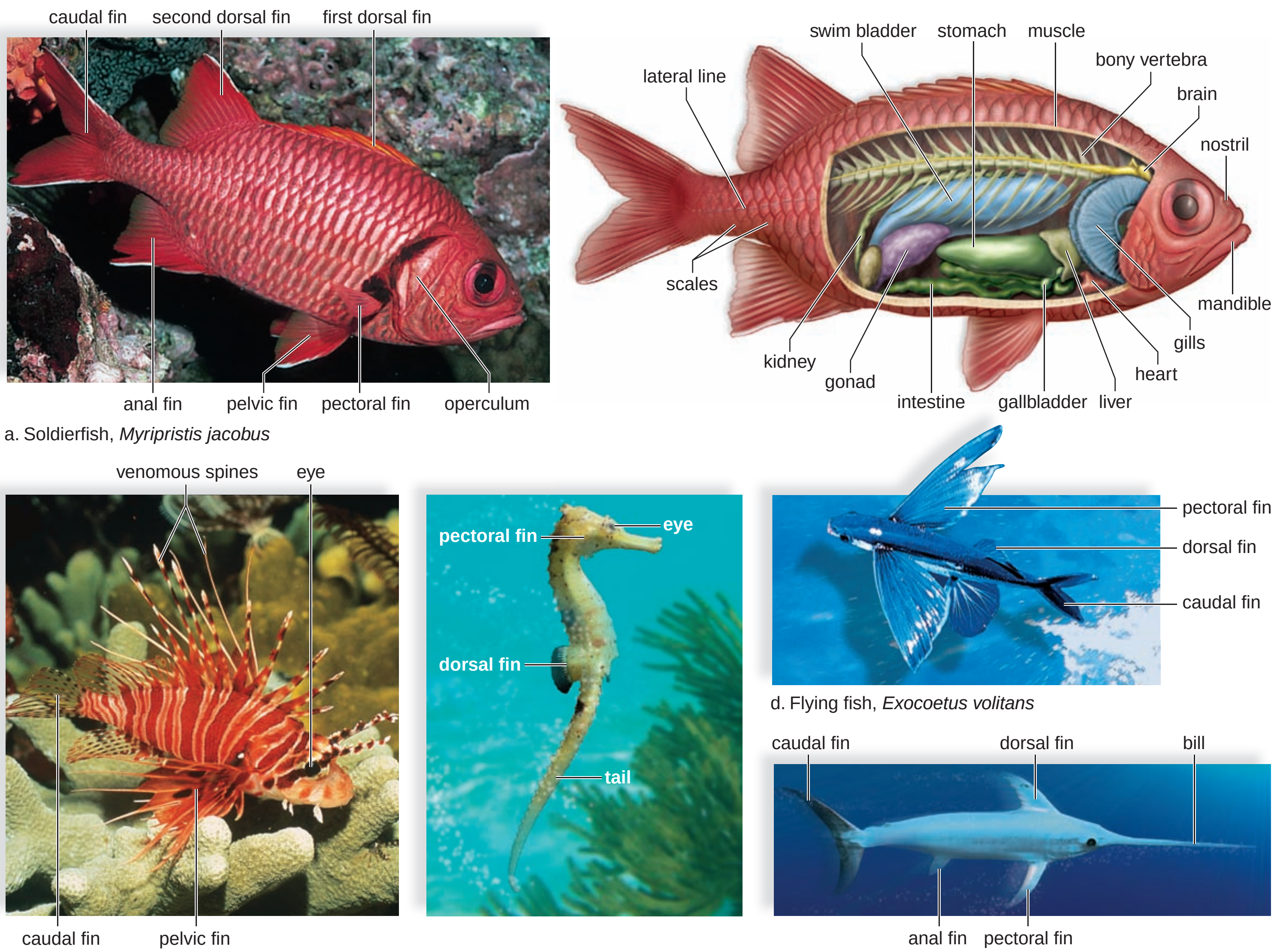


a. Soldierfish, *Myripristis jacobus*

b. Lionfish, *Pterois volitans*

c. Seahorse, *Hippocampus kuda*

d. Flying fish, *Exocoetus volitans*

e. Swordfish, *Xiphias gladius*

FIGURE 29.7 Ray-finned fishes.

a. A soldierfish has the typical appearance and anatomy of a ray-finned fish. A lionfish (**b**), a seahorse (**c**), a flying fish (**d**), and a swordfish (**e**) show how diverse ray-finned fishes can be.

In 1938, a coelacanth was caught from the deep waters of the Indian Ocean off the eastern coast of South Africa. It took the scientific world by surprise because these animals were thought to be extinct for 70 million years. Approximately 200 coelacanths have been captured in recent years (Fig. 29.8).

FIGURE 29.8 Coelacanth, *Latimeria chalumnae*.

A coelacanth is a lobe-finned fish once thought to be extinct.

Check Your Progress 29.3

1. List and describe the characteristics that fishes have in common.
2. What characteristics distinguish cartilaginous fishes?

29.4 The Amphibians

Amphibians (class Amphibia [Gk. *amphibios,* living both on land and in water]), which have these characteristics, were abundant during the Carboniferous period:

Limbs. Typically, amphibians are tetrapods [Gk. *tetra,* four, and *podos,* foot], meaning that they have four limbs. The skeleton, particularly the pelvic and pectoral girdles, is well developed to promote locomotion.

Smooth and nonscaly skin. The skin, which is kept moist by mucous glands, plays an active role in water balance and respiration and can also help in temperature regulation when on land through evaporative cooling. A thin, moist skin does mean, however, that most amphibians stay close to water, or else risk drying out.

Lungs. If lungs are present, they are relatively small, and respiration is supplemented by exchange of gases across the porous skin called cutaneous respiration.

Double-loop circulatory pathway. (Fig. 29.9*b, c*). A three-chambered heart with a single ventricle and two atria pumps blood to both the lungs and to the body.

Sense organs. Special senses, such as sight, hearing, and smell, are fine-tuned for life on land. Amphibian brains are larger than those of fish, and the cerebral cortex is more developed. These animals have a specialized tongue for catching prey, eyelids for keeping their eyes moist, and a sound-producing larynx.

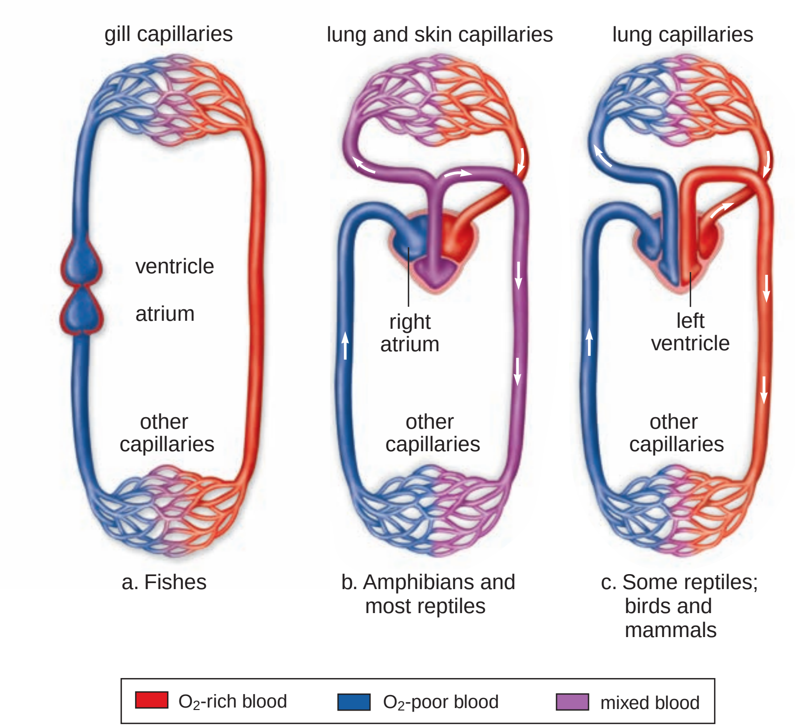


FIGURE 29.9 Vertebrate circulatory pathways.

a. The single-loop pathway of fishes has a two-chambered heart. **b.** The double-loop pathway of other vertebrates sends blood to the lungs and to the body. In amphibians and most reptiles, there is limited mixing of O_2-rich and O_2-poor blood in the single ventricle of their three-chambered heart. **c.** The four-chambered heart of some reptiles (crocodilians and birds) and mammals sends only O_2-poor blood to the lungs and O_2-rich blood to the body.

Ectothermy. Like fishes, amphibians are ectotherms but are able to live in environments where the temperature fluctuates greatly. During winters in the temperate zone, they become inactive and enter torpor. The European common frog can survive in temperatures dropping to as low as −6°C.

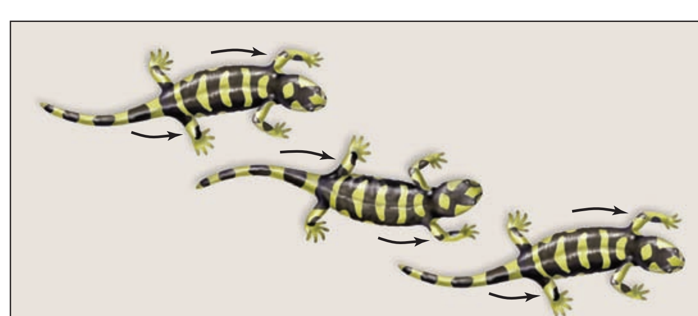
Aquatic reproduction. Their name, amphibians, is appropriate because many return to water for the purpose of reproduction. They deposit their eggs and sperm into the water, where external fertilization takes place. Generally, the eggs are protected only by a jelly coat and not by a shell. When the young hatch, they are tadpoles (aquatic larvae with gills) that feed and grow in the water. After they undergo a **metamorphosis** (change in form), amphibians emerge from the water as adults that breathe air. Some amphibians, however, have evolved mechanisms that allow them to bypass this aquatic larval stage and reproduce on land.

Evolution of Amphibians

Amphibians evolved from the lobe-finned fishes with lungs by way of transitional forms. Two hypotheses have been suggested to account for the evolution of amphibians from lobe-finned fishes. Perhaps lobe-finned fishes had an advantage over others because they could use their lobed fins to move from pond to pond. Or, perhaps the supply of food on land in the form of plants and insects—and the absence of predators—promoted further adaptations to the land environment. Paleontologists have recently found a well-preserved transitional fossil from the late Devonian period in Arctic Canada that represents an intermediate between lobe-finned fishes and tetrapods with limbs. This fossil, named *Tiktaalik roseae* (Fig. 29.10, *left*), provides unique insights into how the legs of tetrapods arose (Fig. 29.10, *right*).

