom gland in the tail; other rays have electric organs that can stun prey with as much as 200 volts of electricity. Thirty or so species of chimaeras prefer eating small mollusks. All have a venom gland in front of the dorsal fin.



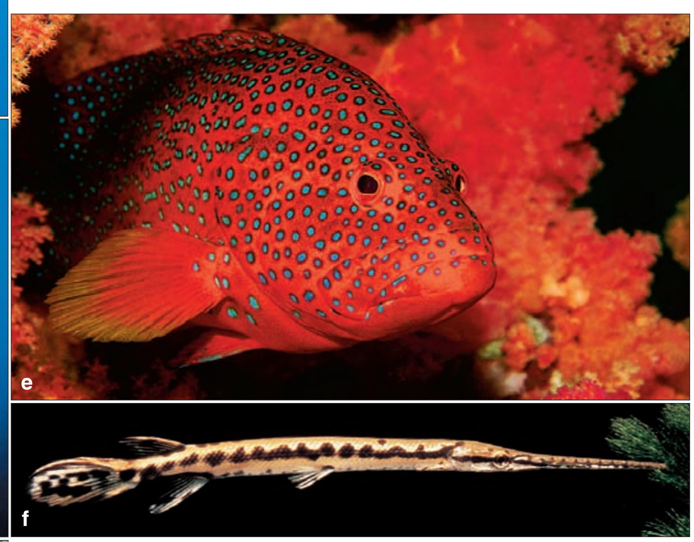


Figure 26.9 Cartilaginous fishes. (**a**) Galápagos sharks. (**b**) Manta ray. Two projections on its head unfurl and waft plankton to a mouth between them. Notice the gill slits on both fishes. (**c**) Chimaera, or ratfish.

Representative ray-finned fishes. This is the largest and most diverse group of bony fishes. (**d**) Sea horse, which anchors itself to substrates with its tail. (**e**) Coral grouper, one of the many species of bony fishes that fishermen are overharvesting. (**f**) Long-nose gar.

"BONY FISHES"

Jawed fishes having a bony endoskeleton evolved 400 million years ago. The **ray-finned fishes** have flexible fin supports derived from skin and thin scales. With more than 21,000 species in freshwater and marine habitats, they are the most diverse vertebrates of all. Paddlefish, sturgeons, and gars are in one group. The group called *teleosts* encompasses about 95 percent of the world's fish species, and half of them inhabit reefs and shallow seas. Teleosts include herrings, true eels, moray eels, puffers, killifishes, scorpionfishes, and the perciforms. Perches, salmon, mullets, groupers, basses, parrotfishes, blennies, cichlids, tuna, mackerels, and the barracudas are representative perciforms. So are sea horses, which are poor swimmers but good hiders.

You can see a few examples of ray-finned fishes in Figure 26.9 and in Sections 1.1, 27.5, 45.6, and 46.5.

Coelacanths (*Latimeria*) are the only surviving group of **lobe-finned fishes**. We know of two populations that may be separate species. The ventral fins of these fishes are fleshy extensions of the body, with skeletal support elements inside (Figure 26.10*a*). Like the ray-finned fishes, coelacanths have gills.

Lungfishes (Figure 26.10*b*) have gills *and* one or two small, modified outpouchings of the gut wall. These sacs help take in oxygen and remove carbon dioxide. Lungfishes must surface and gulp air; they drown if held under water. When streams dry out seasonally, lungfishes encase themselves in slimy secretions and mud. They stay inactive until the rainy season starts.

Do such fishes share a common ancestor with four-legged walkers—**tetrapods**? Probably. Like tetrapods, a lungfish has a separate blood circuit to the lungs. Its skullbones are arranged the same way. It has the same tooth enamel. Also, the fins of both lobe-finned fishes and lungfishes are about the same as tetrapod limbs in structure, position, and sizes. A lungfish even uses its limbs to move forward on underwater substrates.

Limb joints, digits, and other traits of fossils imply that walking originated in water, not on land. By the late Devonian, some swimming and crawling species were using limbs and digits (Figure 26.10*c–e*).

Ray-finned fishes are now the most diverse and abundant vertebrates. The lobe-finned fishes have fleshy ventral fins reinforced with skeletal parts. The lungfishes have simple lunglike sacs that supplement respiration by gills.

Walking probably started under water during the Devonian, among the aquatic forerunners of tetrapods on land.

Figure 26.10 (**a**) Living coelacanth (*Latimeria*), of the only existing lineage of lobe-finned fishes. (**b**) Australian lungfish. (**c**) Painting of Devonian tetrapods. *Acanthostega*, submerged, and *Ichthyostega* crawling onto land. Both had a fishlike skull, caudal tail, and fins. Unlike fishes, both had a short neck and four limbs with digits. (**d**,**e**) Proposed evolution of skeletal elements inside fins into the limb bones of early amphibians.

26.4 Amphibians—First Tetrapods on Land

LINKS TO SECTIONS 15.3, 17.8, CHAPTER 3, INTRODUCTION

Even a single genetic change could have transformed lobed fins into limbs. Remember those enhancers that control gene transcription? One of them influences how the digits form on limb bones. A mutation in one of the master genes can lead to a big change in morphology.

Figure 26.12 One of the caecilians, a legless tropical amphibian. How do you suppose it burrows into soil?

EVOLUTIONARY HIGH POINTS

Amphibians were the first tetrapods on land. Modern kinds have four legs or an aquatic tetrapod ancestor (Figures 26.11 and 26.12). Body plans and reproductive modes are somewhere between fishes and "reptiles."

What drove certain aquatic tetrapods onto land? Consider: Asteroids hit Earth at least five times in the Devonian. One of the last impacts coincided with a mass extinction in the seas. Remember the Chapter 3 introduction? If the hit caused the release of methane hydrates, carbon dioxide would have displaced much of the vital oxygen that was dissolved in the ocean and swampy coastal habitats. However it happened, tetrapods with lungs had the advantage; they could get enough oxygen by gulping air. Fossils show that some tetrapods were semiaquatic and were spending time on land when the Devonian came to a close.

Life in the new, drier habitats was both dangerous and promising. Temperatures shifted more on land than in the water, air did not support the body as well as water did, and free-standing water was not always available. But air is richer in oxygen. Amphibian lungs were further modified in ways that enhance oxygen uptake. The heart, now divided into three chambers, could pump more oxygen-rich blood to cells. These changes supported richly varied, active life-styles.

New sensory information also challenged the early amphibians. Swamp forests supported vast numbers of insects and other small invertebrate prey. On land, vision, hearing, and balance turned out to be highly advantageous senses. They evolved concurrently with

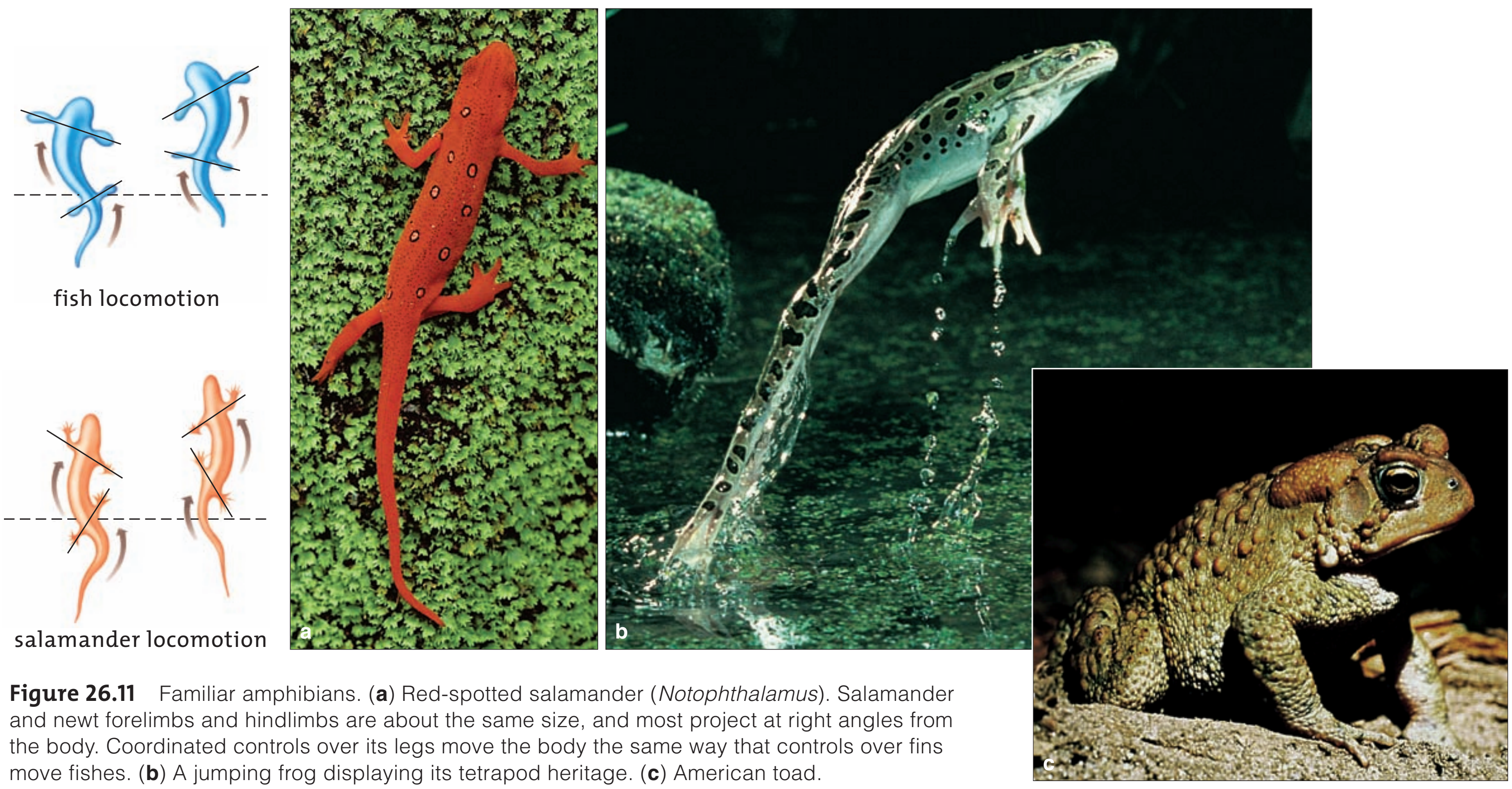


Figure 26.11 Familiar amphibians. (**a**) Red-spotted salamander (*Notophthalamus*). Salamander and newt forelimbs and hindlimbs are about the same size, and most project at right angles from the body. Coordinated controls over its legs move the body the same way that controls over fins move fishes. (**b**) A jumping frog displaying its tetrapod heritage. (**c**) American toad.

expansions of brain regions that received, processed, and responded to the richly novel sensory input.

All living amphibians are descendants of the first tetrapods. None has escaped the water entirely. Even species with gills or lungs also exchange oxygen and carbon dioxide across their thin skin. But respiratory surfaces must be kept moist at all times, and skin dries out easily in air. Some of the modern amphibians are fully aquatic. Most species release their eggs in water, where larvae develop. Species adapted to dry habitats usually lay their eggs in moist places. In a few cases, the embryos develop inside the moist adult body.

MAJOR EXISTING GROUPS

Frogs and toads are familiar amphibians. With more than 4,800 named species, they are the most diverse (Figure 26.11*b*,*c*). Most adults are active predators that capture prey with an extensible, sticky-tipped tongue. Most have epithelial cells that secrete mucus, venom, and antibiotics against diverse pathogens. Frogs have long hindlimbs and strong muscles that help the body catapult into air or barrel through the water. Nearly all frogs and toads lay eggs in water. Their larvae are tadpoles with gills, a tail, and no legs. Later, the gills and tail disappear, and four legs form (Section 43.2).

About 500 salamander species and their relatives, the newts, are carnivores. All live in north temperate zones and in Central and South America. Most are less than 15 centimeters (6 inches) long. Adults retain the larval tail. A few kinds, such as mudpuppies and axolotls, retain additional juvenile features, including external gills. Their bones just stop growing during an early stage. Also, some species are sexually precocious; they can breed before assuming the adult form.

Salamander limbs are positioned at the side of the body, not under it. When most species walk, they must bend from side to side like fishes, as in Figure 26.11*a*. Probably the first tetrapods on land walked this way.

As some amphibians evolved, they lost their limbs and vision, but not their jaws. This group gave rise to caecilians (Figure 26.12). Most of the 165 or so species burrow in moist soil, using senses of touch and smell as they pursue insects. A few aquatic predators detect weak electric currents emanating from moving prey.

In body form and behavior, amphibians show resemblances to aquatic tetrapods and reptiles. Most still rely on access to aquatic or moist habitats to complete their life cycle. Frogs, toads, and salamanders are the most familiar groups.

26.5 Vanishing Acts

FOCUS ON THE ENVIRONMENT

LINKS TO SECTIONS 24.1, 25.5

Amphibians are survivors. Their lineage originated before the dinosaurs, and it outlasted them. These tetrapods have been around a thousand times longer than humans, but now human activities all around the world are putting many species at risk.

There is no question that amphibians are in trouble. Of about 5,500 known species, population sizes of at least 200 are plummeting. The alarming declines have been well documented in North America and Europe, but things look bad worldwide.