Diversity of Living Amphibians

The amphibians of today occur in three groups: salamanders and newts; frogs and toads; and caecilians. Salamanders and newts have elongated bodies, long tails, and usually two pairs of limbs (Fig. 29.11*a*). Salamanders and newts range in size from less than 15 cm to the giant Japanese salamander, which exceeds 1.5 m in length. Most have limbs that are set at right angles to the body and resemble the earliest fossil amphibians. They move like a fish, with side-to-side, sinusoidal (S-shaped) movements:



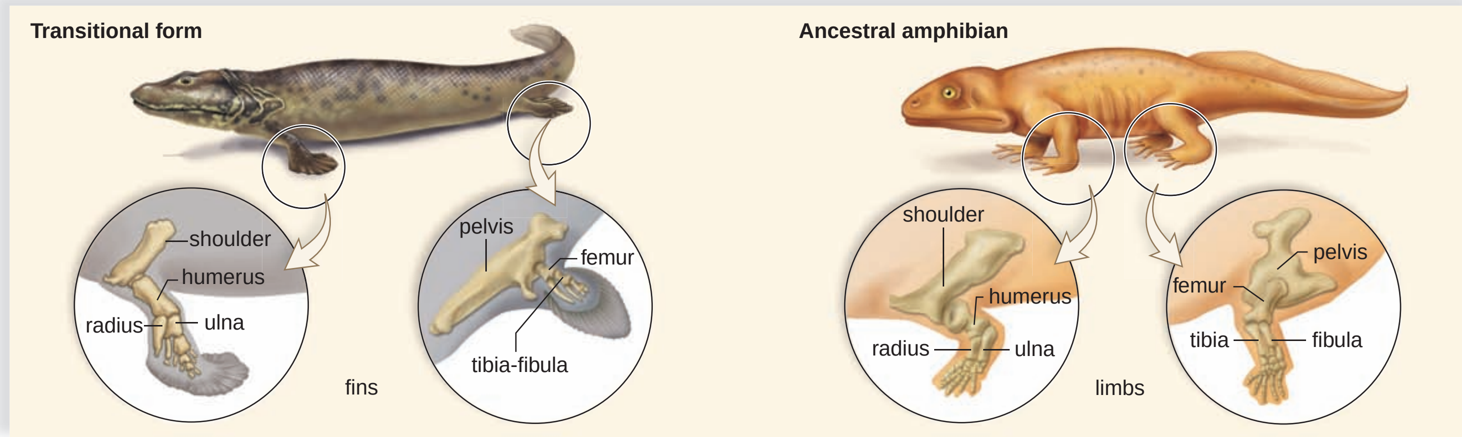


FIGURE 29.10 Lobe-finned fishes to amphibians.

This transitional form links the lobes of lobe-finned fishes to the limbs of ancestral amphibians. Compare the fins of the transitional form (*left*) to the limbs of the ancestral amphibian (*right*).

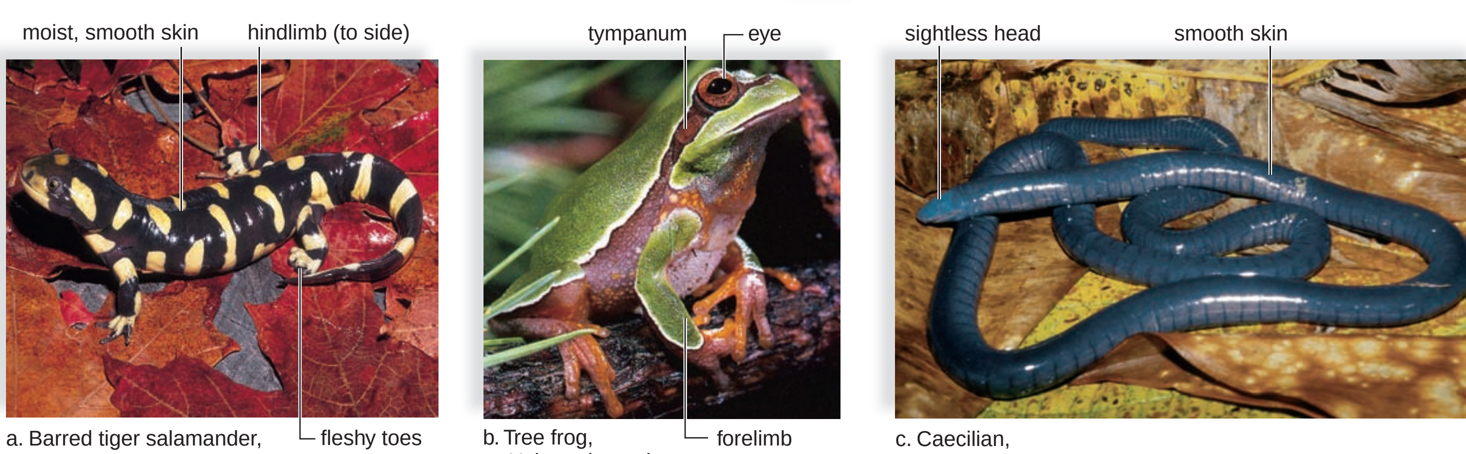
Both salamanders and newts are carnivorous, feeding on small invertebrates such as insects, slugs, snails, and worms. Salamanders practice internal fertilization; in most, males produce a sperm-containing spermatophore that females pick up with their **cloaca** (the terminal chamber common to the urinary, digestive, and genital tracts). Then the fertilized eggs are laid in water or on land, depending on the species. Some amphibians, such as the mudpuppy of eastern North America, remain in the water and retain the gills of the larva.

Frogs and toads, which range in length from less than 1 cm to 30 cm, are common in subtropical to temperate to desert climates around the world. In these animals, which lack tails as adults, the head and trunk are fused, and the long hindlimbs are specialized for jumping (Fig. 29.11*b*). All species are carnivorous and have a tremendous array of specializations depending on their habitats. Glands in the skin secrete poisons that make the animal distasteful to eat and protect them from microbial infections. Some tropical species with brilliant fluorescent green and red coloration are particularly poisonous (see Fig. 29A*a*). Colombian Indians dip their darts in the deadly secretions of these frogs, aptly called poison-dart frogs. The tree frogs have adhesive toepads that allow them to climb trees, while others, the spadefoots, have hardened spades that act as shovels enabling them to dig into the soil.

Caecilians are legless, often sightless, worm-shaped amphibians that range in length from about 10 cm to more than 1 m (Fig. 29.11*c*). Most burrow in moist soil, feeding on worms and other soil invertebrates. Some species have folds of skin that make them look like a segmented earthworm.

Check Your Progress 29.4

1. **a.** List and describe the characteristics that amphibians have in common. **b.** What evidence links lobe-finned fishes to the amphibians?
2. Describe the usual life cycle of amphibians.



a. Barred tiger salamander, *Ambystoma tigrinum*

b. Tree frog, *Hyla andersoni*

c. Caecilian, *Caecilia nigricans*

FIGURE 29.11 Amphibians.

Living amphibians are divided into three orders: **a.** Salamanders and newts. Members of this order have a tail throughout their lives and, if present, unspecialized limbs. **b.** Frogs and toads. Like this frog, members of this order are tailless and have limbs specialized for jumping. **c.** The caecilians are wormlike burrowers.

29.5 The Reptiles

The **reptiles** (class Reptilia) are a very successful group of terrestrial animals consisting of more than 17,000 species, including the birds. Reptiles have these characteristics showing that they are fully adapted to life on land:

Paired limbs. Two pairs of limbs usually with five toes. Reptiles are adapted for climbing, running, paddling, or flying.

Skin. A thick and dry skin is impermeable to water. Therefore, the skin prevents water loss. In reptiles, the skin is wholly or in part scaly (Fig. 29.12). Many reptiles (e.g., snakes and lizards) molt several times a year.

Efficient breathing. The lungs are more developed than in amphibians. Also in many reptiles, an expandable rib cage assists breathing.

Efficient circulation. The heart prevents mixing of blood. A septum divides the ventricle either partially or completely. If it partially divides the ventricle, the mixing of O_2-poor blood and O_2-rich blood is reduced. If the septum is complete, O_2-poor blood is completely separate from O_2-rich blood (see Fig. 29.9*c*).

Efficient excretion. The kidneys are well developed. The kidneys excrete uric acid, and therefore less water is required to rid the body of nitrogenous wastes.

Ectothermy. Most reptiles are ectotherms, and this allows them to survive on a fraction of the food per body weight required by birds and mammals. Ectothermic reptiles are adapted behaviorally to maintain a warm body temperature by warming themselves in the sun.

Well-adapted reproduction. Sexes are separate and fertilization is internal. Internal fertilization prevents sperm from drying out when copulation occurs. The **amniotic egg** contains extraembryonic membranes, which protect the embryo, remove nitrogenous wastes, and provide the embryo with oxygen, food, and water (see Fig. 29.14*e*). These membranes are not part of the embryo itself and are disposed of after development is complete. One of the membranes, the amnion, is a sac that fills with fluid and provides a "private pond" within which the embryo develops.

Evolution of Amniotes

An ancestral amphibian gave rise to the amniotes, which includes animals now classified as the reptiles (including birds) and the mammals. The embryo of an amniote has extracellular membranes, including an amnion. Figure 29.13 shows that the amniotes consist of three lineages: (1) the turtles, in which the skull has no openings behind the orbit—eye socket; (2) all the other reptiles including the birds, in which the skull has two openings behind the orbit; and (3) the mammals, in which the skull has one opening behind the orbit.

This chapter concerns the reptiles, an artificial grouping because it has no common ancestor. In other words, reptiles are a paraphyletic group and not a monophyletic group.

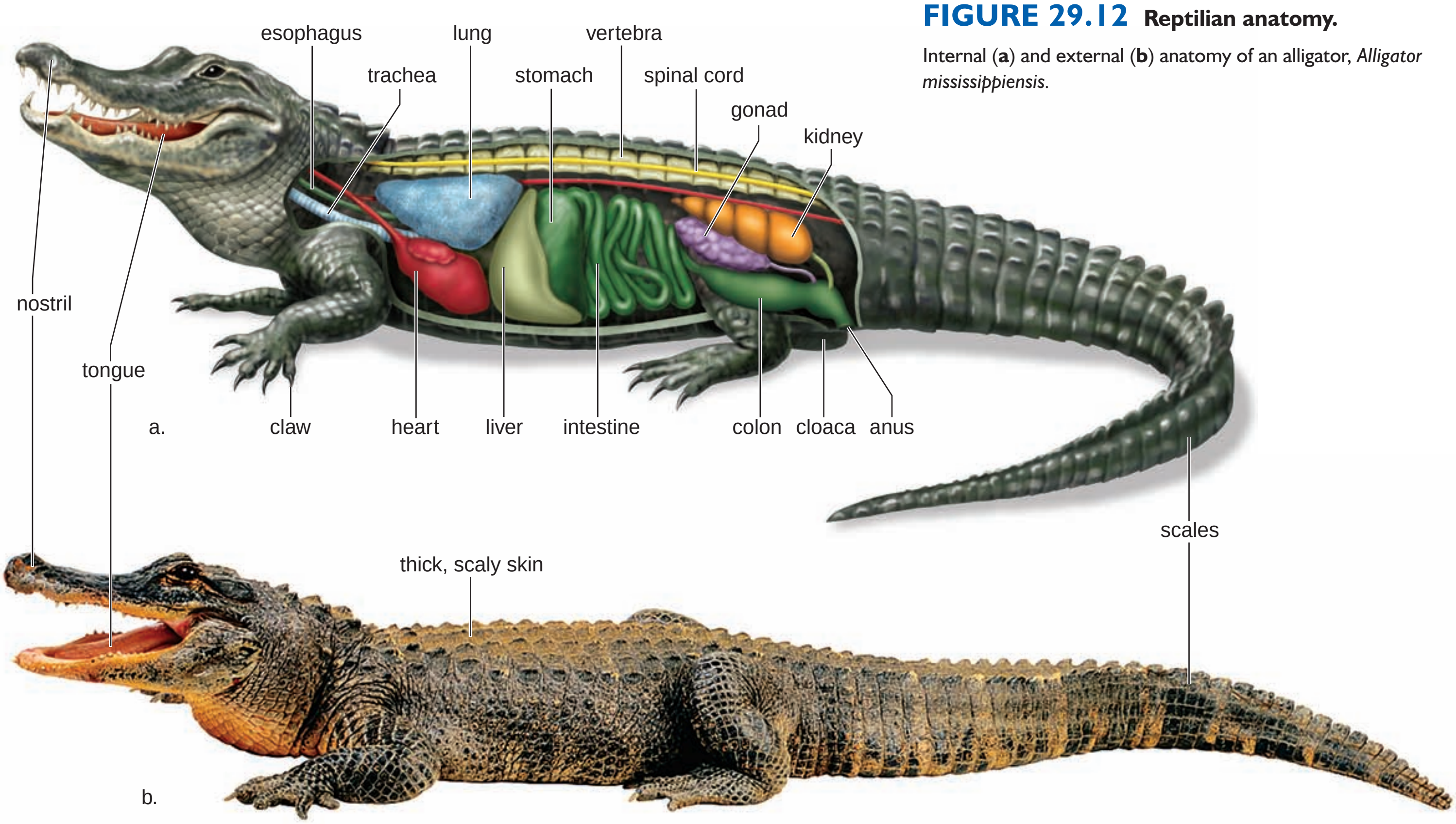


FIGURE 29.12 **Reptilian anatomy.**

Internal (**a**) and external (**b**) anatomy of an alligator, *Alligator mississippiensis*.

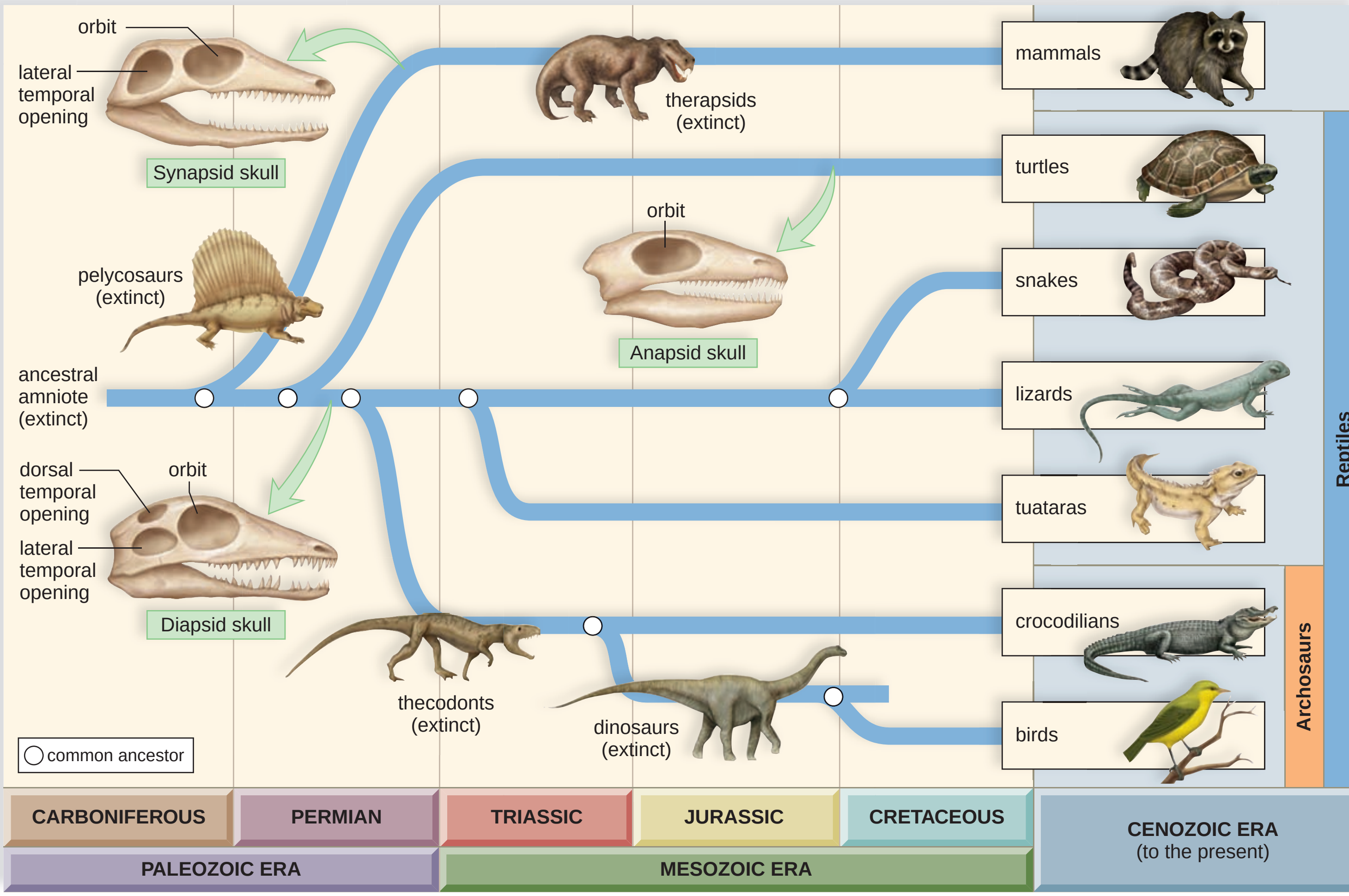


FIGURE 29.13 Phylogenetic tree of reptiles.

This phylogenetic tree shows the presumed evolutionary relationships among major groups of reptiles, starting with an amniote ancestor in the Paleozoic era. Openings in the skull are evidence that there are two major groups of reptiles. The turtles have a different ancestry from the other reptiles.

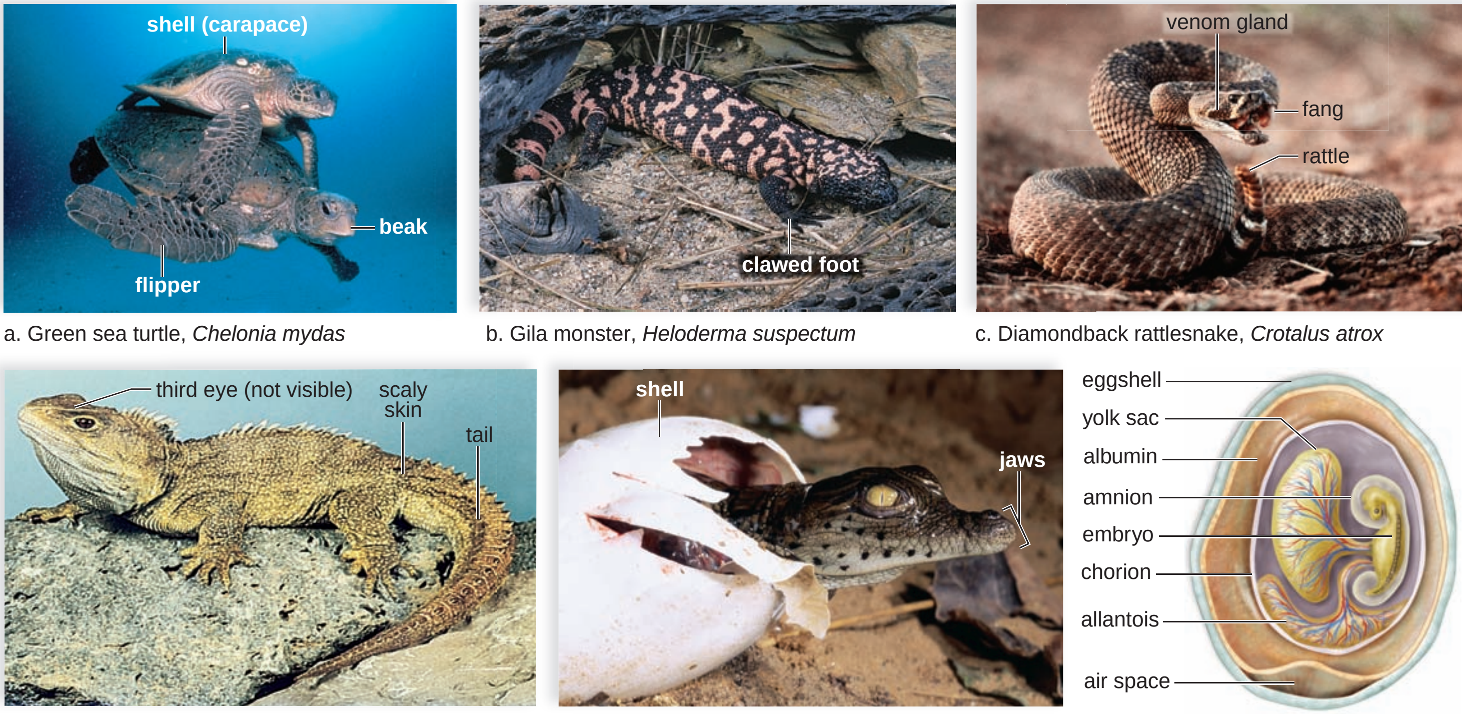
Therefore, authorities are in the process of dividing the reptiles into a number of monophyletic groups.

The other reptiles are *diapsids* because they have a skull with two openings behind the eyes. The thecodonts are diapsids that gave rise to the ichthyosaurs, which returned to the aquatic environment, and the pterosaurs of the Jurassic period, which had a keel for the attachment of large flight muscles and air spaces in their bones to reduce weight. Their wings were membranous and supported by elongated bones of the fourth finger. *Quetzalcoatlus*, the largest flying animal ever to live, had an estimated wingspan of nearly 13.5 m.

Of interest to us, the thecodonts gave rise to the crocodiles and dinosaurs. A sequence of now known transitional forms occurs between the dinosaurs and the birds. The crocodilians and birds share derived features, such as skull openings in front of the eyes and clawed feet. It is customary now to use the designation archosaurs for the crocodilians, dinosaurs, and birds. This means that these animals are more closely related to each other than they are to snakes and lizards.

The **dinosaurs** varied greatly in size and behavior. The average size of a dinosaur was about the size of a chicken. Some of the dinosaurs, however, were the largest land animals ever to live. *Brachiosaurus*, a herbivore, was about 23 m long and about 17 m tall. *Tyrannosaurus rex*, a carnivore, was 5 m tall when standing on its hind legs. A bipedal stance freed the forelimbs and allowed them to be used for purposes other than walking, such as manipulating prey. It was also preadaptive for the evolution of wings in the birds.

Dinosaurs dominated the Earth for about 170 million years before they died out at the end of the Cretaceous period. One hypothesis for this mass extinction is that a massive meteorite struck the Earth near the Yucatán Peninsula. The resultant cataclysmic events disrupted existing ecosystems, destroying many living things. This hypothesis is supported by the presence of a layer of the mineral iridium, which is rare on Earth but common in meteorites in the late Cretaceous strata.



a. Green sea turtle, *Chelonia mydas*

b. Gila monster, *Heloderma suspectum*

c. Diamondback rattlesnake, *Crotalus atrox*

d. Tuatara, *Sphenodon punctatus*

e. American crocodile, *Crocodylus acutus*

FIGURE 29.14 Reptilian diversity other than birds.

Representative living reptiles include (**a**) green sea turtles, (**b**) the venomous Gila monster, (**c**) the diamondback rattlesnake, and (**d**) the tuatara. **e.** A young crocodile hatches from an egg. The eggshell is leathery and flexible, not brittle like birds' eggs. Inside the egg, the embryo is surrounded by three membranes. The chorion aids in gas exchange, the allantois stores waste, and the amnion encloses a fluid that prevents drying out and provides protection. The yolk sac provides nutrients for the embryo.

Diversity of Living Reptiles

Living reptiles are represented by turtles, lizards, snakes, tuataras, crocodilians, and birds. Figure 29.14 shows representatives of all but the birds.