At this writing, six species of frogs, four species of toads, and eleven species of salamanders are listed as threatened or endangered in the United States and Puerto Rico. One of them, the California red-legged frog, is the largest frog native to the western United States. It is the species that inspired Mark Twain's classic short story, "The Celebrated Jumping Frog of Calaveras County."

Researchers correlate many declines with shrinking or deteriorating habitats. Developers and farmers commonly fill in low-lying ground that once filled up seasonally and provided pools of standing water. Nearly all species of amphibians have trouble breeding unless they deposit their eggs in water, where larvae can develop.

Also contributing to the declines are introductions of new species in amphibian habitats, long-term changes in climate, increases in ultraviolet radiation, and the spread of fungal and parasitic diseases into new habitats (Section 24.1 and Figure 26.13). Chemical contamination of aquatic habitats is another contributing factor. Chapter 36 offers a closer look at some effects of habitat contamination.

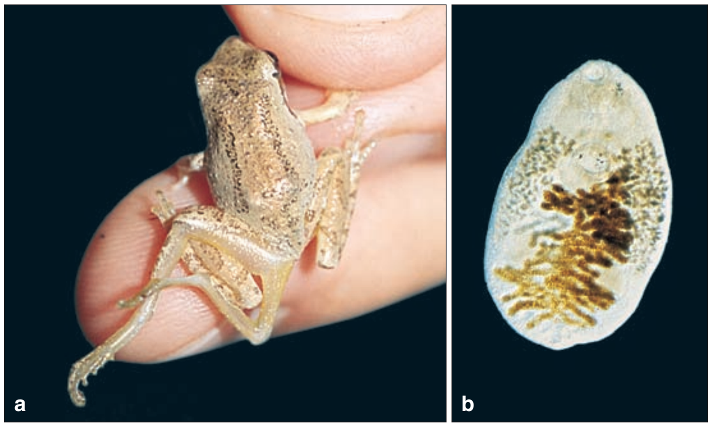


Figure 26.13 (**a**) Example of frog deformities. (**b**) A parasitic fluke (*Ribeiroia*) that burrows into frog tadpole limb buds and physically or chemically alters their cells. Infected tadpoles grow extra legs or none at all. In places where *Ribeiroia* population densities are great, the number of tadpoles that successfully complete metamorphosis is low. Trematode cysts have been found in deformed frogs and salamanders throughout North America.

26.6 The Rise of Amniotes

Amniotes were the first vertebrates to adapt to dry land habitats. They did so through modifications in their organ systems, behavior, and eggs, which have four membranes that conserve water and support embryonic development.

Late in the Carboniferous, **amniotes** arose from some amphibians. These vertebrates alone make eggs with four membranes that are vital for the structural and functional development of the embryos. All amniotes have dry, tough, or scaly skin that helps restrict water loss and two kidneys that efficiently conserve water.

A major group of amniotes, the **synapsids**, includes all mammals and extinct mammal-like species, such as *Lystrosaurus*. This tusked herbivore inhabited Triassic floodplains (Section 17.6). It belonged to the therapsid lineage that probably led to modern mammals.

Another major group of amniotes, the **sauropsids**, includes all "**reptiles**" and birds. *Reptile* is no longer a formal taxon; we now know that the grouping is not monophyletic. The name persists only as a means to refer to lineages that show basic amniote features but not the derived traits that define birds or mammals.

Compared to amphibians, early reptiles chased prey with more cunning and speed. With well-muscled jaws and sharp teeth, they could seize and crush prey with sustained force. The four limbs of many species were good at supporting the weight of the body's trunk on land. Although required for amphibians, gas exchange across skin was abandoned; lungs had become more efficient. Reptiles with bigger brains now engaged in behaviors not seen among amphibians (Figure 26.14).

The first **dinosaurs** evolved from Triassic reptiles and were no bigger than turkeys. They may have had

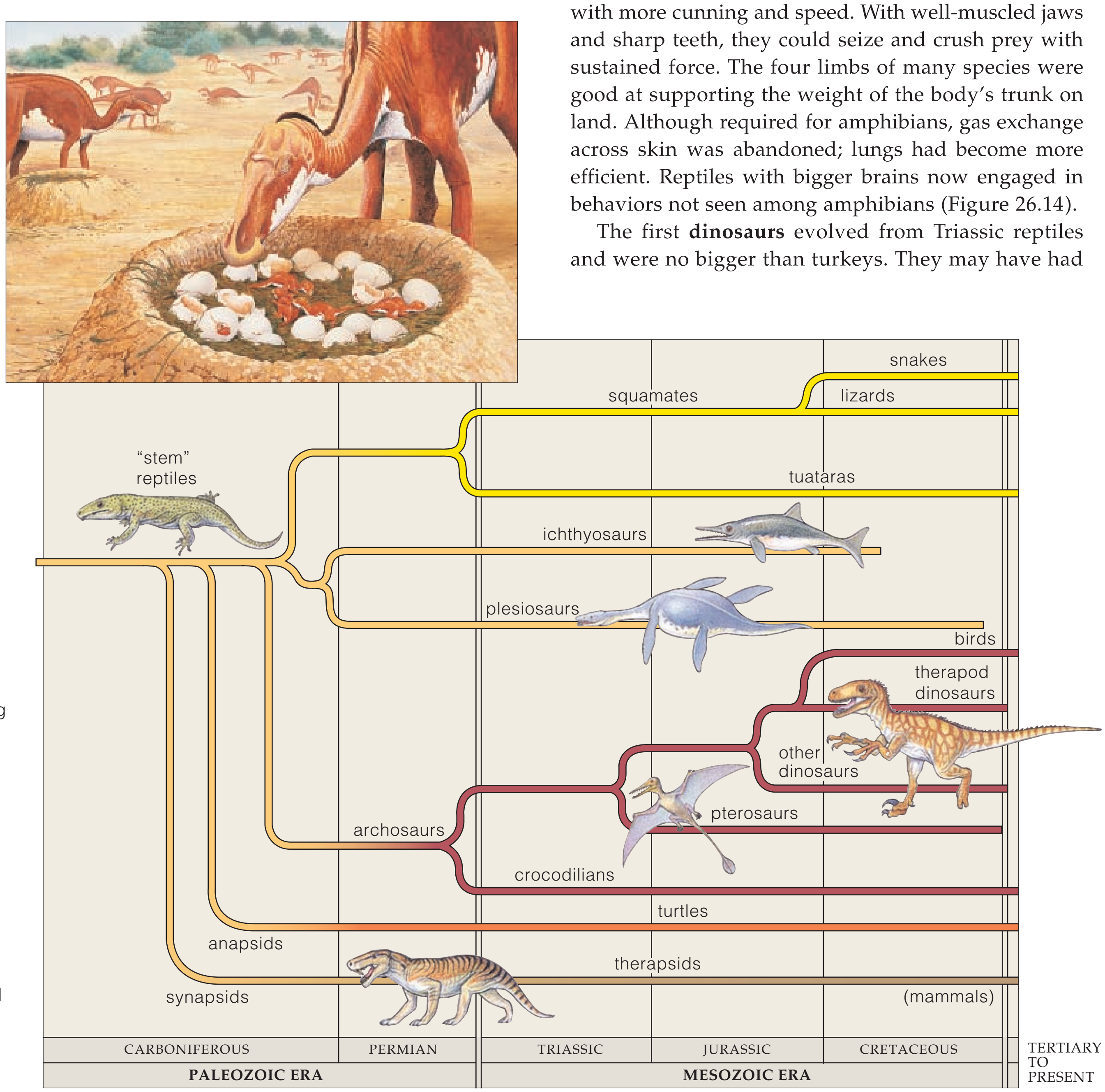


Figure 26.14 Family tree for the amniotes known informally as the reptiles. The painting above depicts the nesting behavior of a duck-billed, plant-eating dinosaur (*Maiasaura*). This species lived about 80 million years ago in what is now Montana. Like the existing crocodilians and many birds, it protected its eggs and may have cared for the hatchlings. Like some other dinosaurs, this one traveled in herds.

Figure 26.15 *Temnodontosaurus*. This ichthyosaur hunted large squids, ammonites, and other prey in the warm, shallow seaways of the early Jurassic. Fossils measuring nine meters (thirty feet) long have been found in England and Germany.

high metabolic rates, and possibly they were warm-blooded. Many moved on two legs. Adaptive zones opened up for them about 213 million years ago, after huge fragments from an asteroid or comet fell on the spinning Earth and hit what is now France, Quebec, Manitoba, and North Dakota. Nearly all animals that survived these impacts were small, had high rates of metabolism, and tolerated big temperature changes.

Surviving dinosaur groups, such as those shown in the chapter's introduction, became "ruling reptiles." For 125 million years they dominated the land even as different groups, including ichthyosaurs, flourished in the seas (Figure 26.15). Many lineages of dinosaurs were lost in a mass extinction that ended the Jurassic, others in pulses of lava outpourings and global climate change during the Cretaceous. Some did recover, and new ones arose in forests, swamps, and open habitats.

The Cretaceous ended as cosmic bad luck wiped out nearly all dinosaurs. A feathered group—the birds—survived. So did some reptiles. Descendants include the crocodilians, turtles, tuataras, snakes, and lizards.

Eggs with four membranes that help embryos develop, water-conserving skin and kidneys, and active life-styles helped early amniotes radiate into dry land habitats.

One amniote group, the synapsids, includes mammals and now-extinct mammal-like species. Another group, the sauropsids, includes reptiles and birds.

Much of amniote history was a matter of luck, of being in the right or wrong places on a changing geologic stage.

26.7 So Long, Dinosaurs

FOCUS ON EVOLUTION

LINK TO CHAPTER 17 INTRODUCTION

How often have various people, puffed up with self-importance, set out to conquer neighbors, lands, and the seas? Think about it. Then think about the dinosaurs. Did they reign supreme? No question about it. Their lineage dominated the land for 140 million years. In the end, did it matter? Not a bit. Sixty-five million years ago, the remaining members of their lineage perished. Why? Bad luck.

Reflect, now, on the passing reference in Chapter 17 to a mass extinction that occurred at the Cretaceous–Tertiary (K–T) boundary. After methodically analyzing iridium levels in soils, maps of gravitational fields, and other evidence from around the world, scientists Walter Alvarez and Luis Alvarez announced that a direct hit by an asteroid the size of Mount Everest was the culprit.

Later, researchers identified the impact site. Crustal movements had transported it to its present location in the Gulf of Mexico (Figure 17.1). The impact crater is 9.6 kilometers deep and 300 kilometers across, wider than Connecticut. That crater, and other evidence, supports what is now called the **K–T asteroid impact theory**.

To make a crater that big, the asteroid had to hit the Earth at 160,000 kilometers per hour. It blasted at least 200,000 cubic kilometers of dense gases and debris into the sky. The crust heaved violently. Monstrous waves 120 meters high raced across the ocean. They obliterated life on islands, then slammed into the continents.

Some researchers thought that atmospheric debris must have blocked sunlight for months. They were trying to explain the fossil record, which indicated that many kinds of plants and other producers on land withered and died, and that many animals starved to death. However, the volume of debris blasted aloft would not have been large enough to have had such global consequences. So what did happen? It was a mystery.

Then comet Shoemaker–Levy 9 slammed into Jupiter. Particles blasted into the Jovian atmosphere triggered an intense heating of an area larger than Earth. That event supports a **global broiling hypothesis**, first proposed by H. Melosh and his colleagues. In their view, the amount of energy released at the K–T impact site was equivalent to detonating 100 million nuclear bombs. Trillions of tons of vaporized debris rose in a colossal fireball, which rapidly condensed and formed particles the size of sand grains.

Seconds later, a cooler fireball of unmelted rock, carbon dioxide, and steam formed. When the debris plummeted to Earth, it raised the temperature of the atmosphere by thousands of degrees.

The sky would have been excruciatingly hotter than it gets above Death Valley in summer. In one horrific glowing hour, nearly all plants around the world erupted in flames and all animals out in the open—including nearly all of the remaining dinosaurs—were broiled alive.

An asteroid impact ended the golden age of dinosaurs.

26.8 Portfolio of Existing "Reptiles"

The name reptile *is derived from the Latin* repto, *which means to creep. Some existing forms do creep. Others race, lumber, or swim about. These diverse lineages include all living amniotes that are not birds and not mammals.*

GENERAL CHARACTERISTICS

More than 8,160 species of turtles, lizards, tuataras, snakes, and crocodilians live in a variety of habitats on land and in water. All are cold-blooded. Both sexes have a cloaca, an opening that functions in excretion and reproduction. The females are fertilized internally. Even aquatic species typically lay their eggs on land. Figure 26.16 shows one of the distinctive body plans.

MAJOR GROUPS

Turtles About 305 existing species of turtles live in a shell attached to their skeleton. If threatened, turtles can pull their head and limbs inside (Figure 26.17*a*,*b*). Their body plan has been around since Triassic times, although the shell's size became reduced in lineages of sea turtles and other highly mobile types.

Instead of teeth, turtles have horny plates that are used to grip and chew food. Strong jaws and a fierce disposition help fend off predators. But turtle eggs are vulnerable to many predators on land. Add hunting and destruction of nesting sites to the mix, and most sea turtles are now poised at the brink of extinction.