Along with tortoises, turtles can be found in marine, freshwater, and terrestrial environments. Most turtles have ribs and thoracic vertebrae that are fused into a heavy shell. They lack teeth but have a sharp beak. The legs of sea turtles are flattened and paddlelike (Fig. 29.14*a*), while terrestrial tortoises have strong limbs for walking.

Lizards have four clawed feet and resemble their prehistoric ancestors in appearance (Fig. 29.14*b*), although some species have lost their limbs and superficially resemble snakes. Typically, they are carnivorous and feed on insects and small animals, including other lizards. Marine iguanas of the Galápagos Islands are adapted to spending time each day at sea, where they feed on sea lettuce and other algae. Chameleons are adapted to live in trees and have long, sticky tongues for catching insects some distance away. They can change color to blend in with their background. Geckos are primarily nocturnal lizards with adhesive pads on their toes. Skinks are common elongated lizards with reduced limbs and shiny scales. Monitor lizards and Gila monsters, despite their names, are not a dangerous threat to humans.

Although most snakes (Fig. 29.14*c*) are harmless, several venomous species, including rattlesnakes, cobras, mambas, and copperheads, have given the whole group a reputation of being dangerous. Snakes evolved from lizards and have lost their limbs as an adaptation to burrowing. A few species such as pythons and boas still possess the vestiges of pelvic girdles. Snakes are carnivorous and have a jaw that is loosely attached to the skull; therefore, they can eat prey that is much larger than their head size. When snakes and lizards flick out their tongue, it is collecting airborne molecules and transferring them to a Jacobson's organ at the roof of the mouth and sensory cells on the floor of the mouth. A Jacobson's organ is an olfactory organ for the analysis of airborne chemicals. Snakes possess internal ears that are capable of detecting low-frequency sounds and vibrations. Their ears lack external ear openings

Two species of tuataras are found in New Zealand (Fig. 29.14*d*). They are lizardlike animals that can attain a length of 66 cm and can live for nearly 80 years. These animals possess a well-developed "third" eye, known as a pineal eye, which is light sensitive and buried beneath the skin in the upper part of the head. The tuataras are the only member of an ancient group of reptiles that included the common ancestor of modern lizards and snakes.

The majority of crocodilians (including alligators and crocodiles) live in fresh water feeding on fishes, turtles, and terrestrial animals that venture too close to the water. They have long, powerful jaws (Fig. 29.14*e*) with numerous teeth and a muscular tail that serves as both a weapon and a paddle. Male crocodiles and alligators bellow to attract mates. In some species, the male protects the eggs and cares for the young.

science focus

Vertebrates and Human Medicine

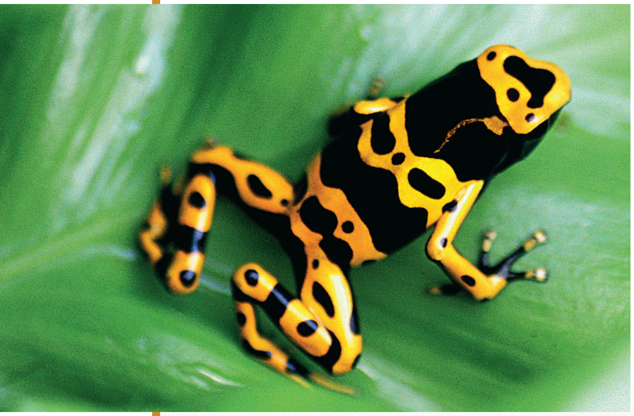
Hundreds of pharmaceutical products come from other vertebrates, and even those that produce poisons and toxins give us medicines that benefit us. The Thailand cobra paralyzes its victim's nerves and muscles with a potent venom that eventually leads to respiratory arrest. However, that venom is also the source of the drug Immunokine, which has been used for ten years in multiple sclerosis patients. Immunokine, which is almost without side effects, actually protects the patient's nerve cells from destruction by their immune system. A compound known as ABT-594, derived from the skin of the poison-dart frog, is approximately 50 times more powerful than morphine in relieving chronic and acute pain without the addictive properties. The southern copperhead snake and the fer-de-lance pit viper are two of the unlikely vertebrates that either serve as the source of pharmaceuticals or provide a chemical model for the synthesis of effective drugs in the laboratory. These drugs include anticoagulants ("clot busters"), painkillers, antibiotics, and anticancer drugs.

A variety of friendlier vertebrates produce proteins that are similar enough to human proteins to be used for medical treatment. Until 1978, when recombinant DNA human insulin was produced, diabetics injected insulin purified from pigs. Currently, the flu vaccine is produced in fertilized chicken eggs. The production of these drugs, however, is often time-consuming, labor intensive, and expensive. In 2003, pharmaceutical companies used 90 million chicken eggs and took nine months to produce the flu vaccine.

Some of the most powerful applications of genetic engineering can be found in the development of drugs and therapies for human diseases. In fact, this new biotechnology has actually led to a new industry: animal pharming. Animal pharming uses genetically altered vertebrates, such as mice, sheep, goats, cows, pigs, and chickens, to produce medically useful pharmaceutical products. The human gene for some useful product is inserted into the embryo of the vertebrate. That embryo is implanted into a foster mother, which gives birth to the transgenic animal, so called because it contains genes from two sources. An adult transgenic vertebrate produces large quantities of the pharmed product in its blood, eggs, or milk, from which the product can be easily harvested and purified. A pharmed product advanced in development and the FDA approval process is ATIII, a bioengineered form of human antithrombin. This medication is important in the treatment of individuals who have a hereditary deficiency of this protein and so are at high risk for life-threatening blood clots, especially during such events as surgery or childbirth procedures.

Xenotransplantation, the transplantation of nonhuman vertebrate tissues and organs into humans, is another benefit of genetically altered animals. There is an alarming shortage of human donor organs to fill the need for hearts, kidneys, and livers. The first animal–human transplant occurred in 1984 when a team of surgeons implanted a baboon heart into an infant, who unfortunately lived only a short while before dying of circulatory complications. In the late 1990s, two patients were kept alive using a pig liver outside of their body to filter their blood until a human organ was available for transplantation. Although baboons are phylogenetically closer to humans than pigs, pigs are generally healthier, produce more offspring in a shorter time, and are already farmed for food. Despite the fears of some, scientists think that viruses unique to pigs are unlikely to cross the species barrier and infect the human recipient. Currently, pig heart valves and skin are routinely used for treatment of humans. Miniature pigs, whose heart size is similar to humans, are being genetically engineered to make their tissues less foreign to the human immune system, in order to avoid rejection.

The use of transgenic vertebrates for medical purposes does raise health and ethical concerns. What viral AIDS-like epidemic might be unleashed by cross-species transplantation? What other unseen health consequences might there be? Is it ethical to change the genetic makeup of vertebrates, in order to use them as drug or organ factories? Are we redefining the relationship between humans and other vertebrates to the detriment of both? These questions will continue to be debated as the research goes forward. Meanwhile, several U.S. regulatory bodies, including the FDA, have adopted voluntary guidelines for this new technology.



a. Poison-dart frogs, source of a medicine

b. Pigs, source of organs

c. Heart for transplantation

FIGURE 29A Use of other vertebrates for medical purposes.
a. *The poison-dart frog is the source of a pain medication.* ***b.*** *Pigs are now being genetically altered to provide a supply of (****c****) hearts for heart transplant operations.*

Birds

Birds share a common ancestor with crocodilians and have traits, such as the presence of scales (feathers are modified scales), a tail with vertebrae, and clawed feet, that show they are indeed reptiles.

To many people, **birds** are the most conspicuous, melodic, beautiful, and fascinating group of vertebrates. Birds range in size from the tiny "bee" hummingbird at 1.8 g (less than a penny) and 5 cm long to the ostrich at a maximum weight of 160 kg and a height of 2.7 m.

Nearly every anatomical feature of a bird can be related to its ability to fly (Fig. 29.15). These features are involved in the action of flight, providing energy for flight or the reduction of the bird's body weight, making flight less energetically costly:

Feathers. Soft down keeps birds warm, wing feathers allow flight, and tail feathers are used for steering. A feather is a modified reptilian scale with the complex structure shown in Figure 29.15*a*. Nearly all birds molt (lose their feathers) and replace their feathers about once a year.

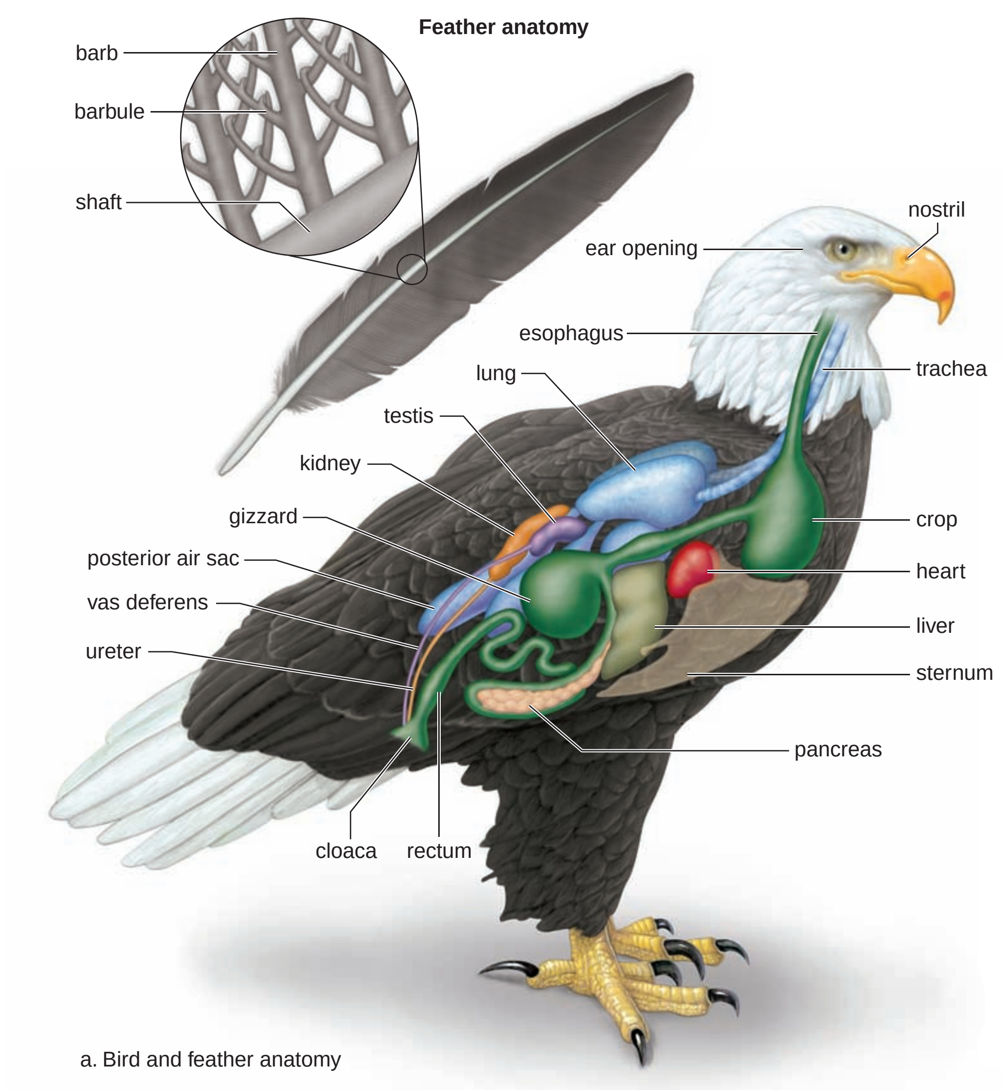
Modified skeleton. Unique to birds, the collarbone is fused (the wishbone), and the sternum has a keel (Fig. 29.15*b*). Many other bones are fused, making the skeleton more rigid than the reptilian skeleton. The breast muscles are attached to the keel, and their action accounts for a bird's ability to fly.