Lizards With 4,710 species, the lizards are the most diverse reptiles. The smallest, *Sphaerodactylus ariasae*, can fit on a dime (*left*). The largest, *Varanus komodoensis* (Komodo dragon) is a monitor lizard that may grow 3 meters (10 feet long). This ambush predator lurches out of bushes at deer, wild boar, an occasional human, and other prey. Like most predatory lizards, it snags its prey with sharp, peglike teeth. Chameleons (page 557) use accurate flicks of a sticky tongue, which can be longer than their body. Iguanas, including marine iguanas of the Galápagos, are herbivores.

Being small themselves, most lizards are prey for other animals. Some try to outrun predators; others try to startle them by flaring their throat fan (Figure 26.17*c*,*d*). Many will give up their tail when a predator grabs it. The detached tail wriggles for a bit and may distract a predator from its fleeing owner.

Tuataras Two species of tuataras survive on small islands near New Zealand (Figure 26.17*e*). They are descendants of a group that had its heyday in the Triassic. They are reptiles, yet they resemble modern amphibians in their brain and locomotion. Like some lizards, the tuataras have a third, middle "eye" under the skin, with retina, a rudimentary lens, and links to the brain. It may detect changes in daylength and light intensity and affect hormonal control of reproduction.

Snakes In the Cretaceous, short-legged, long-bodied lizards gave rise to elongated, limbless snakes. Some snakes retain bony remnants of ancestral hindlimbs. Most move their body in S-shaped waves, much like salamanders do (Section 42.7). All 2,955 living species are carnivores that have flexible skull bones and jaws. Many swallow prey wider than they are. Rattlesnakes and other fanged species bite and subdue prey with venom (Figure 26.17*f*). Snakes in general tend not to attack humans, but venomous types bite about 7,000 people annually in the United States and kill a few of them. About 40 percent of those bitten reported that they were handling the snake or otherwise disturbing it. Worldwide, the annual death toll from snake bites is estimated at 30,000–40,000.

All snakes are vulnerable during their life cycle, because birds and other predators relish snake eggs. Female snakes store sperm and lay several clutches

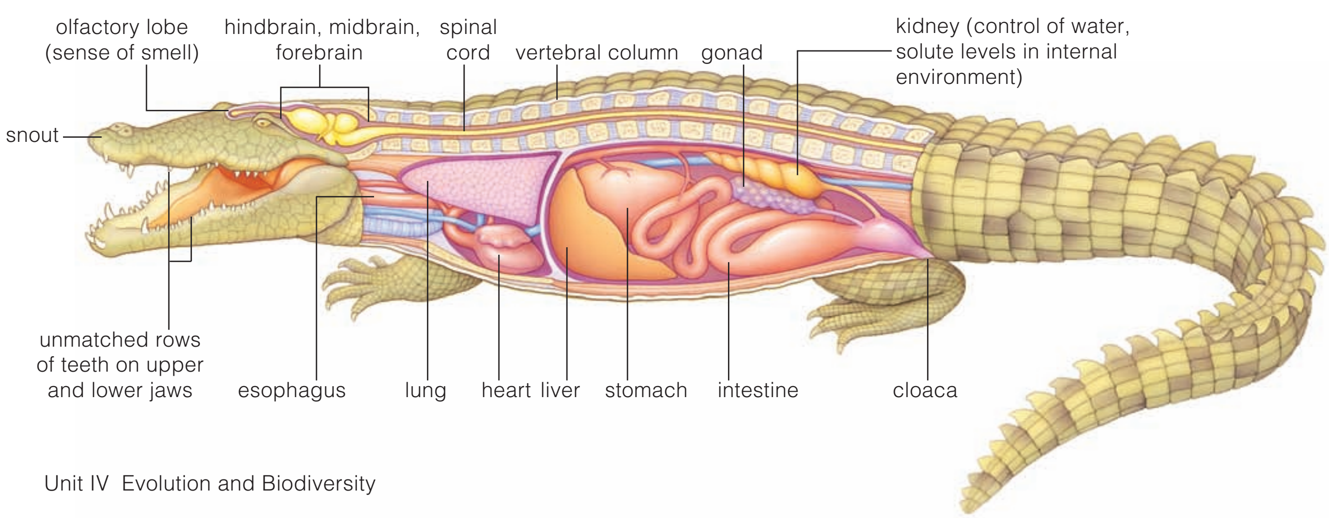
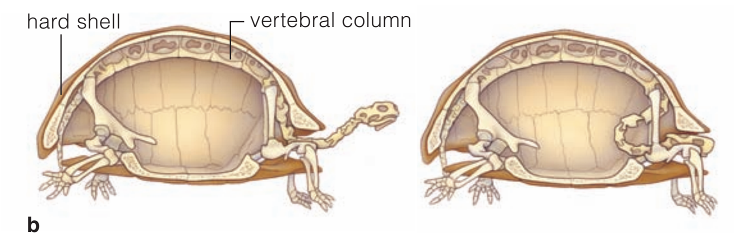


Figure 26.16 ***Animated!*** Body plan of a crocodile which, like its life-style, has remained much the same for nearly 200 million years. The group's future is not rosy. Human habitats now encroach on many crocodilian habitats. Alligator belly skin is in high demand for wallets, handbags, and shoes.



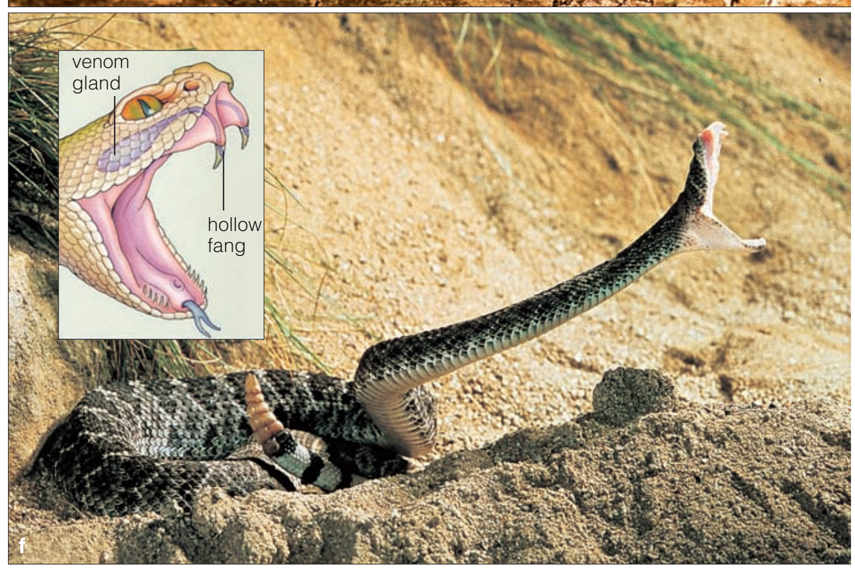


Figure 26.17 (**a**) Galápagos tortoise. (**b**) Turtle shell and skeleton. (**c**) Lizard fleeing and (**d**) lizard confronting. (**e**) Tuatara (*Sphenodon*). (**f**) Rattlesnake. (**g**) Spectacled caiman, a crocodilian. Its upper and lower rows of teeth do not match up, as mammalian teeth do.

of fertilized eggs at intervals after they mate, which improves the odds that at least some will hatch.

Crocodilians Almost a dozen species of crocodiles, alligators, and caimans are the closest living relatives of birds. All are predators in or near water. They have powerful jaws, a long snout, and sharp teeth (Figure 26.17*g*). They all drag prey into water, tear it apart as they spin around, and gulp down chunks. The feared southern Asia crocodile and Nile crocodile can weigh as much as 0.25 to 1 ton (500 to 2,000 pounds).

Like other reptiles and birds, the crocodilians can adjust body temperature by altering certain behaviors and adjusting metabolic rates (Section 42.7). However, they are the only reptiles that have a four-chambered heart, as mammals and birds do. Also like most birds, crocodilians engage in parental behavior, as when they guard their nests and assist the hatchlings.

Turtles and tuataras have body plans that have changed very little since the Triassic. Lizards and snakes are the most diverse reptilians. Crocodilians have the most complex brain and heart structure. They are the closest relatives of birds.

26.9 Birds—The Feathered Ones

A capacity for flight evolved in pterosaurs, which are now extinct, and in insects, birds, and bats. But only birds, like a few extinct dinosaurs that preceded them, make ***feathers****—lightweight structures used in flight, as body insulation, and often in courtship displays (Figures 26.18 and 26.19).*

Birds are warm-blooded, feathered vertebrates. Like the dinosaurs and crocodilians, their closest relatives, they have scales on their legs and some of the same internal organs, including a cloaca that functions in excretion and reproduction. Birds, too, make amniote eggs that are fertilized internally in females (Figure 26.20). Internal and external modifications to the basic body plan led to the capacity for flight.

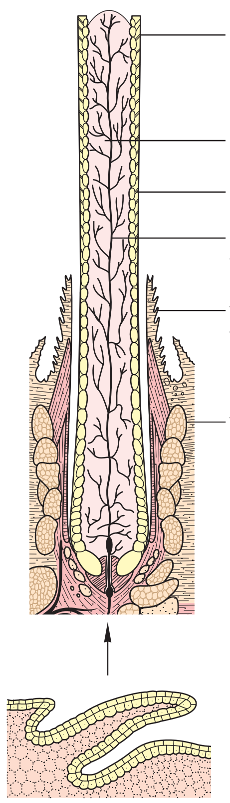
Birds originated when Mesozoic reptiles began an adaptive radiation. They diverged from a lineage of small theropod dinosaurs, a type of carnivore that ran about on two legs, and their feathers evolved from highly modified reptilian scales. *Archaeopteryx* was in or near that lineage; *Confuciusornis sanctus* definitely was an early bird (Figures 26.1 and 26.18).

Unlike reptiles, birds have built-in mechanisms that adjust body temperature. They gain most of their heat not from outside sources but from metabolism. When it gets cold outside, they fluff feathers as insulation. When it gets too hot, elastic air sacs connected to the lungs speed the outflow of warm air, which can help dissipate excess metabolic heat (Sections 40.3 and 42.7).

The evolution of bird flight involved far more than feathers. It involved modification of the entire body, from internal bone structure to highly efficient modes of respiration and circulation. The high metabolic rates that sustain flight depend on a strong flow of oxygen through the body. The elastic air sacs greatly enhance oxygen uptake. Also, like mammals, birds have a four-chambered heart that pumps oxygen-rich blood to the lungs and to the rest of the body in separate circuits, as it probably did in reptilian ancestors of birds.

Flight also demands an airstream, low weight, and a powerful downstroke that can provide *lift*, or a force at right angles to an airstream. Each wing, a modified forelimb, consists of feathers and lightweight bones attached to powerful muscles. Its bones do not weigh much, owing to profuse air cavities in the bone tissue. The flight muscles attach to an enlarged breastbone (sternum) and to the upper limb bones attached to it. When the muscles contract, they produce a powerful downstroke (Figures 26.21 and 26.22).

Figure 26.18 *Confuciusornis sanctus*, which lived about the same time as *Archaeopteryx*. It is the earliest known bird with a bill. Fossils show how the clawed limbs of its four-legged ancestor were modified into wings. Each wing had three digits, one a reduced claw with flight feathers.



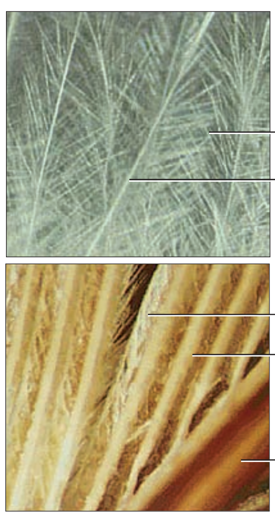


Figure 26.19 Feathers. (**a**) in chick embryos, a typical feather develops from actively dividing epidermal cells. A cone-shaped bud starts growing out from the skin. Its base sinks, and the space around it becomes a follicle. Horny cells at the cone's surface differentiate and form a sheath, then a feather forms inside it. Blood vessels in the underlying dermis form pulp, which nourishes the growing feather.

(**b**) Flight feathers. Their hollow central shaft and interlocked lattice of barbs and barbules impart strength without adding much weight. (**c**) Innermost down feathers are insulative.

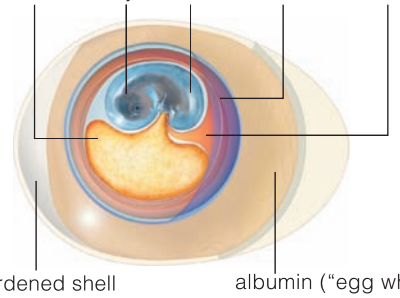


Figure 26.20 ***Animated!*** One type of amniote egg.

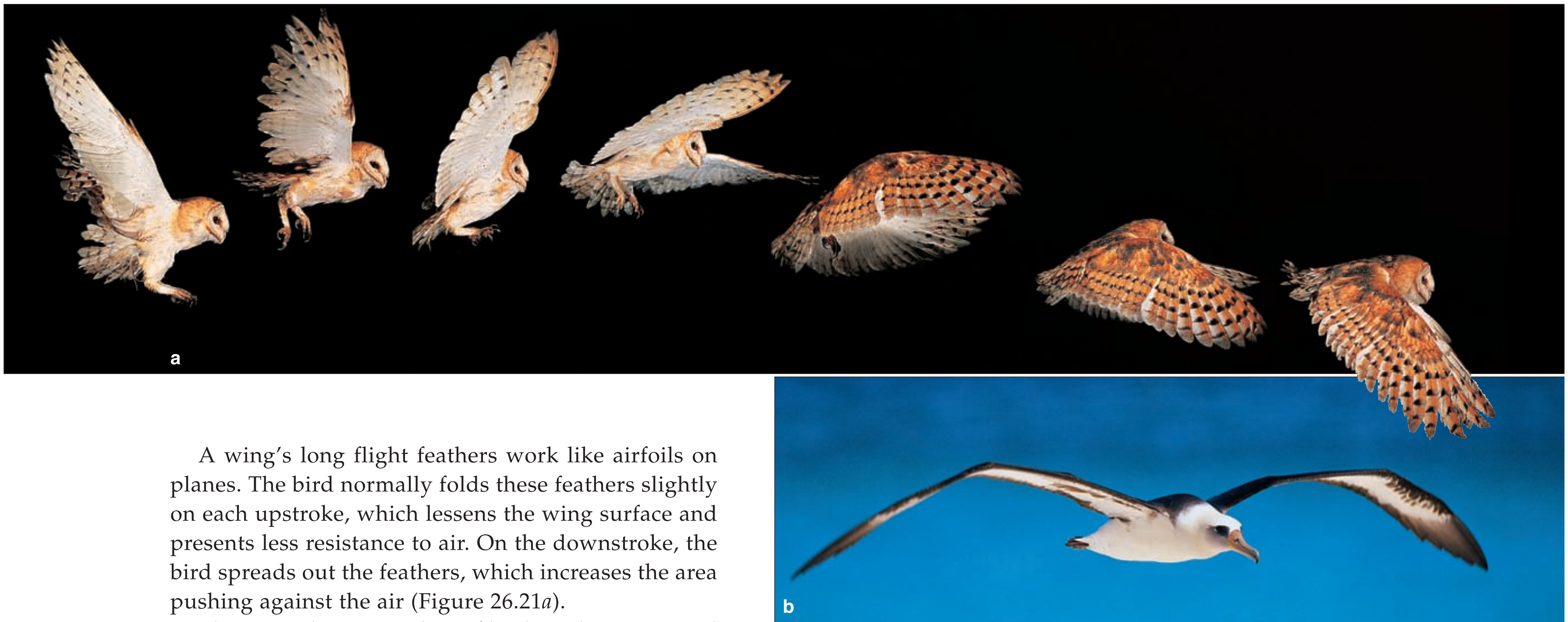


Figure 26.21 Bird flight. (**a**) Of all living animals, only birds and bats fly by *flapping* wings. A bird wing is a system of lightweight bones and feathers. Section 19.4 looks at the evolution of wing bones. (**b**) Laysan albatross. Its wingspan is more than two meters, yet this seabird weighs less than 10 kilograms (22 pounds). It is so at home in the air, it even sleeps while riding the winds. One bird monitored by researchers flew 24,843 miles in ninety days as it searched for food and then brought it back to its nestlings. That is the equivalent of a trip around the globe.

A wing's long flight feathers work like airfoils on planes. The bird normally folds these feathers slightly on each upstroke, which lessens the wing surface and presents less resistance to air. On the downstroke, the bird spreads out the feathers, which increases the area pushing against the air (Figure 26.21*a*).

There are about 28 orders of birds and 9,000 named species that vary in size, proportions, coloration, and capacity for flight. The tiniest, the bee hummingbird, weighs 1.6 grams (0.6 ounce). The ostrich, the largest living bird, can weigh 150 kilograms (330 pounds). It cannot fly, but powerful leg muscles help it sprint. Warblers, parrots, and some other perching species that show complex social behaviors often have vivid feather colors and patterns. Bird song and other forms of behavior are among the topics of Chapter 49.

We see one of the most dramatic forms of behavior among birds that migrate with the changing seasons. **Migration** is a recurring pattern of movement from one region to another in response to environmental rhythms. Seasonal change in daylength is one factor that influences the internal timing mechanisms that we call "biological clocks." It causes physiological and behavioral changes that induce migratory birds to make round trips between breeding grounds and wintering grounds. Arctic terns migrate the farthest. They spend summers in arctic regions and winters in antarctic regions. One monitored bird took off from an island near Great Britain and landed three months later in Melbourne, Australia. It racked up more than 22,000 kilometers (14,000 miles) on that one journey.

Of all animals, birds alone produce feathers, which they use in flight, heat conservation, and socially significant communication displays. A bird's feathers, lightweight bones, and highly efficient respiratory and circulatory systems sustain flight.

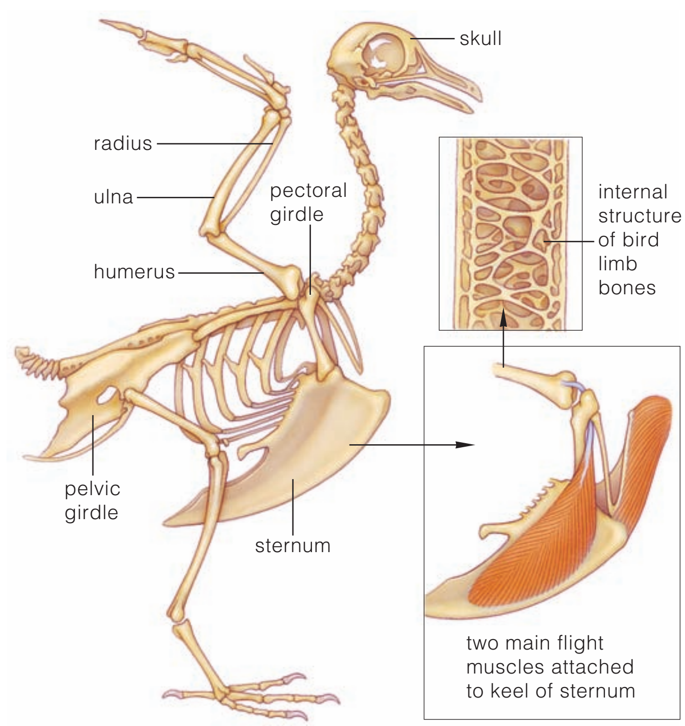


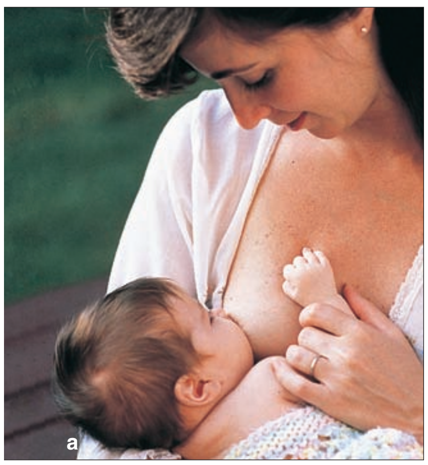
Figure 26.22 *Animated!* Flight muscles and the keeled breastbone (sternum).

26.10 The Rise of Mammals

LINKS TO SECTIONS 17.6, 17.8, CHAPTER 3 INTRODUCTION

Remember the premise of cause and effect? Christine Janis put it this way: In a world dominated by the dinosaurs, mammals survived by being small, efficient at exploiting food, and flexible in behavior. They originated before the dinosaurs and outlasted them, largely by being artful dodgers and because of chance, catastrophic events.

Which traits set **mammals** apart from other animals? These are the only animals that make hair, although species differ in the amount, type, and distribution. Female mammals alone secrete milk for their young. This nutrient-rich fluid forms in mammary glands that have ducts to the body surface. Jaws and teeth also help set mammals apart. Most have four types of upper and lower teeth that match up (Figure 26.23).



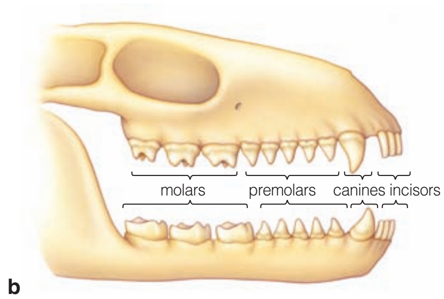


Figure 26.23 Distinctly mammalian traits. (**a**) A human baby, already with a mop of hair, being nourished by milk from mammary glands. (**b**) Four types of mammalian teeth; upper and lower rows match up.

Reptiles have a hinged two-part jaw, and all teeth are one type only and do not match up. Most mammals care for their offspring during an extended period of dependency. The young typically have the capacity to learn and repeat behaviors with survival value. Some species show notable *behavioral flexibility*—a capacity to expand on basic activities with novel behaviors.

Mammals are the only synapsids that made it to the present. Synapsids, again, were the first amniotes to branch from stem reptiles in the late Carboniferous. They became dominant on land, but many were lost in a mass extinction that ended the Permian (Chapter 3).

The therapsid branch endured. During the Triassic, the four limbs of certain species became positioned under the body instead of at its sides. The change made it easier to walk erect, but a trunk higher from the ground was not as stable. Not coincidentally, the volume of the cerebellum—a brain region that controls balance and spatial positions—expanded at that time.

Modern mammals evolved early in the Jurassic. By 130 million years ago, there were three lineages: the **monotremes** (egg-laying mammals), the **marsupials** (pouched kinds), and **eutherians** (placental kinds). In the Paleocene, with no more pressure from dinosaurs, a great mammalian radiation began. Climates were mild; forests or woodlands extended into polar areas. Carnivores, omnivores, and herbivores evolved. Their teeth could nip, shred, or grind food (Figure 26.24).

Figure 26.24 A few of the early Paleocene mammals that lived in sequoia forests in what is now Wyoming. On the ground, raccoonlike *Chriacus* faces a tree-climbing rodent (*Ptilodus*). Higher up is *Peradectes*, a marsupial.

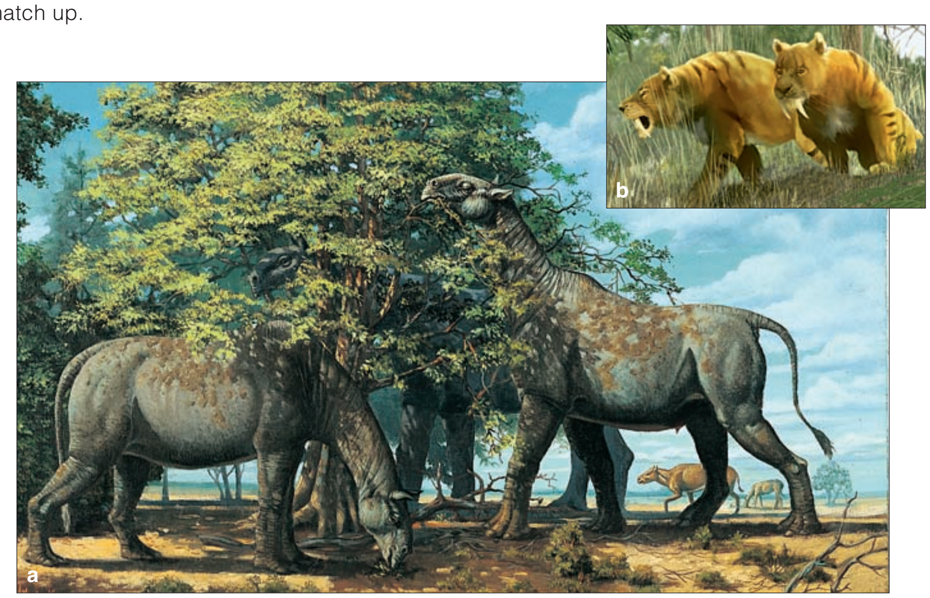


Figure 26.25 (**a**) *Indricotherium*, the "giraffe rhinoceros." At 15 tons and 5.5 meters high at the shoulder, it was the largest mammal we know about. (**b**) Saber-tooth cat (*Smilodon*) in a dry woodland of the Pleistocene. *Smilodon* fossils have been recovered from the pitch pools in Rancho LaBrea, California.

a About 150 million years ago, during the Jurassic, the first monotremes and marsupials evolved and migrated throughout the supercontinent Pangea.

b Between 130 and 85 million years ago, in the Cretaceous, placental mammals emerged and started to spread. Monotremes and marsupials of the southern supercontinent evolved in isolation from placental mammals.

c About 20 million years ago, in the Miocene, placental mammals expanded in range and diversity. On Antarctica, mammals vanished. Marsupials and early placental mammals displaced monotremes in South America.

d About 5 million years ago, in the Pliocene, advanced placental mammals invaded South America. They drove most marsupials and the early placental species to extinction.

Figure 26.26 ***Animated!*** (**a**–**d**) Adaptive radiations of mammals. *Right*, one consequence—a case of convergent evolution. (**e**) Australia's spiny anteater, one of two living monotremes. (**f**) Africa's aardvark and (**g**) South America's giant anteater. Compare the specialized ant-snuffling snouts.