A horny beak has replaced jaws equipped with teeth, and a slender neck connects the head to a rounded, compact torso.

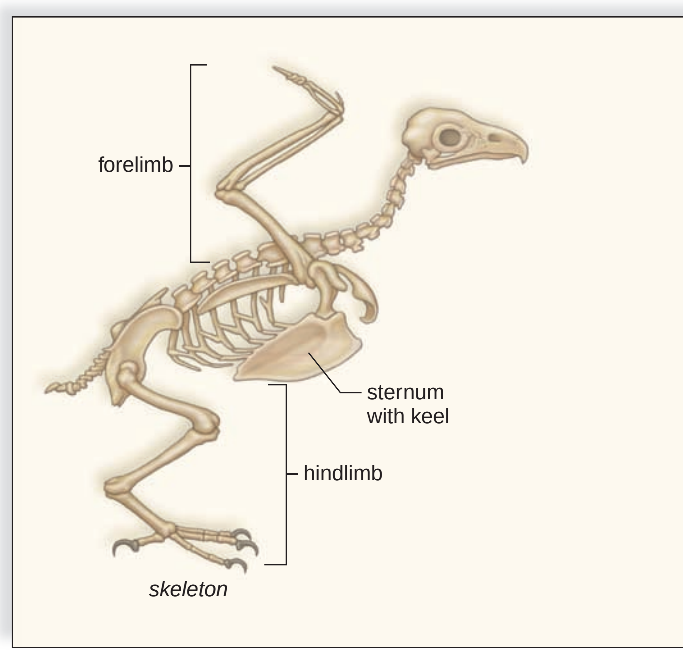
Modified respiration. In birds, unlike other reptiles, the lobular lungs connect to anterior and posterior air sacs. The presence of these sacs means the air circulates one way through the lungs, and gases are continuously exchanged across respiratory tissues. Another benefit of air sacs is that they lighten the body and bones for flying. Some of the air sacs are present in cavities within the bones.

Endothermy. Birds, unlike other reptiles, generate internal heat. Many **endotherms** can use metabolic heat to maintain a constant internal temperature. Endothermy may be associated with their efficient nervous, respiratory, and circulatory systems.

Well-developed sense organs and nervous system. Birds have particularly acute vision and well-developed brains. Their muscle reflexes are excellent. An enlarged portion of the brain seems to be the area



a. Bird and feather anatomy



b. Bald eagle, *Haliaetus*

FIGURE 29.15 Bird anatomy and flight.

a. Bird anatomy. *Top:* In feathers, a hollow central shaft gives off barbs and barbules, which interlock in a latticelike array. *Bottom:* The anatomy of an eagle is representative of bird anatomy. **b.** Bird flight. *Left:* The skeleton of an eagle shows that birds have a large, keeled sternum to which flight muscles attach. The bones of the forelimb help support the wings. *Right:* Birds fly by flapping their wings. Bird flight requires an airstream and a powerful wing downstroke for lift, a force at right angles to the airstream.

a. Bald eagle, *Haliaetus leucocephalus*

b. Pileated woodpecker, *Dryocopus pileatus*

c. Flamingo, *Phoenicopterus ruber*

d. Blue-and-yellow macaw, *Ara ararauna*

e. Cardinal, *Cardinalis cardinalis*

FIGURE 29.16

Bird beaks.

a. A bald eagle's beak allows it to tear apart prey. **b.** A woodpecker's beak is used to chisel in wood. **c.** A flamingo's beak strains food from the water with bristles that fringe the mandibles. **d.** A parrot's beak is modified to pry open nuts. **e.** A cardinal's beak allows it to crack tough seeds.

responsible for instinctive behavior. A ritualized courtship often precedes mating. Many newly hatched birds require parental care before they are able to fly away and seek food for themselves. A remarkable aspect of bird behavior is the seasonal migration of many species over long distances. Birds navigate by day and night, whether it is sunny or cloudy, by using the sun and stars and even the Earth's magnetic field to guide them. Birds are very vocal animals. Their vocalizations are distinctive and so convey an abundance of information.

Diversity of Living Birds

The majority of birds, including eagles, geese, and mockingbirds, have the ability to fly. However, some birds, such as emus, penguins, kiwis, and ostriches, are flightless. Traditionally, birds have been classified according to beak and foot type (Fig. 29.16) and, to some extent, on their habitat and behavior. The birds of prey have notched beaks and sharp talons; shorebirds have long, slender, probing beaks and long, stiltlike legs; woodpeckers have sharp, chisel-like beaks and grasping feet; waterfowl have broad beaks and webbed toes; penguins have wings modified as paddles; songbirds have perching feet; and parrots have short, strong "plierlike" beaks and grasping feet.

Check Your Progress 29.5

1. How are reptiles adapted to a land environment?
2. Contrast the characteristics of alligators to those of snakes.
3. The common ancestor for birds was a dinosaur. Does this make birds a reptile? Explain.

29.6 The Mammals

The **mammals** include the largest animal ever to live, the blue whale (130 metric tons); the smallest mammal, the Kitti's bat (1.5 g); and the fastest land animal, the cheetah (110 km/hr). These characteristics distinguish mammals:

Hair. The most distinguishing characteristics of mammals are the presence of hair and milk-producing mammary glands. Hair provides insulation against heat loss, and being endothermic allows mammals to be active even in cold weather. The color of hair can camouflage a mammal and help the animal blend into its surroundings. In addition, hair can be ornamental and can serve sensory functions.

Mammary glands. These glands enable females to feed (nurse) their young without leaving them to find food. Nursing also creates a bond between mother and offspring that helps ensure parental care while the young are helpless and provides antibodies to the young from the mother through the milk.

Skeleton. The mammalian skull accommodates a larger brain relative to body size than does the reptilian skull. Also, mammalian cheek teeth are differentiated as premolars and molars. The vertebrae of mammals are highly differentiated, typically the middle region of the vertebral column is arched, and the limbs are under the body.

Internal organs. Efficient respiratory and circulatory systems ensure a ready oxygen supply to muscles whose contraction produces body heat. Like birds, mammals have a double-loop circulatory pathway and a four-chambered heart. The kidneys are adapted to conserving water in terrestrial mammals. The nervous system of mammals is highly developed. Special senses in mammals are well developed, and mammals exhibit complex behavior.

Internal development. In most mammals, the young are born alive after a period of development in the uterus, a part of the female reproductive tract. Internal development shelters the young and allows the female to move actively about while the young are maturing.

Evolution of Mammals

Mammals share an amniote ancestor with reptiles (see Fig. 29.13). Their more immediate ancestors in the Mesozoic era had a synapsid skull (two openings behind the eyes). The first true mammals appeared during the Triassic period, about the same time as the first dinosaurs, and were similar in size to mice. During the reign of the dinosaurs (170 million years), mammals were a minor group that changed little. The two earliest mammalian groups, represented today by the monotremes and marsupials, are not abundant today. The marsupials probably originated in the Americas and then spread through South America and Antarctica to Australia before these continents separated. Placental mammals, the third branch of the mammalian lineage, originated in Eurasia and spread to the Americas also by land connections that existed between the continents during the Mesozoic. The placental mammals underwent an adaptive radiation into the habitats previously occupied by the dinosaurs.

Monotremes

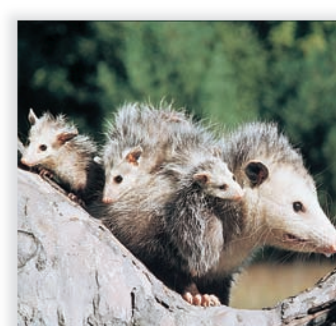
Monotremes [Gk. *monos*, one, and *trema*, hole] are egg-laying mammals that include only the duckbill platypus (Fig. 29.17*a*) and two species of spiny anteaters. The term monotreme refers to the presence of a single opening, the cloaca. Monotremes unlike other mammals lay hard-shelled amniotic eggs. No embryonic development occurs inside the female's body. The female duckbill platypus lays her eggs in a burrow in the ground. She incubates the eggs, and after hatching, the young lick up milk that seeps from modified sweat glands on the mother's abdomen. Spiny anteaters, which actually feed mainly on termites and not ants, have pores that seep milk in a shallow belly pouch formed by skin folds on each side. The egg moves from the cloaca to this pouch, where hatching takes place and the young remain for about 53 days. Then they stay in a burrow, where the mother periodically visits and nurses them.

Marsupials

The **marsupials** [Gk. *marsupium*, pouch] are also known as the pouched mammals. Marsupials include kangaroos, koalas, Tasmanian devils, wombats, sugar gliders, and opossums. The young of marsupials begin their development inside the female's body, but they are born in a very immature condition. Newborns are typically hairless, have yet to

a. Duckbill platypus, *Ornithorhynchus anatinus*

b. Koala, *Phascolarctos cinereus*



c. Virginia opossum, *Didelphis virginianus*

FIGURE 29.17 Monotremes and marsupials.

a. The duckbill platypus is a monotreme that inhabits Australian streams. **b.** The koala is an Australian marsupial that lives in trees. **c.** The opossum is the only marsupial in North America. The Virginia opossum is found in a variety of habitats.

a. White-tailed deer, *Odocoileus virginianus*

b. African lioness, *Panthera leo*

c. Squirrel monkey, *Saimiri sciureus*

d. Killer whale, *Orcinus orca*

FIGURE 29.18

Placental mammals.

Placental mammals have adapted to various ways of life. **a.** Deer are herbivores that live in forests. **b.** Lions are carnivores on the African plain. **c.** Monkeys inhabit tropical forests. **d.** Whales are sea-dwelling placental mammals.

open their eyes, yet crawl up into a pouch on their mother's abdomen. Inside the pouch, they attach to nipples of mammary glands and continue to develop. Frequently, more are born than can be accommodated by the number of nipples, and it's "first come, first served."

Today, marsupial mammals are most abundant in Australia and New Guinea, filling all the typical roles of placental mammals on other continents. For example, among herbivorous marsupials in Australia today, koalas are tree-climbing browers (Fig. 29.17*b*), and kangaroos are grazers. A significant number of marsupial species are also found in South and Central America. The opossum is the only North American marsupial (Fig. 29.17*c*).

Placental Mammals

The **placental mammals** are the dominant group of mammals on Earth. Developing placental mammals are dependent on the **placenta,** an organ of exchange between maternal blood and fetal blood. Nutrients are supplied to the growing offspring, and wastes are passed to the mother for excretion. While the fetus is clearly parasitic on the female, in exchange, she is able to freely move about while the fetus develops.

Placental mammals lead an active life. The senses are acute, and the brain is enlarged due to the convolution and expansion of the foremost part—the cerebral hemispheres. The brain is not fully developed for some time after birth, and there is a long period of dependency on the parents, during which the young learn to take care of themselves.

Most mammals live on land, but some (e.g., whales, dolphins, seals, sea lions, and manatees) are secondarily adapted to live in water, and bats are able to fly. While bats are the only mammal that can fly, three types of placentals can glide: the flying squirrels, scaly-tailed squirrels, and the flying lemurs. These are the main types of placental mammals:

The *ungulates* are hoofed mammals, which comprise about a third of all living and extinct mammalian groups. The hoofed mammals have a reduced number of toes and are divided according to whether an odd number remain (e.g., horses, zebras, tapirs, rhinoceroses) or whether a even number of toes remain (e.g., pigs, cattle, deer, hippopotamuses, buffaloes, giraffes) (Fig. 29.18*a*). Many of the hoofed animals have elongated limbs and are adapted for running, often across open grasslands. Both groups of animals are herbivorous and have large, grinding teeth.

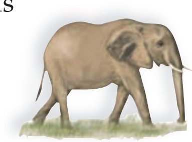
The *carnivores* (e.g., dogs, cats, bears, raccoons, and skunks) are predaceous meat eaters with large and conical-shaped canine teeth (Fig. 29.18*b*). Some carnivores are aquatic (e.g., seals, sea lions, and walruses) and must return to land to reproduce.

The *primates* are tree-dwelling fruit eaters (e.g., lemurs, monkeys, gibbons, chimpanzees, gorillas, and humans) (Fig. 29.18*c*). Humans are ground dwellers, well known for their opposable thumb and well-developed brain.

The *cetaceans* are well-known marine whales and dolphins (Fig. 29.18*d*), which have very little hair or fur. Baleen whales feed by straining large quantities of water containing plankton. Toothed whales feed mainly on fish and squid.

The *chiroptera* are the flying mammals (e.g., bats), whose wings consist of two layers of skin and connective tissue stretched between the elongated bones of all fingers but the first. Many species use echolocation to navigate at night and to locate their usual insect prey. But there are also bird-, fish-, frog-, plant-, and blood-eating bats.

The *rodents* are most often small plant eaters (e.g., mice, rats, squirrels, beavers, and porcupines). The incisors of these gnawing animals suffer heavy wear and tear, and they grow continuously.



The *proboscideans*, the herbivorous elephants, are the largest living land mammals, whose upper lip and nose have become elongated and muscularized to form a trunk.

The *lagomorphans* are the rodentlike jumpers (e.g., rabbits, hares, and pikas). These herbivores have two pairs of continually growing incisors, and their hind legs are longer than their front legs.

The *insectivores* are the small burrowing mammals (e.g., shrews and moles), which have short snouts and live primarily underground.

At one time, it was thought that insectivores were most like the original placentals. More recent analysis suggests that the *edentates* (anteaters) and pangolins (scaly anteaters) are the more primitive groups of living placentals.

Check Your Progress 29.6

1. What are the major characteristics of mammals? What are the evolutionary advantages of these characteristics?
2. Describe the three groups of mammals and several groups of the placental mammals.

Connecting the Concepts

How do you measure success? As human beings, we may assume that vertebrate chordates, such as ourselves, are the most successful organisms. But depending on the criteria used, organisms that are in some ways less complex may come out on top!

For example, vertebrates are eukaryotes, which have been assigned to one domain, while the prokaryotes are now divided into two domains. In fact, the total number of prokaryotes is greater than the number of eukaryotes, and there are possibly more types of prokaryotes than any other living form. Therefore, the unseen world is much larger than the seen world. Furthermore, prokaryotes are adapted to use most energy sources and to live in almost any type of environment.

As terrestrial mammals, humans might assume that terrestrial species are more successful than aquatic ones. However, if not for the myriad types of terrestrial insects, there would be more aquatic species than terrestrial ones on Earth. The adaptative radiation of mammals has taken place on land, and this might seem impressive to some. But actually, the number of mammalian species (4,800) is small compared to, say, the molluscs (110,000 species), which radiated in the sea.

The size and complexity of the brain is also sometimes cited as a criterion by which vertebrates are more successful than other living things. However, this very characteristic has been linked to others that make an animal prone to extinction. Studies have indicated that large animals have a long life span, are slow to mature, have few offspring, expend much energy caring for their offspring, and tend to become extinct if their normal way of life is destroyed. And finally, vertebrates, in general, are more threatened than other types of organisms by our present biodiversity crisis—a crisis brought on by the activities of the vertebrate with the most complex brain of all, *Homo sapiens*.

Chapter 30 traces the increase in complexity of the human brain by exploring the evolution of the primates, a group that includes humans.

summary

29.1 The Chordates

Chordates (sea squirts, lancelets, and vertebrates) have a notochord, a dorsal tubular nerve cord, pharyngeal pouches, and a postanal tail at some time in their life history.

Lancelets and sea squirts are the nonvertebrate chordates. Lancelets are the only chordate to have the four characteristics in the adult stage. Sea squirts lack chordate characteristics (except gill slits) as adults, but they have a larva that could be ancestral to the vertebrates.

29.2 The Vertebrates

Vertebrates have the four chordate characteristics as embryos. As adults, the notochord is replaced by the vertebral column. Vertebrates undergo cephalization, and have an endoskeleton, paired appendages, and well-developed internal organs.

Vertebrate evolution is marked by the evolution of vertebrae, jaws, a bony skeleton, lungs, limbs, and the amniotic egg.

29.3 The Fishes

The first vertebrates lacked jaws and paired appendages. They are represented today by the hagfishes and lampreys. Ancestral bony fishes, which had jaws and paired appendages, gave rise during the Devonian period to two groups: today's cartilaginous fishes (skates, rays, and sharks) and the bony fishes, including the ray-finned fishes and the lobe-finned fishes. The ray-finned fishes (actinopterygii) became the most diverse group among the vertebrates. Ancient lobe-finned fishes (sarcopterygii) gave rise to the coelacanths and amphibians.

29.4 The Amphibians

Amphibians are tetrapods represented primarily today by frogs and salamanders. Most frogs and some salamanders return to the water to reproduce and then metamorphose into terrestrial adults.

29.5 The Reptiles

Reptiles (today's alligators and crocodiles, birds, turtles, tuataras, lizards, and snakes) lay a shelled amniotic egg, which allows them to reproduce on land. Turtles with an anapsid skull have a separate ancestry from the other reptiles mentioned. The other reptiles with a diapsid skull include the crocodilians, dinosaurs, and the birds. Birds have reptilian features, including scales (feathers are modified scales), tail with vertebrae, and clawed feet.

The feathers of birds help them maintain a constant body temperature. Birds are adapted for flight: Their bones are hollow, their shape is compact, their breastbone is keeled, and they have well-developed sense organs.

29.6 The Mammals

Mammals share an amniote ancestor with reptiles but they have a synapsid skull (two openings behind the eyes). Mammals remained small and insignificant while the dinosaurs existed, but when dinosaurs became extinct at the end of the Cretaceous period, mammals became the dominant land organisms.

Mammals are vertebrates with hair and mammary glands. Hair helps them maintain a constant body temperature, and the mammary glands allow them to feed and establish an immune system in their young. Monotremes lay eggs, while marsupials have a pouch in which the newborn crawls and continues to develop. The placental mammals, which are the most varied and numerous, retain offspring inside the female until birth.

understanding the terms

agnathan 543
amniote 542
amniotic egg 548
amphibian 546
bird 552
bony fish (Osteichthyes) 544
cartilaginous fish (Chondrichthyes) 543
cephalochordate 540
chordate 540
cloaca 547
dinosaur 549
ectotherm 543
endotherm 552
fin 544
fishes 543
gills 540
gnathostome 542
jawless fishes 543
lobe-finned fishes (Sarcopterygii) 544
lungfishes 544
mammal 554
marsupial 554
metamorphosis 546
monotreme 554
notochord 540
operculum 544
ostracoderm 543
placenta 555
placental mammal 555
placoderm 543
ray-finned bony fishes 544
reptile 548
sarcopterygii 544
swim bladder 544
tetrapod 542
urochordate 541

Match the terms to these definitions:

a. ______________ Animal (bird or mammal) that maintains a uniform body temperature independent of the environmental temperature.

b. ______________ Egg-laying mammal—for example, duckbill platypus and spiny anteater.

c. ______________ Terrestrial vertebrates with internal fertilization, scaly skin, and a shelled egg; includes turtles, lizards, snakes, crocodilians, and birds.

d. ______________ Dorsal supporting rod that exists in all chordates sometime in their life history; replaced by the vertebral column in vertebrates.

reviewing this chapter

1. What four characteristics do all chordates have at some time in their development? 540
2. Describe the two groups of nonvertebrate chordates, and explain how the sea squirts might be ancestral to vertebrates. 540–41
3. Discuss the distinguishing characteristics and the evolution of vertebrates. 542
4. Describe the jawless fishes, including ancient ostracoderms. 543
5. Describe the characteristics of fishes with jaws. What is the significance of having jaws? Describe today's cartilaginous and bony fishes. The amphibians evolved from what type of ancestral fish? 543–45
6. Discuss the characteristics of amphibians, stating which ones are especially adaptive to a land existence. Explain how their name (amphibians) characterizes these animals. 546–47
7. What is the significance of the amniotic egg? What other characteristics make reptiles less dependent on a source of external water? 548
8. Draw a simplified phylogenetic tree that includes the anapsid, diapsid, and synapsid skulls. 548–50
9. What is the significance of wings? In what other ways are birds adapted to flying? 552–53
10. What are the three major groups of mammals, and what are their primary characteristics? 554–56

testing yourself

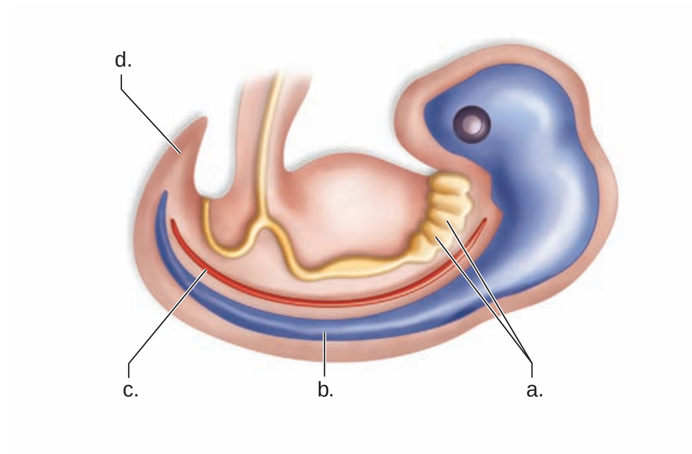
Choose the best answer for each question.

1. Which of these is not a chordate characteristic?
   a. dorsal supporting rod, the notochord
   b. dorsal tubular nerve cord
   c. pharyngeal pouches
   d. postanal tail
   e. vertebral column
2. Adult sea squirts
   a. do not have all five chordate characteristics.
   b. are also called tunicates.
   c. are fishlike in appearance.
   d. are the first chordates to be terrestrial.
   e. All of these are correct.
3. Cartilaginous fishes and bony fishes are different in that only
   a. bony fishes have paired fins.
   b. bony fishes have a keen sense of smell.
   c. bony fishes have an operculum.
   d. cartilaginous fishes have a complete skeleton.
   e. cartilaginous fishes are predaceous.
4. Amphibians evolved from what type of ancestral fish?
   a. sea squirts and lancelets
   b. cartilaginous fishes
   c. jawless fishes
   d. ray-finned fishes
   e. lobe-finned fishes

5. Which of these is not a feature of amphibians?
   a. dry skin that resists desiccation
   b. metamorphosis from a swimming form to a land form
   c. small lungs and a supplemental means of gas exchange
   d. reproduction in the water
   e. a single ventricle
6. Reptiles
   a. were dominant during the Mesozoic era.
   b. include the birds.
   c. lay shelled eggs.
   d. are ectotherms, except for birds.
   e. All of these are correct.
7. Which of these is a true statement?
   a. In all mammals, offspring develop completely within the female.
   b. All mammals have hair and mammary glands.
   c. All mammals have one birth at a time.
   d. All mammals are land-dwelling forms.
   e. All of these are true.
8. Which of these is not an invertebrate? Choose more than one answer if correct.
   a. tunicate
   b. frog
   c. lancelet
   d. squid
   e. roundworm
9. Which of these is not a characteristic of vertebrates? Choose more than one answer if correct.
   a. All vertebrates have a complete digestive system.
   b. Vertebrates have a closed circulatory system.
   c. Sexes are usually separate in vertebrates.
   d. Vertebrates have a jointed endoskeleton.
   e. Most vertebrates never have a notochord.
10. Bony fishes are divided into which two groups?
   a. hagfishes and lampreys
   b. sharks and ray-finned fishes
   c. ray-finned fishes and lobe-finned fishes
   d. jawless fishes and cartilaginous fishes
11. Which of these is an incorrect difference between reptiles and birds?