Many modern species, such as rodents, primates, bats, even-toed hoofed mammals (hippos, camels, and other artiodactyls), and odd-toed mammals such as the tiny, earliest horse (*Hyracotherium*) arose in the early Eocene. Later on, parts of Pangea that would become Australia and Antarctica drifted apart, rafting some monotremes and marsupials away from the placental mammals radiating through other land masses. Then a passage opened between the Arctic and the North Atlantic oceans, and deep circulation patterns shifted. An Antarctic ice cap formed, and northern lands grew cooler and drier. Woodlands and vast open grasslands replaced tropical forests, and plant growth patterns changed. Most early mammals became extinct.

From the Oligocene on through the Pliocene, many grazing and browsing animals evolved, including gazelle-like camels, the "giraffe rhinoceros," and the saber-tooth cat (Figure 26.25). On the land mass that became South America, monotremes were replaced by marsupials and early placental mammals. Using a land bridge from North America, the highly evolved placental mammals radiated southward and rapidly replaced many of their previously isolated relatives (Figure 26.26). Only the opossums and a few other species invaded land masses in the other direction.

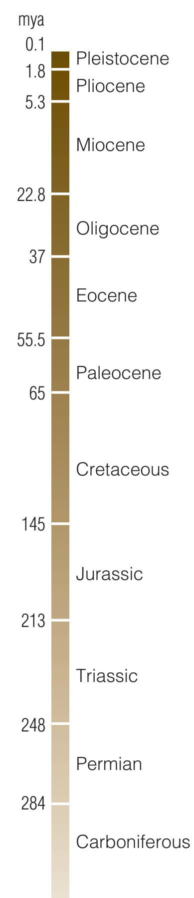
What gave placental mammals a competitive edge? They could use higher metabolic rates to control body temperature, and they had a better way to nourish embryos. Later chapters explain these traits. For now, note that the adaptive radiation of highly specialized placental mammals came about at the expense of less competitive relatives.

The climate cooled again in the Miocene as great mountain ranges arose and altered air circulation and rainfall patterns. Grasslands formed, and new kinds of herbivores emerged. Beginning in the Pliocene, ice ages started alternating with interglacials, or warmer periods. Species richness declined in deserts, prairies, steppes, and pampas, which are still with us today. As you will see, early humans faced these challenges.

One more point: Many lineages originally evolved on separate continents but became adapted to similar habitats. In time, they came to resemble one another in form and function. For example, Australia's spiny anteater, South America's giant anteater, and Africa's aardvark all have similar snouts adapted to preying on ants (Figure 26.26*e*–*g*). Such species are examples of *convergent* evolution, as described in Section 17.4.

Mammals are the only animals with hair, and only female mammals produce milk from mammary glands.

The three major groups are the egg-laying monotremes, the pouched marsupials, and the placental mammals. Placental mammals are now the dominant group in most regions.



26.11 Portfolio of Existing Mammals

Reflect now on the current range of mammalian diversity—the monotremes, marsupials, and placental mammals.

The only living monotremes are two species of spiny anteaters (Figure 26.26) and the duck-billed platypus (Figure 26.27*a*). One spiny anteater lives in Australia, and the other in Papua New Guinea. These burrowing mammals eat ants. Like porcupines, they bristle with protective spines (modified hairs). As is the case for platypuses, females lay eggs. Unlike platypuses, they do not dig out nests. They incubate a single egg, and their hatchling suckles and completes its development in a skin pouch that forms temporarily (through muscle contractions) on the mother's ventral surface.

Most of the 260 existing species of marsupials are native to Australia and nearby islands; a few live in the Americas (Figure 26.27*b*,*c*). Tiny, blind, hairless newborns suckle and finish developing in a permanent pouch on the mother's ventral surface. The Tasmanian devil, the largest carnivorous marsupial, bares fangs as a threat display (Figure 26.27*c*). It makes hair-raising screeches, coughs, and snarls but is only a scavenger, famous for its rowdy communal feeds at carcasses.

Placental mammals are named after the **placenta**, a spongy organ made of maternal and fetal membranes (Figure 26.28*a*). A placenta forms in a chamber (uterus) that protects an embryo as it develops. It gets oxygen and nutrients to the embryo and removes its metabolic wastes (Section 44.11). In general, such embryos have a developmental advantage over their closest relatives. They can grow faster than marsupial embryos do in a pouch. Also, many species are fully formed, thus less vulnerable to predators, at birth. Appendix I lists the major groups; Figure 26.28 shows representatives.

The body form, function, behavior, and ecology of mammals will occupy our attention later in the book. In the next chapter, we will take a look at mammals that are now threatened by a current mass extinction. Here, we leave the three existing lineages by inviting you to reflect on Table 26.1. It highlights classic cases of convergent evolution that occurred among them.

Most existing monotremes and marsupials are native to the southern continents and islands. Placental mammals show far greater distribution and diversity.

Figure 26.27 (**a**) Platypus, a monotreme. Two marsupials: (**b**) Adult koala (*Phascolarctos cinereus*). Its ancestors evolved millions of years ago, when the climate turned drier and drought-resistant plants evolved. Koalas eat only eucalyptus leaves. European settlers in Australia cleared eucalyptus forests for farmland. Millions of slow-moving koalas were shot for their pelts. In the 1930s they became a protected species, but their numbers declined because nothing protected the eucalyptus trees. This still is the case in much of their home range. (**c**) Young Tasmanian devil.

Table 26.1 Convergences Among Groups of Mammals

Life-Style	Home	Mammalian Family
Aquatic invertebrate eater	North America Central America Australia	Water shrew (Soricidae) Water mouse (Cricetidae) Platypus (Ornithorhynchidae)
Carnivore on land	North America Australia	Wolf (Canidae) Tasmanian wolf (Thylacinidae)
Anteater on land	South America Africa Australia	Giant anteater (Myrmecophagidae) Aardvark (Orycteropodidae) Spiny anteater (Tachyglossidae)
Ground-dwelling leaf, tuber eater	North America South America Eurasia	Pocket gopher (Geomyidae) Tuco-tuco (Ctenomyidae) Mole rat (Spalacidae)
Tree-dwelling leaf eater	South America Africa Madagascar Australia	Howler monkey (Cebidae) Colobus monkey (Cercopithecidae) Woolly lemur (Indriidae) Koala (Phascolarctidae)
Tree-dwelling nut, seed eater	Southeast Asia Africa Australia	Flying squirrel (Sciuridae) Flying squirrel (Anomaluridae) Flying squirrel (Phalangeridae)

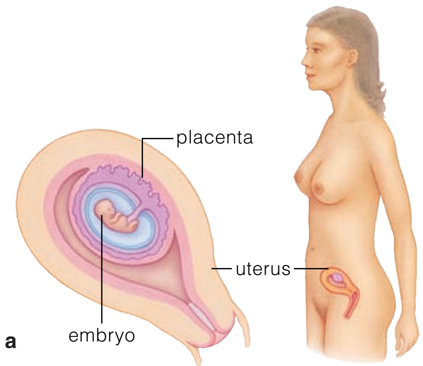
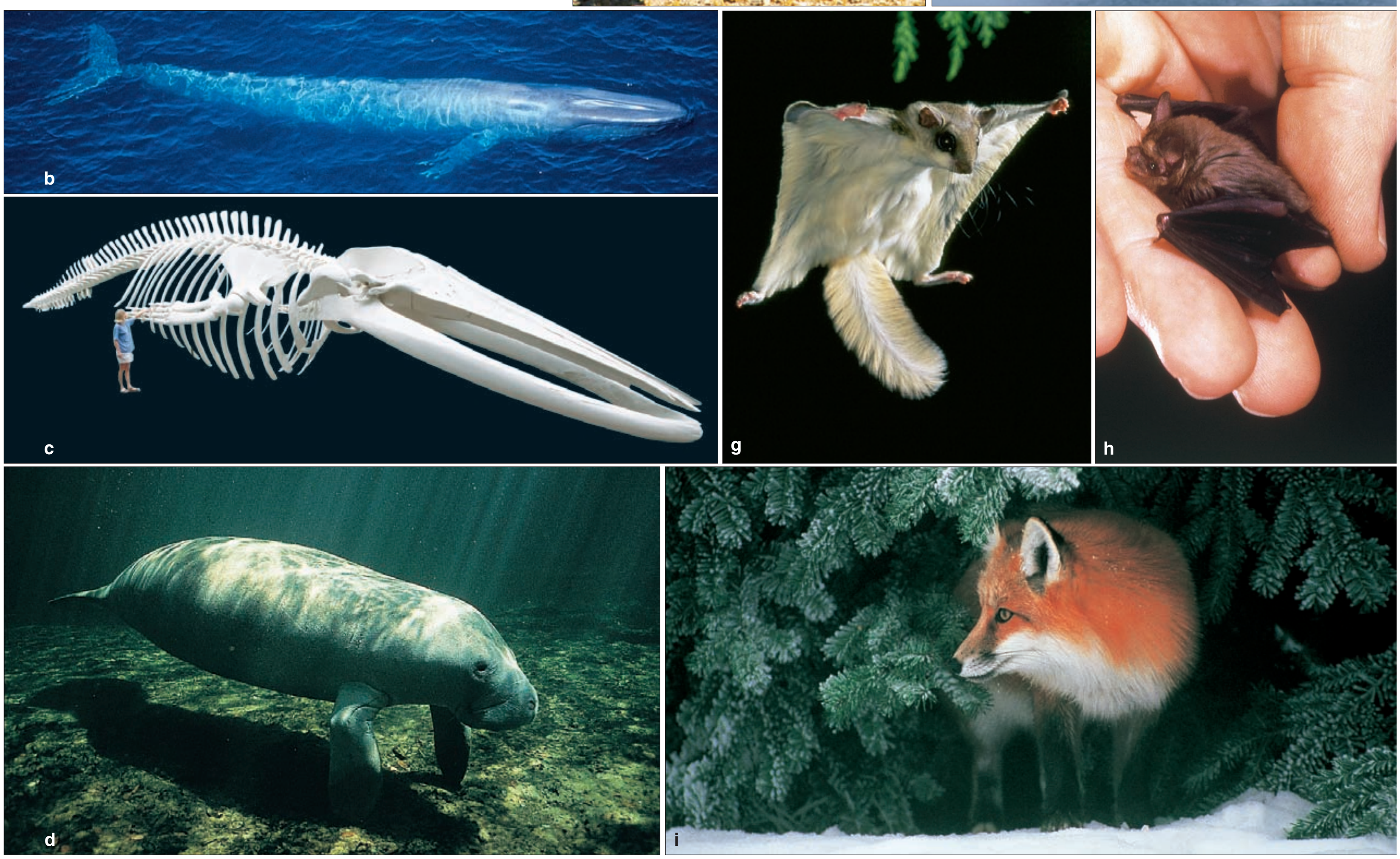


Figure 26.28 Placental mammals. (**a**) Location of the placenta in a pregnant human female. (**b**) Blue whale and (**c**) the size of its skeleton relative to a human. At 200 tons, an adult is the biggest living animal. (**d**) A manatee lives in water and eats seaweed. Early sailors imagined it was a mermaid. (**e**) A camel traverses hot deserts while (**f**) harp seals swim in frigid waters after prey and sunbathe on ice. (**g**) Flying squirrel, really just a glider. The only flying mammals are bats (**h**); this one is a Kitti's hog-nosed bat. (**i**) Red fox hiding in blue spruce. Thick, insulative fur protects it from winter cold.



26.12 Trends in Primate Evolution

LINK TO SECTION 17.4

So far, you have traveled 570 million years through time, from tiny flattened invertebrates to craniates, then on to the jawless and jawed fishes with a backbone. You encountered some early tetrapods, which were walking on four limbs that had evolved from fleshy lobed fins. You moved on to amniotes—reptiles, birds, and mammals. Now you are about to travel primate roads that led to modern humans.

WHAT IS A PRIMATE?

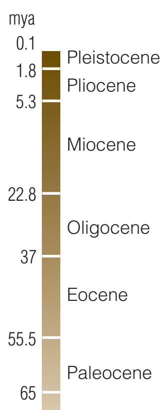
The **primate** lineage originated from squirrel-sized mammals of the Mesozoic. By 60 million years ago, its earliest forms—*prosimians*—had evolved. These tree-dwelling (arboreal) species radiated through northern forests. Before the Oligocene, one branch gave rise to *monkeys* and *apes* that would, from the Miocene on, displace prosimians as the dominant primates. Today, prosimians endure only in isolated places, including Madagascar, or where they can forage at night while monkeys and apes are sleeping.

Gibbon, siamang, orangutan, gorilla, chimpanzee, bonobo—these primates are classified as the apes. All monkeys, apes, and *humans* are further classified as **anthropoids**. In biochemistry and body form, apes and humans are close relatives. They, and their closest extinct ancestors, are the only **hominoids**. All human-like and human species, past and present, are known as the **hominids**. They will be our focus here.

KEY EVOLUTIONARY TRENDS

Most primates live in the trees of forests, woodlands, or savannas (grasslands with a scattering of trees). Few features set them apart from other mammals, and each lineage has its own defining traits. The five trends that define the lineage that led to modern humans were set in motion among the first tree-dwelling lineages.

First, a reliance on the sense of smell became less important than daytime vision. *Second*, skeletal changes promoted **bipedalism**—upright walking—which freed hands for new tasks. *Third*, altered bones and muscles made hands more versatile. *Fourth,* teeth became less specialized. *Fifth*, the evolution of the brain, behavior, and culture became interlocked. **Culture** is the sum of a social group's behavioral patterns, passed on through the generations by learning and symbolic behavior. In brief, *"uniquely" human traits emerged by modification of traits that had evolved earlier, in ancestral forms.*



Enhanced Daytime Vision Early primates had an eye on each side of the head, which was held parallel to the ground. Later on, many species had eyes facing forward, which was better for sampling shapes and movement in three-dimensional space. Visual systems became increasingly responsive to variations in light intensity (dim to bright) and to colors.

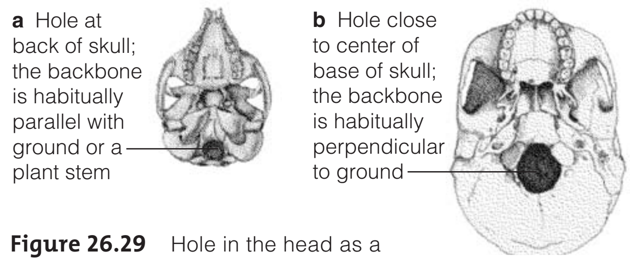


Figure 26.29 Hole in the head as a diagnostic tool—the foramen magnum.

Upright Walking How a primate walks depends on the length, shape, and skeletal position of its bones, especially the backbone, shoulder blades, and pelvic girdle. At the base of its skull bones is an opening, the **foramen magnum**, where the spinal cord can connect with the brain (Figure 26.29). If this hole is at the back of the skull, you can be sure that the animal moved on all fours. If it is almost centered at the skull's base, the animal held its backbone perpendicular to the ground.

Tarsiers and monkeys are four-legged walkers, with front and back limbs of about the same length; gorillas walk on two legs and knuckles of their long arms. But their foramen magnum is not at the back of the skull, as it was in their ancestors. When sitting, they can hold their head erect. In humans, the foramen magnum is close to center at the base of the skull. Of all primates, humans have the shortest, most flexible backbone, one curved into an S shape. These are structural traits that make bipedalism possible (Figures 26.29*b* and 26.30).

Power Grip and Precision Grip So how did we get our versatile hands? Early mammals spread their toes apart to support their weight as they walked or ran on four legs. In ancient tree-dwelling primates, the bones of each hand changed, so fingers could curl around objects (*prehensile* movements), and the thumb could touch all the fingertips (*opposable* movements). In time, the hands were freed from load-bearing functions and became modified in ways that permitted powerful or precision gripping of objects:

Figure 26.30 Comparison of skeletal organization and stances of a few primates. The images are not at the same scale. (**a**) Tarsier, small enough to fit on a human hand. It is a climber and leaper. (**b**,**c**) Spider monkey, an agile four-legged climber, leaper, and runner. It has long, thin limbs relative to its torso, and its long, thin digits are good at gripping, not at supporting the body's weight. (**d**,**e**) Gorillas use their forelimbs to climb and support body weight when walking on knuckles and two legs. (**f**) A human is a two-legged walker. (**g**) In captivity, a bonobo is upright 2 percent of the time on land, and 90 percent of the time when it is wading after edible fishes and aquatic invertebrates.

Having the capacity for versatile hand positions gave the ancestors of humans the capacity to make and use tools. Refined prehensile and opposable movements led to the development of technologies and cultures.

Teeth for All Occasions As you will see shortly, modifications to the jaws and teeth in certain groups accompanied a shift from eating insects, to fruits and leaves, to a mixed diet. Rectangular jaws and lengthy canines evolved in monkeys and apes. Among early hominids, a bow-shaped jaw evolved. So did teeth that were smaller and all about the same length.

Brains, Culture, and Behavior Over time, shifts in reproductive and social behavior accompanied a shift to life in the trees. In many lineages, parents put more effort in fewer offspring, and maternal care became intense. The more the young had to learn to survive on their own, the longer they depended on parents.

Culture is the sum of a human group's patterns of social behavior. It endures largely because of a system of recognized signs and symbols—language. It evolved in hominids as selection pressures acted on the brain regions dealing with sensory inputs. The brain became larger and more complex, but only after mutations led to increases in the volume of its bony chamber.

Complex, forward-directed vision; bipedalism, refined hand movements, generalized teeth, and interlocked elaboration of brain regions, behavior, and culture were key adaptations on the road from arboreal primates to modern humans.

26.13 From Early Primates to Hominids

LINKS TO SECTIONS 17.4, 19.4

Fossils from central, eastern, and southern Africa show that the Miocene through the Pliocene was a "bushy" time of hominid evolution, meaning many forms were rapidly evolving. We still do not know how they are related.

ORIGINS AND EARLY DIVERGENCES

Primate-like mammals emerged between 85 million and 65 million years ago, in tropical Paleocene forests. Like small tree shrews (Figure 26.31), they had a long snout and a good sense of smell, suitable for snuffling food or predators. They clambered about in stems and branches, although not with speed or grace. They, too, had huge appetites. They foraged at night for seeds, buds, insects, and eggs under trees.

Prosimians evolved by the Eocene. These primates climbed higher and their snout was shorter. They had a larger brain, better daytime vision, and better ways to grasp objects. *How did these traits evolve?*

Consider the trees. Trees provided food and safety from ground-dwelling predators, but they also were zones of uncompromising selection. Picture an Eocene morning, leaves swaying in the breeze, colorful fruit, and predatory birds. An odor-sensitive, lengthy snout would not have been of much use, because breezes disperse odors. But skeletal changes and a brain that could assess motion, depth, shape, and color must have been favored. For instance, eye sockets were now facing front, not on the skull's sides, which is better for depth perception. For climbers and leapers, a brain that could estimate body weight, distance, wind speed, and suitable destinations would have been favored; adjustments had to be quick for a body in motion.

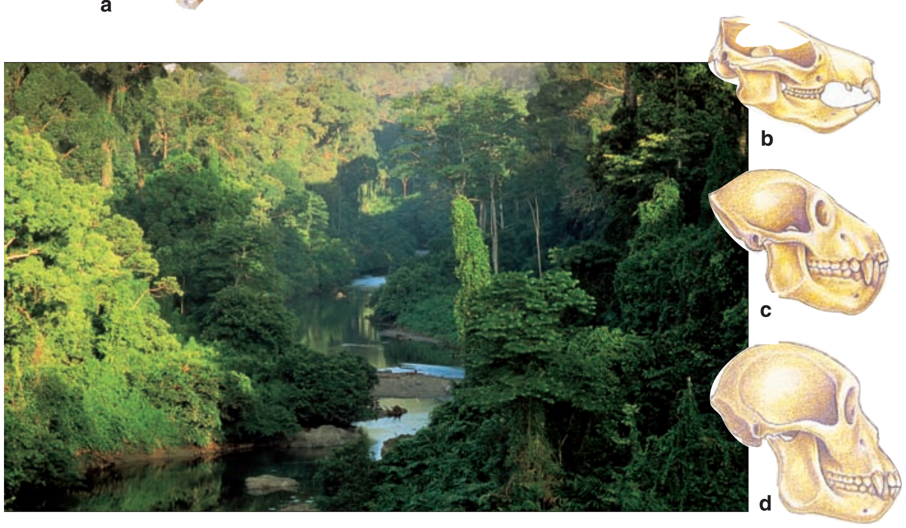
By 36 million years ago, anthropoids had evolved. These tree-dwellers were on or close to the lineage that led to monkeys and apes. One kind had forward-directed eyes, a flattened face, and an upper jaw that sported shovel-shaped front teeth. It probably used the digits on its forelimbs to grasp food. Some lived in swamp forests infested with predatory reptiles. Was that a reason why it became imperative to think fast, grip strongly, and avoid the ground? Possibly.

THE FIRST APELIKE AND HUMANLIKE FORMS

Between 23 and 18 million years ago, in the Miocene, apes evolved. They were the first of the *hominoids*, and they spread through Africa, Asia, and Europe when the climate was changing (Figure 26.32). Africa became cooler and drier, with more seasonal change. Tropical forests, with their fruits, leaves, and insects, gave way to open woodlands and, later, to savannas. Food had become drier, harder, and more difficult to find.

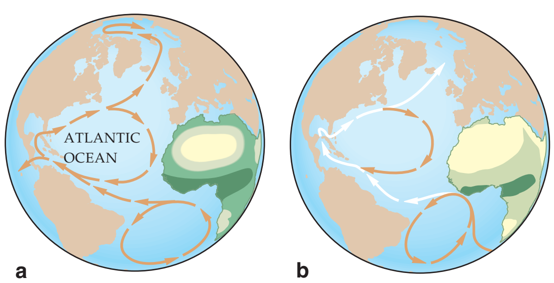
Hominoids that had evolved in lush forests could move into new adaptive zones or die out. Most died, but not the common ancestor of modern apes and humans. Did upright stances and nimble fingers help their descendants survive? Did both traits evolve on land or in water? (Captive bonobos stay upright when wading into lakes and estuaries in pursuit of fishes and invertebrates.) Another puzzle: Increased cranial volume could not have occurred without mutation in

a



b c d

Figure 26.31 (**a**) Tree shrew (*Tupaia*), a squirrel-size primate of tropical forests in Southeast Asia. Skull shape and teeth of early primates: (**b**) This Paleocene primate, *Plesiadapis*, had rodentlike teeth. (**c**) Monkey-sized *Aegyptopithecus*, an Oligocene anthropoid, predates the split to Old World apes and monkeys. (**d**) Apelike Miocene dryopith. Some dryopiths were as big as chimpanzees.



a b

Figure 26.32 Model for a long-term shift in global climate. (**a**) Before the Isthmus of Panama formed, the salinity of surface ocean currents was similar around the world. Ocean circulation kept Arctic waters from getting too cold. (**b**) After the isthmus formed, circulation patterns changed. The North Atlantic surface currents grew saltier and heavier, and sank before reaching the Arctic. Water got colder in polar regions. An Arctic ice cap formed; climates became cooler and drier.

Figure 26.33 ***Animated!*** Fossils of African hominids that lived between 7 and 1.5 million years ago.

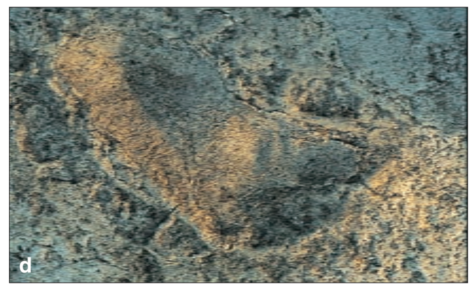


Figure 26.34 (**a**) Fossilized bones of a female dubbed "Lucy" (*Australopithecus afarensis*), a two-legged wader or walker that lived 3.2 million years ago.

Unlike chimpanzees and other apes, the early hominids did not have a splayed-out big toe (**b**). So how do we know? (**c**,**d**) At Laetoli in Tanzania, Mary Leakey found footprints made in soft, damp, volcanic ash 3.7 million years ago. The arch, big toe, and heel marks of these footprints are signs of bipedal hominids.

the genes that control metabolism and bone growth (Section 17.9). Concurrently, the diet would have had to provide enough fuel for a larger, more active brain. By one hypothesis, a switch to eating fishes, so rich in fatty acids, fueled the expansion in brain volume.

Sahelanthropus tchadensis was an ape or a hominid that lived in Central Africa about 6 or 7 million years ago. Its brain was chimpanzee-sized (Figure 26.33). Even so, like hominids that evolved later on, it had a flattened face, a prominent brow ridge, and smaller canines. It lived near the shore of a lake.

Australopithecus and *Paranthropus* were two groups, known informally as **australopiths** ("southern apes"). *A. anamensis*, *A. afarensis*, and *A. africanus* had slight builds (Figure 26.34*a*). *P. boisei* and *P. robustus* were muscular and heavily built. Like apes, all had a large face relative to brain size, and their jaws protruded. Given their thick-enameled molars, they had to be eating harder food. Also, they walked upright, either straight forward or with a side-to-side motion, like a skater or someone wading through water.

However upright walking arose, we know that the hominids were already bipedal by 3.7 million years ago, because they left footprints. At that time, two *A. afarensis* individuals scuttled across a layer of newly deposited volcanic ash. A light rain was falling, and it transformed the ash into fast-drying cement—which preserved the footprints. Compare Figure 26.34*d*.

By the Eocene, prosimians—the first primates—had evolved from mammals that resembled modern tree shrews. The first apelike forms (hominoids) evolved in the Oligocene. One branch gave rise to apes in the Miocene.

Australopiths and certain hominids that preceded them walked upright. Long-term climate change drove them out of the trees in pursuit of food, either by wading in lakes and estuaries or by walking about in open woodlands.

26.14 Emergence of Early Humans

Judging from the fossil record, the earliest members of the human lineage emerged about 2.5 million years ago, in the great East African Rift Valley.

What do the fossilized fragments of early hominids tell us about human origins? The record is still too sketchy for us to interpret how all the diverse forms were related, let alone which might have been our ancestors. Besides, exactly which traits should we use to define **humans**—members of the genus *Homo*?