	Reptiles	**Birds**
a.	shelled egg	partial internal development
b.	scales	feathers
c.	tetrapods	wings
d.	ectothermy	endothermy
e.	no air sacs	air sacs

12. Which of these does not produce an amniotic egg? Choose more than one answer if correct.
   a. bony fishes
   b. duckbill platypus
   c. snake
   d. robin
   e. frog
13. Label the following diagram of a chordate embryo.



14. The amniotes include all but the
   a. birds.
   b. mammals.
   c. reptiles.
   d. amphibians.
15. Which of the following groups has a three-chambered heart?
   a. all birds
   b. all reptiles
   c. all mammals
   d. all amphibians
16. Ancestors to the mammals known only in the fossil record are
   a. synapsids.
   b. marsupials.
   c. monotremes.
   d. placentals.

thinking scientifically

1. *Archaeopteryx* was a birdlike reptile that had a toothed beak. Give an evolutionary explanation for the elimination of teeth in a bird's beak.
2. While amphibians have rudimentary lungs, skin is also a respiratory organ. Why would a thin skin be more sensitive to pollution than lungs?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

30

Human Evolution

Sometimes you hear people say that evolutionists believe humans evolved from apes. This is a mistake; instead, evolutionists tell us that modern humans and certain of the apes followed their own evolutionary pathways after evolving from a common ancestor. Among the apes, gorillas and chimpanzees are our cousins, and we couldn't have evolved from our cousins because we are all contemporaries—living on Earth at the same time. The pattern of descent is just like that between you and your cousin in that cousins are descended from the same grandparents.

Scientists have discovered that the same patterns of evolution characterize human evolution as any other group of organisms. Various prehuman groups died out, migrated, or interbred with other groups all within a very short period of time, making the evolutionary descent of humans very complex. Additional fossils are always being found; the photo below shows how scientists have reconstructed the appearance of Sahelanthropus tchadensis *from his fossil remains. This fossil has been dated somewhat later than the time when humans and apes parted, but the skull opening for the spine indicates that* Sahelanthropus tchadensis *walked erect, just as we do. This chapter traces the ancestry of primates, including humans, from their origins.*

Reconstruction of *Sahelanthropus tchadensis*, a possible human ancestor that lived 7 million years ago (MYA).

concepts

30.1 Evolution of Primates

Primates [L. *primus*, first] include prosimians, monkeys, apes, and humans (Fig. 30.1). In contrast to other types of mammals, primates are adapted for an **arboreal** life—that is, for living in trees. The evolution of primates is characterized by trends toward mobile limbs; grasping hands; a flattened face; stereoscopic vision; a large, complex brain; and a reduced reproductive rate. These traits are particularly useful for living in trees.

Mobile Forelimbs and Hindlimbs

Primates have evolved grasping hands and feet, which have five digits each. In most primates, flat nails have replaced the claws of ancestral primates, and sensitive pads on the undersides of fingers and toes assist the grasping of objects. All primates have a thumb, but it is only truly opposable in Old World monkeys, great apes, and humans. Because an **opposable thumb** can touch each of the other fingers, the grip is both powerful and precise (Fig. 30.2). In all but humans, primates with an opposable thumb also have an opposable toe.

The evolution of the primate limb was a very important adaptation for their life in trees. Mobile limbs with clawless opposable digits allow primates to freely grasp and release tree limbs. They also allow primates to easily reach out and bring food, such as fruit, to the mouth.

Stereoscopic Vision

A foreshortened snout and a relatively flat face are also evolutionary trends in primates. These may be associated with a general decline in the importance of smell and an increased reliance on vision. In most primates, the eyes are located in the front, where they can focus on the same object from slightly different angles (Fig. 30.3). The **stereoscopic** (three-dimensional) **vision** and good depth perception that result permit primates to make accurate judgments about the distance and position of adjoining tree limbs.

Some primates, humans in particular, have color vision and greater visual acuity because the retina contains cone cells in addition to rod cells. Rod cells are activated in dim light, but the blurry image is in shades of gray. Cone cells require bright light, but the image is sharp and in color. The lens of the eye focuses light directly on the fovea, a region of the retina where cone cells are concentrated.

PROSIMIANS

Ring-tailed lemur, *Lemus catta*

Tarsier, *Tarsius bancanus*

a.

NEW WORLD MONKEY

White-faced monkey, *Cebus capucinus*

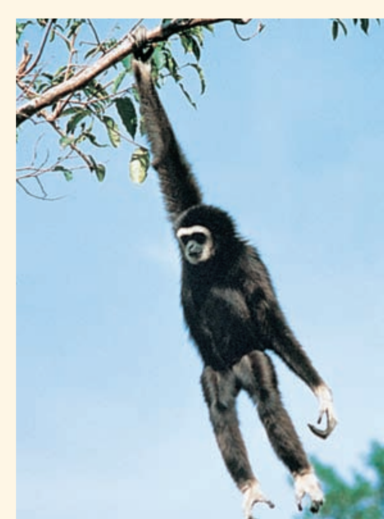
OLD WORLD MONKEY

Anubis baboon, *Papio anubis*

b.

ASIAN APES

Orangutan, *Pongo pygmaeus*



White-handed gibbon, *Hylobates lar*

c.

Large, Complex Brain

Sense organs are only as beneficial as the brain that processes their input. The evolutionary trend among primates is toward a larger and more complex brain. This is evident when comparing the brains of prosimians, such as lemurs and tarsiers, with that of apes and humans. In apes and humans, the portion of the brain devoted to smell is smaller, and the portions devoted to sight have increased in size and complexity. Also, more of the brain is devoted to controlling and processing information received from the hands and the thumb. The result is good hand-eye coordination. A larger portion of the brain is devoted to communication skills, which supports primates' tendency to live in social groups.

Reduced Reproductive Rate

One other trend in primate evolution is a general reduction in the rate of reproduction, associated with increased age of sexual maturity and extended life spans. Gestation is lengthy, allowing time for forebrain development. One birth at a time is the norm in primates; it is difficult to care for several offspring while moving from limb to limb. The juvenile period of dependency is extended, and there is an emphasis on learned behavior and complex social interactions.

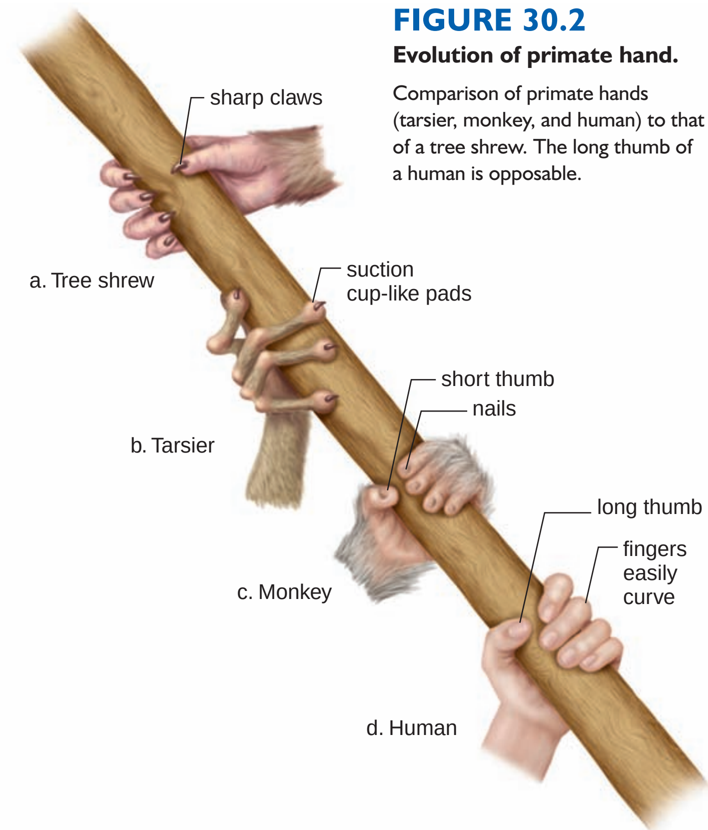


FIGURE 30.2
Evolution of primate hand.
Comparison of primate hands (tarsier, monkey, and human) to that of a tree shrew. The long thumb of a human is opposable.

AFRICAN APES

Chimpanzee, *Pan troglodytes*

Western lowland gorilla, *Gorilla gorilla*

Humans, *Homo sapiens*

d.

FIGURE 30.1
Primate diversity.
a. Today's prosimians may resemble the first group of primates to evolve. **b.** Today's monkeys are divided into the New World monkeys and the Old World monkeys. **c.** Today's apes can be divided into the Asian apes (orangutans and gibbons) and the African apes (chimpanzees and gorillas). **d.** Humans are also primates.

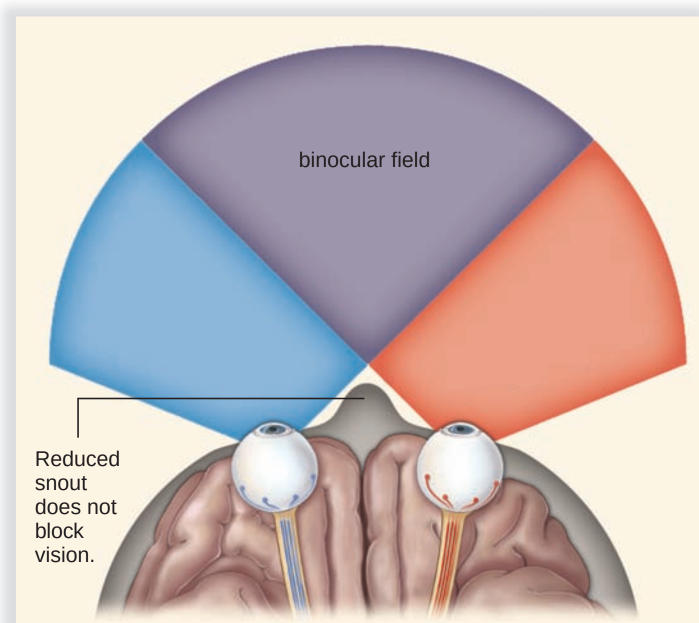


FIGURE 30.3 Stereoscopic vision.
In primates, the snout is reduced, and the eyes are at the front of the head. The result is a binocular field that aids depth perception and provides stereoscopic vision.