Well, what about brains? Our brain is the basis of unsurpassed analytical skills, verbal skills, complex social behavior, and technological innovations. Our brain sets us apart from apes that have a far smaller cranial volume (Figure 26.35). Yet this feature alone cannot tell us when a lineage of hominids made the evolutionary leap to becoming human. Their brain size fell within the range of apes. They did use simple tools, but so do chimps and some birds. We have no clue to their social behavior.

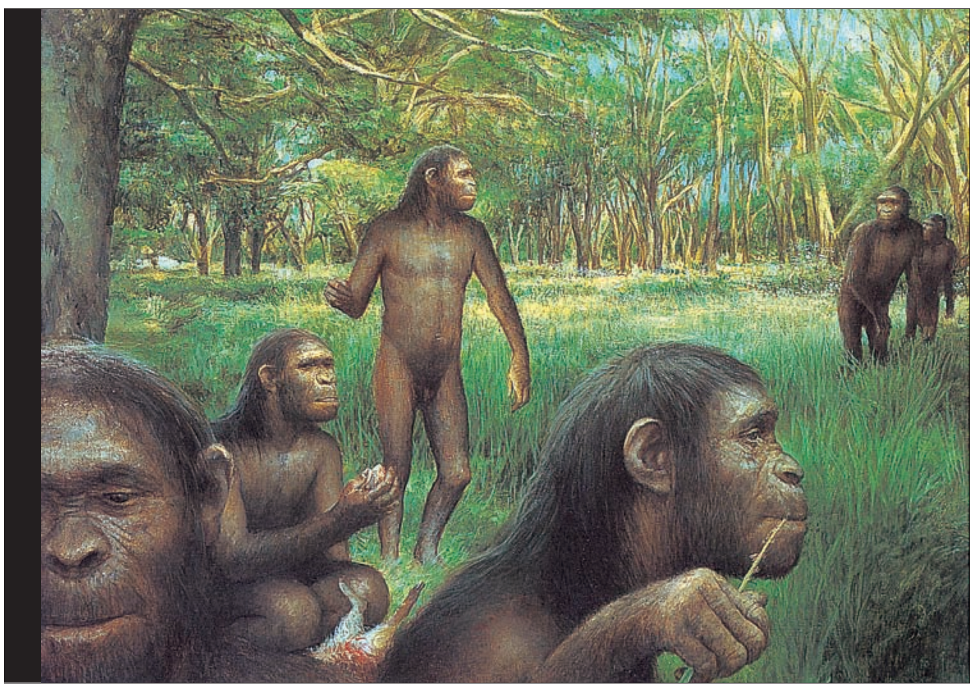
We are left to speculate on the evidence of physical traits among diverse fossils. They include a skeleton that permitted bipedalism, nimble fingers, a smaller face, a larger cranium, and smaller, thickly enameled teeth. These traits emerged late in the Miocene and are features of what might be the first humans—*Homo habilis*. The name means "handy man" (Figure 26.36).

Most of the early known forms of *Homo* evolved in Olduvai Gorge, Lake Turkana, and other formations of the East African Rift Valley (Figure 26.37). This long valley had started to form earlier in the Miocene, when crustal plates were colliding. Later in time, woodlands flourished on its western slope. However, mountains blocked most of the seasonal rainfall to the west, and there, savannas formed.

Figure 26.35 Comparison of brain size for a chimpanzee (*left*) and a modern human (*right*).

Fossil teeth indicate that these early humans ate hard-shelled nuts, dry seeds, soft fruits and leaves, and insects—all seasonal foods. *H. habilis* had to think ahead, and plan when to gather and store foods that could last through the cool, dry seasons ahead.

H. habilis shared its habitat with carnivores such as saber-tooth cats, which could impale prey and tear flesh but could not crush open the marrow bones. Carcasses with meat shreds clinging to bones offered nutrients in nutrient-stingy places. Judging from its



Homo rudolfensis
2.4–1.8 million years

H. habilis
1.9–1.6 million years

Figure 26.36 *Left:* Painting of a band of *Homo habilis* in an East African woodland. Two australopiths are shown in the distance. *Above:* Two fossils of early humans.

Figure 26.37 Olduvai Gorge in Africa, and a sampling of stone tools. *Left to right:* crude chopper, more refined chopper, hand ax, and cleaver.

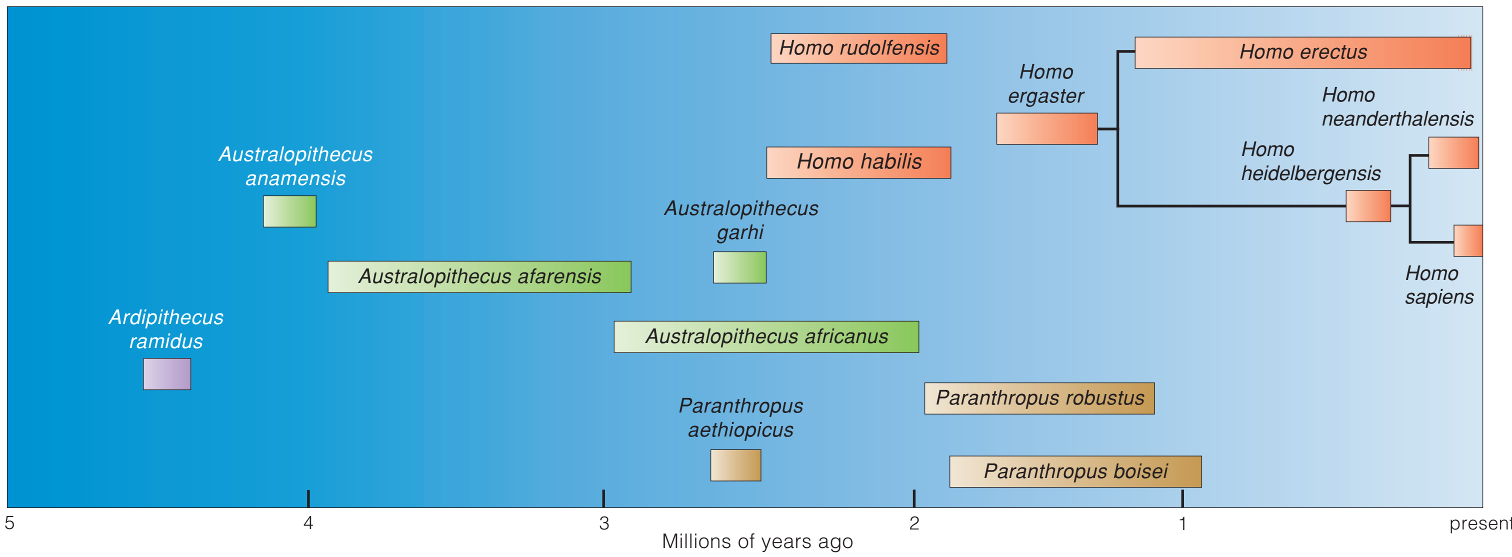


Figure 26.38 Timeline for the appearance and extinction of major hominid species, currently placed in four genera. Graph lines at upper right depict one view of the evolutionary relationships among the most recent species. The number of species, which fossils should be assigned to each group, and how species are related are all matters of heated debate among paleontologists.

array of teeth, *H. habilis* apparently was not one of the full-time carnivores. However, it might have enriched its diet opportunistically, by scavenging carcasses.

Which was the first toolmaker? The earliest stone tools we know about, from a site in Ethiopia, date to about 2.5 million years ago. Pieces of volcanic rock, chipped to create a sharp edge, were found alongside bones of animals that appear to have been butchered with similar tools. Fossils of *A. garhi* that were found nearby date to the same period. Did *A. garhi* make the tools? Perhaps.

The layers of Tanzania's Olduvai Gorge document later refinements in toolmaking skills (Figure 26.37). The deepest of these sedimentary rock layers date to about 1.8 million years ago and hold crudely chipped pebbles similar to the earliest ones in Ethiopia. They also hold the fossil remains of australopiths and of *H. habilis*. We don't know which group created the tools. More recently deposited layers hold somewhat more complex tools. But all innovations in tool form were limited. The same types appear in layers that formed slowly, over a period of about 1 million years.

Before turning the page, take a look at Figure 26.38 to get a sense of where we have been on the primate evolutionary road, and where we go from here.

Once again, biological and geologic evolution converged. Crustal movements formed the great East African Rift Valley, which became cloaked in woodlands and forests that promoted the evolution of the first humans.

26.15 Emergence of Modern Humans

LINKS TO SECTIONS 17.8, 19.4

Ancestors of modern humans remained in Africa until Homo erectus *evolved. Then cultural evolution took off.*

EARLY BIG-TIME WALKERS

Homo erectus is a species related to modern humans (Figures 26.39 and 26.40). Its name means "upright man." Its forerunners walked upright, but some *H. erectus* populations did the name justice. They walked out of Africa, turned left into Europe, and also right, all the way to China. Middle East and Southeast Asia fossils date from 1.8 million to 1.6 million years ago. So *H. erectus* had to adapt to brutally cold climates of that period, and to ice sheets that advanced several times into northern Europe and North America.

Whatever pressures triggered the far-flung travels, this was a time of physical changes, as in skull size and leg length. It was a time of cultural lift-off for the human lineage. *H. erectus* had a larger brain and was a more creative toolmaker. Its social organization and communication skills must have been well developed. How else can we explain its dispersal? From southern Africa to England, populations used the same kinds of hand axes and other tools. They met environmental challenges by building fires and using fur for clothing, starting with an early Pleistocene ice age.

One fossil from Ethiopia shows that *Homo sapiens* had evolved by about 160,000 years ago. Compared to *H. erectus,* that species had smaller teeth, facial bones, and jawbones. Many individuals had a novel feature —a chin. They had a higher, rounder skull, a bigger brain, and possibly complex language.

A different group, the massively built and large-brained Neandertals, lived in Europe and the Near East from 200,000 to 30,000 years ago (Figure 26.39). Their extinction coincided with the arrival of modern humans in the same regions. Did they interbreed or war with the new arrivals? We cannot say. Neandertal mitochondrial DNA does have unique sequences that are not found in modern gene pools. By all molecular evidence, they have no modern descendants.

Figure 26.39 Fossils of early modern human forms.

H. erectus 2 million–53,000? years | *H. neandertalensis* 200,000–30,000 years

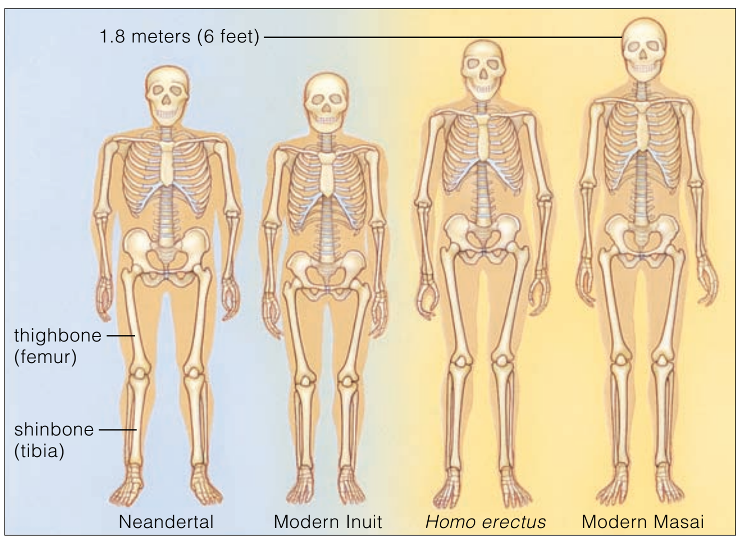


Figure 26.40 Body build correlated with climate. Humans adapted to cold climates have a heat-conserving body: stockier and with shorter legs, compared to humans adapted to hot climates.

WHERE DID MODERN HUMANS ORIGINATE?

Was Africa the cradle for us all? At this writing, no one has discovered fossils of *Homo* that are older than 2 million years *except* in Africa. Between 2 million and 500,000 years ago, some *H. erectus* groups left Africa in waves. Some still lived in Southeast Asia between 53,000 and 37,000 years ago.

But when did *H. sapiens* originate? *Here we find one case of how the same body of evidence can be interpreted in different ways.* The *multiregional* model and the *African emergence* model explain the distribution of early and modern humans differently. Even so, they both rely on measurements of genetic distance between modern populations. Biochemical and immunological studies correlate *H. sapiens* fossils to specific times and places in the past (Figure 26.41). They also reveal that the greatest genetic distance is between the populations native to Africa and all other populations. The next greatest distance separates populations of Southeast Asia and Australia from others (Figure 26.42).

According to the **multiregional model**, groups of *H. erectus* in different regions faced different selection pressures, and they gave rise to subpopulations (races) of *H. sapiens*. In 2003, fossils of early humans that date to 18,000 years ago turned up on an Indonesian island (Flores). They were about as tall as australopiths. Like *H. erectus*, they had a small brain relative to body size and heavy brow ridges. But *H. erectus* vanished 200,000 years ago. The species, named *H. floresiensis*, may have

H. sapiens
fossil from Ethiopia,
160,000 years old

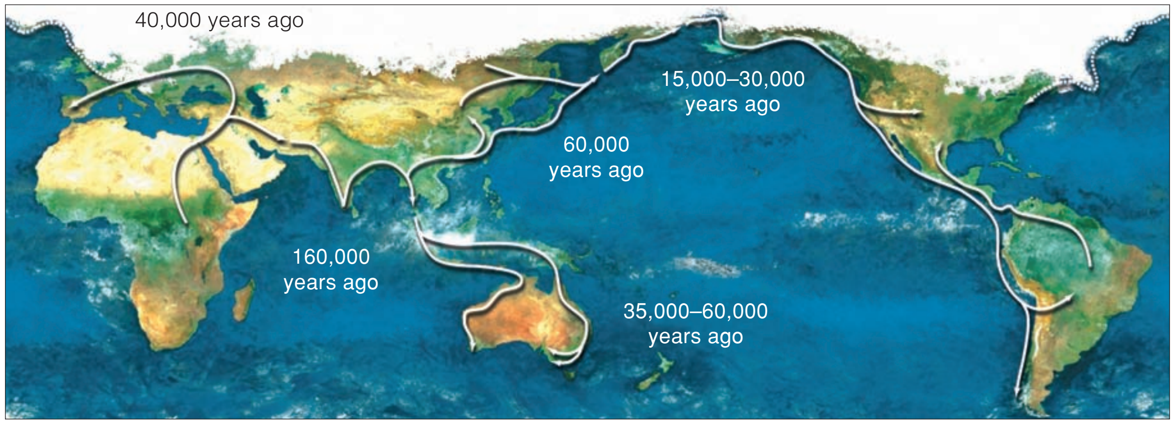


Figure 26.41 Estimated times when early *H. sapiens* colonized different parts of the world, based on radiometric dating of fossils. White lines are presumed dispersal routes. Molecular and immunological data imply that only a few populations left Africa. Genetically, all modern populations are highly similar.

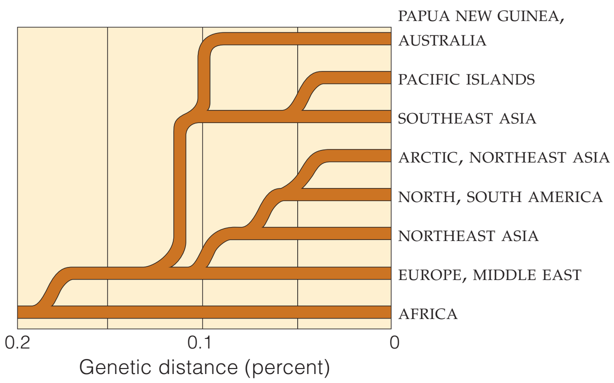


Figure 26.42 One proposed family tree for *Homo sapiens* populations native to different regions. The tree is based on analysis of many genes (such as those for mitochondrial DNA and the ABO blood group) and immunological comparisons.

Figure 26.43 Cave paintings at Lascaux, France.

descended from *Homo erectus*. As we know from many studies in biogeography, reduction in the body size of big organisms actually is a common adaptation to life on small islands, which have limited resources.

The **African emergence model** does not contradict fossil evidence that *H. erectus* migrated out of Africa and evolved further in different regions. But it has *H. sapiens* arising in sub-Saharan Africa, then dispersing into other regions (Figure 26.41). As modern humans spread out of Africa, they replaced archaic *H. erectus* populations that had preceded them. Only later did regional phenotypic differences—races—evolve.

Fossil evidence and considerable DNA sequence data from mitochondria, X and Y chromosomes, and autosomes support the African emergence model. So does evidence from archaeology. The oldest *H. sapiens* fossils are from Africa. In Zaire, intricately wrought barbed-bone tools indicate that populations in Africa were as skilled at making tools as *Homo* populations in Europe. Gene patterns from forty-three ethnic Asian groups suggest modern humans moved from Central Asia, along India's coast, then on into Southeast Asia and southern China. They dispersed north and west into China and Siberia, then into the Americas.

From 40,000 years ago to today, culture became an immense part of human evolution, and we must leave that story. A point to remember: Humans dispersed rapidly through the world by devising *cultural* means to deal with the environment, and their art reflects a hunting heritage (Figure 26.43). Today, hunters and gatherers persist in parts of the world; other groups moved on from "stone-age" technology to the age of "high tech." The coexistence of these groups attests to the deep behavioral plasticity of the human species.

Cultural evolution has outpaced the biological evolution of the only remaining human species, H. sapiens. Today, humans everywhere rely on cultural innovation to adapt rapidly to a broad range of environmental challenges.

http://biology.brookscole.com/starr11

Summary

Section 26.1 Four features help define chordates. Their embryos develop a notochord, a dorsal hollow nerve cord, a pharynx with gill slits, and a tail that extends past the anus. Some or all features persist in adults. Tunicates and lancelets are invertebrate filter-feeding chordates.

BiologyNow
Examine the body plan of a lancelet with the animation on BiologyNow.

Section 26.2 Craniates are chordates with a brain chamber of cartilage or bone. Vertebrates are craniates with a vertebral column (cartilaginous or bony segments). Jaws, paired fins, and later, lungs, were key innovations that led to the adaptive radiation of vertebrates.

BiologyNow
Explore the chordate family tree with the animation on BiologyNow.

Section 26.3 Cartilaginous fishes and bony fishes are aquatic vertebrates. The most diverse vertebrates are the bony fishes. Late in the Devonian, bony fishes that had lobed fins and lungs gave rise to the tetrapods.

Sections 26.4, 26.5 Amphibians, the first tetrapods on land, share traits with aquatic tetrapods and reptiles. Most life cycles still go through aquatic stages. Existing groups include salamanders, frogs, and toads. Because of habitat losses and other factors, many species are now declining.

BiologyNow
Read the Infotrac article "Amphibian Declines and Emerging Disease," Joseph Kliesecker, American Scientist, *March–April 2004.*

Sections 26.6, 26.7 Amniotes, the first vertebrates to escape reproductive dependence on outside water, have water-conserving skin and kidneys, and amniote eggs. Synapsids (mammals and mammal-like species, such as therapsids) are one major group. Sauropsids ("reptiles" and birds) are another major group.

Section 26.8 Modern reptilian groups live on land, in fresh water, and in the seas. Eggs are fertilized inside the body and usually laid on land. Lizards and snakes are the most diverse. Tuataras have some amphibian-like traits. Crocodilians are the closest relatives of birds.

Section 26.9 Birds are warm-blooded amniotes and the only existing animals with feathers. In most species, the body plan has been highly modified for flight.

BiologyNow
Learn what's inside a bird egg and how birds are adapted for flight with the animation on BiologyNow.

Sections 26.10, 26.11 Mammals are the only animals in which females nourish the young with milk from mammary glands. Three lineages are egg-laying mammals (monotremes), pouched mammals (marsupials), and placental mammals (eutherians). Placental mammals are the most diverse group.

BiologyNow
See how the current distribution of mammalian groups arose with the animation on BiologyNow.

Section 26.12 Primates are prosimians, tarsiers, and anthropoids (monkeys, apes, humans). The first primates were tiny shrewlike animals. Certain lineages reflect a trend toward better daytime vision, upright walking, more refined hand movements, smaller teeth, bigger brains, and extended parental care.

Sections 26.13–26.15 Hominoids are apes and hominids (humans and their most recent ancestors). They arose in Africa in the Oligocene. Australopiths (early hominids) walked upright. Early humans (*Homo*) arose between 2.4 million and 1.6 million years ago, and some *H. erectus* populations moved on into Europe and Asia. Neandertalers were early humans that apparently did not contribute to the gene pool of modern humans.

H. sapiens had evolved by 160,000 years ago. By a multiregional model for modern human origins, the differences among human subpopulations arose as an outcome of different selection pressures operating on *H. erectus* populations in different regions. By the African emergence model, as modern humans spread out of Africa, they replaced older populations of *H. erectus* that had preceded them. Only later did regional phenotypic differences—races—evolve. Molecular and archaeological data support this model.

BiologyNow
Compare hominid fossils with the animation on BiologyNow.
Read the Infotrac article "Rethinking Neanderthals," Joe Alper, Smithsonian, *June 2003.*

Self-Quiz

Answers in Appendix II

1. All chordates have ______ .
   a. a backbone c. jaws
   b. a notochord d. both b and c

2. Vertebrate gills function in ______ .
   a. respiration d. water regulation
   b. blood circulation e. both a and c
   c. food trapping

3. A divergence from ______ gave rise to tetrapods.
   a. ray-finned fishes c. cartilaginous fishes
   b. lizards d. lobe-finned fishes

4. Which of the following is an amniote?
   a. shark b. turtle c. toad d. sea squirt

5. Reptiles are adapted to life on land by ______ .
   a. tough skin d. amniote eggs
   b. internal fertilization e. all of the above
   c. good kidneys f. none of the above

6. ______ are the closest living relatives of birds.
   a. Crocodilians c. Prosimians
   b. Tuataras d. Lizards

Figure 26.44 *Ciona savignyi*. This sea squirt is native to seas near Japan, but it has invaded waters along the west coast of the United States, including the San Francisco Bay.

Figure 26.45 Duck-billed platypus (*Ornithorhynchus anatinus*), native to Australia and Tasmania. In addition to other unusual traits, it is the only mammal that produces venom.

7. Only birds have ________ .
   a. a cloaca
   b. a four-chambered heart
   c. feathers
   d. all of the above

8. A chimpanzee is a ________ .
   a. craniate
   b. vertebrate
   c. hominoid
   d. amniote
   e. placental mammal
   f. all of the above

9. *Homo erectus* ________ .
   a. was the earliest member of the genus *Homo*
   b. was one of the australopiths
   c. evolved in Africa and spread to diverse regions
   d. was the first to make stone tools

10. Match the organisms with the appropriate description.
    ____ fishes
    ____ amphibians
    ____ reptiles
    ____ birds
    ____ monotremes
    ____ marsupials
    ____ hominids
    a. first land tetrapods
    b. feathered amniotes
    c. egg-laying mammals
    d. humans and close relatives
    e. cold-blooded amniotes
    f. pouched mammals
    g. most diverse vertebrates

Additional questions are available on **Biology Now™**

Critical Thinking

1. The National Human Genome Research Institute is currently funding a project to sequence the genome of *Ciona savignyi*, a sea squirt (Figure 26.44). What might these studies tell us about the human genome?

2. Kathie and Gary, two amateur fossil hunters, dug up the complete fossil of a mammal. How can they determine whether it was a herbivore, carnivore, or omnivore?

3. In 1798, a stuffed platypus specimen was delivered to the British Museum. Many thought it was a fake. It had brown fur, a beaverlike tail, a ducklike bill, and webbed feet (Figure 26.45). Reports that the animal laid eggs only added to the confusion. We now know that platypuses burrow in riverbanks and forage for prey under water. Webbing on their feet can be retracted to reveal claws. Sensory receptors in the bill allow the animal to detect prey even with its eyes and ears tightly shut.

To modern biologists, a platypus is clearly a mammal. Like other mammals, it has fur and the females produce milk. Young animals have more typical mammalian teeth that are replaced by hardened pads as the animal matures. Why do you think modern biologists can more easily accept the idea that a mammal can have some reptilian traits, such as laying eggs? What do they know that gives them an advantage over scientists living in 1798?

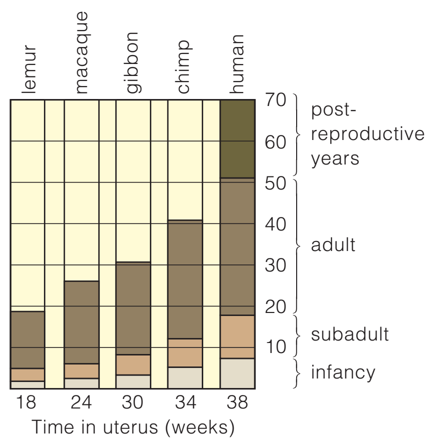


Figure 26.46 Comparison among primates of the most ancient to the most recent lineages. The graph plots how long it takes for embryos to develop inside pregnant females. It shows the years spent as infants and juveniles, when they are most vulnerable and still learning survival skills from adults. The graph also compares the average life spans. The trend is toward longer life spans and greater dependency of offspring on adults.

4. During the Triassic, hundreds of species of tuatara-like reptiles roamed Pangea. Now only two species survive on a few small, cold islands off the coast of New Zealand. Speculate on why this relic population has survived there despite disappearing from the rest of its former range.

5. Reflect on the flight muscles of birds and their high demands for oxygen. Which organelle would you expect to be profuse in flight muscles? Why?

6. The average cranial volume of early *H. sapiens* was 1,200 cubic centimeters. It now averages 1,400 cubic centimeters. By one hypothesis, females chose the most clever mates, the advantage being offspring with genes that favorably affect intelligence. What kind of data might a researcher gather to test this sexual selection hypothesis?

7. Figure 26.46 compares five primates. Note the trend toward longer life spans and the length of time before adulthood. Research the life-styles and selection pressures on these primates. Formulate a hypothesis that might explain the differences among them.

8. Amniotes are defined partly by their eggs, which have four membranes that nourish and protect the embryo while it develops in the mother's body (Section 44.9). Do some research on how these amniote eggs help reptiles, including snakes (Figure 26.47) survive in dry or seasonally dry habitats on land.

Figure 26.47 Eastern hog-nosed snakes emerging from amniote eggs.