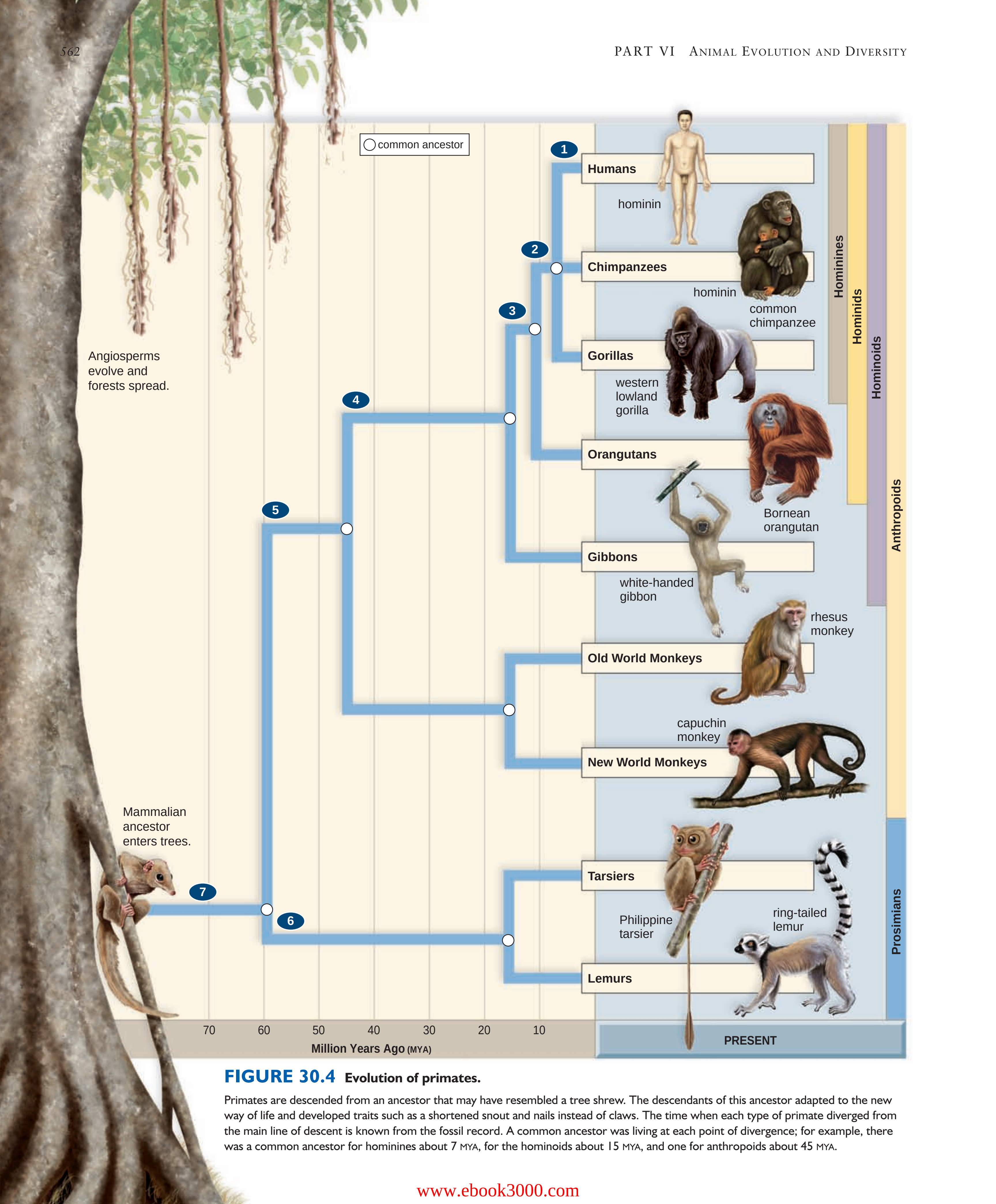


FIGURE 30.4 **Evolution of primates.**

Primates are descended from an ancestor that may have resembled a tree shrew. The descendants of this ancestor adapted to the new way of life and developed traits such as a shortened snout and nails instead of claws. The time when each type of primate diverged from the main line of descent is known from the fossil record. A common ancestor was living at each point of divergence; for example, there was a common ancestor for hominines about 7 MYA, for the hominoids about 15 MYA, and one for anthropoids about 45 MYA.

Sequence of Primate Evolution

Figure 30.4 traces the evolution of primates during the Cenozoic era. 1 **Hominins** (the designation that includes chimpanzees, humans, and species very closely related to humans) first evolved about 5 MYA. 2 Molecular data shows that hominins and gorillas are closely related and these two groups must have shared a common ancestor sometime during the Miocene. Hominins and gorillas are now grouped together as **hominines.** 3 The **hominids** [L. *homo,* man; Gk. *eides,* like] include the hominines and the orangutan. 4 The **hominoids** include the gibbon and the hominids. The hominoid common ancestor first evolved at the beginning of the Miocene about 23 MYA.

5 The **anthropoids** [Gk. *anthropos,* man, and *eides,* like] include the hominoids and the Old World monkeys and New World monkeys. Old World monkeys lack tails and have protruding noses. Some of the better-known Old World monkeys are the baboon, a ground dweller, and the rhesus monkey, which has been used in medical research. The New World monkeys often have long prehensile (grasping) tails and flat noses. Two of the well-known New World monkeys are the spider monkey and the capuchin, the "organ grinder's monkey."

Primate fossils similar to monkeys are first found in Africa, dated about 45 MYA. At that time, the Atlantic Ocean would have been too expansive for some of them to have easily made their way to South America, where the New World monkeys live today. It is hypothesized that a common ancestor to both the New World and Old World monkeys arose much earlier when a narrower Atlantic would have made crossing much more reasonable. The New World monkeys evolved in South America, and the Old World monkeys evolved in Africa.

6 Notice that **prosimians** [L. *pro,* before, and *simia,* ape, monkey], represented by lemurs and tarsiers, were the first type of primate to diverge from the common ancestor for all the primates. 7 All primates share one common mammalian ancestor, which lived about 55 MYA. This ancestor may have resembled today's tree shrews.

Hominoid Evolution

About 15 MYA, there were dozens of hominoid species, but the anatomy of a fossil classified as *Proconsul* makes it a probable transitional link between the monkeys and the hominoids. *Proconsul* was about the size of a baboon, and the size of its brain (165 cc) was also comparable. This fossil species didn't have the tail of a monkey (Fig. 30.5), and its elbow is similar to that of modern apes, but its limb proportions suggest that it walked as a quadruped on top of tree limbs as monkeys do. Although primarily a tree dweller, *Proconsul* may have also spent time exploring nearby grasslands for food.

Proconsul was probably ancestral to the **dryopithecines,** from which the hominoids arose. About 10 MYA, Africarabia (Africa plus the Arabian Peninsula) joined with Asia, and the apes migrated into Europe and Asia. In 1966, Spanish paleontologists announced the discovery of a specimen of *Dryopithecus* dated at 9.5 MYA near Barcelona. The anatomy of these bones clearly indicates that *Dryopithecus* was a tree dweller and locomoted by swinging from branch to branch as gibbons do today. They did not walk along the top of tree limbs as *Proconsul* did.

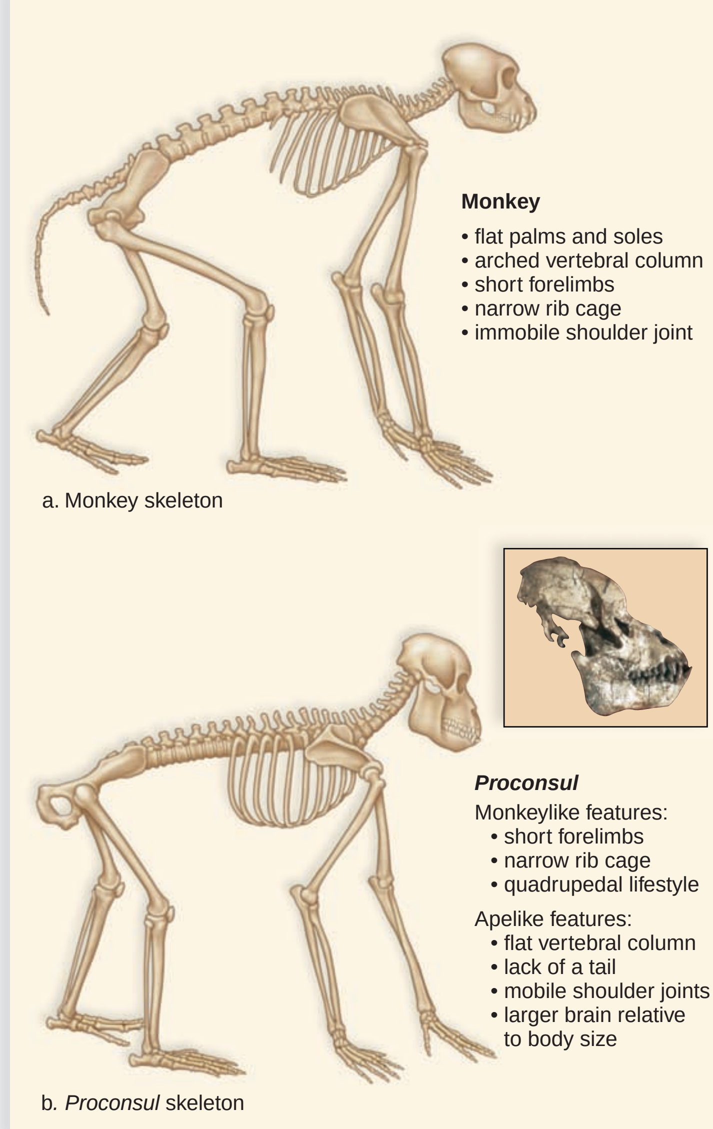


FIGURE 30.5 Monkey skeleton compared to *Proconsul* skeleton.

Comparison of a monkey skeleton (**a**) with that of *Proconsul* (**b**) shows various dissimilarities, indicating that *Proconsul* is more related to today's apes than to today's monkeys.

Check Your Progress 30.1

1. Match these terms to a number in Figure 30.4: prosimians, anthropoids, hominoids, hominins, hominines.
2. What type of evidence tells us that we humans are very closely related to the chimpanzees and gorillas?

30.2 Evolution of Humanlike Hominins

The relationship of hominins to the other primates is shown in the classification box at the right. Molecular data have been used to determine when hominin evolution began. When two lines of descent first diverge from a common ancestor, the genes of the two lineages are nearly identical. But as time goes by, each lineage accumulates genetic changes. Genetic changes compared to the other hominines suggest that hominin evolution began about 5 MYA.

CLASSIFICATION

ORDER: Primates

- Adapted to an arboreal life
- Prosimians, Anthropoids

FAMILY: Hominidae (hominids)

SUBFAMILY: Homininae (hominines)

TRIBE*: Hominini (hominins)

Early Humanlike Hominins → *Sahelanthropus*, ardipithecines,

Later Humanlike Hominins → australopithecines

GENUS: *Homo* (humans) → *Homo habilis, Homo rudolfensis, Homo ergaster, Homo erectus*

Early *Homo*
Brain size greater than 600 cc; tool use and culture

Later *Homo* → *Homo heidelbergensis, Homo neandertalensis, Homo sapiens*
Brain size greater than 1,000 cc; tool use and culture

* A new taxonomic level that lies between subfamily and genus.

Derived Characters of Humans

Although humans are closely related to chimpanzees, they stand erect and are, therefore, bipedal. Standing erect causes humans to have several distinct differences from the apes, as illustrated in Figure 30.6.

In humans, the spine exits inferior to the center of the skull, and this places the skull in the midline of the body. The longer, S-shaped spine of humans causes the trunk's center of gravity to be squarely over the feet. The broader pelvis and hip joint of humans keep them from swaying when they walk. The longer neck of the femur in humans causes the femur to angle inward at the knees. The human knee joint is modified to support the body's weight—that is, the femur is larger at the bottom, and the tibia is larger at the top. The human toe is not opposable; instead, the foot has an arch, which enables humans to walk long distances and run with less chance of injury.

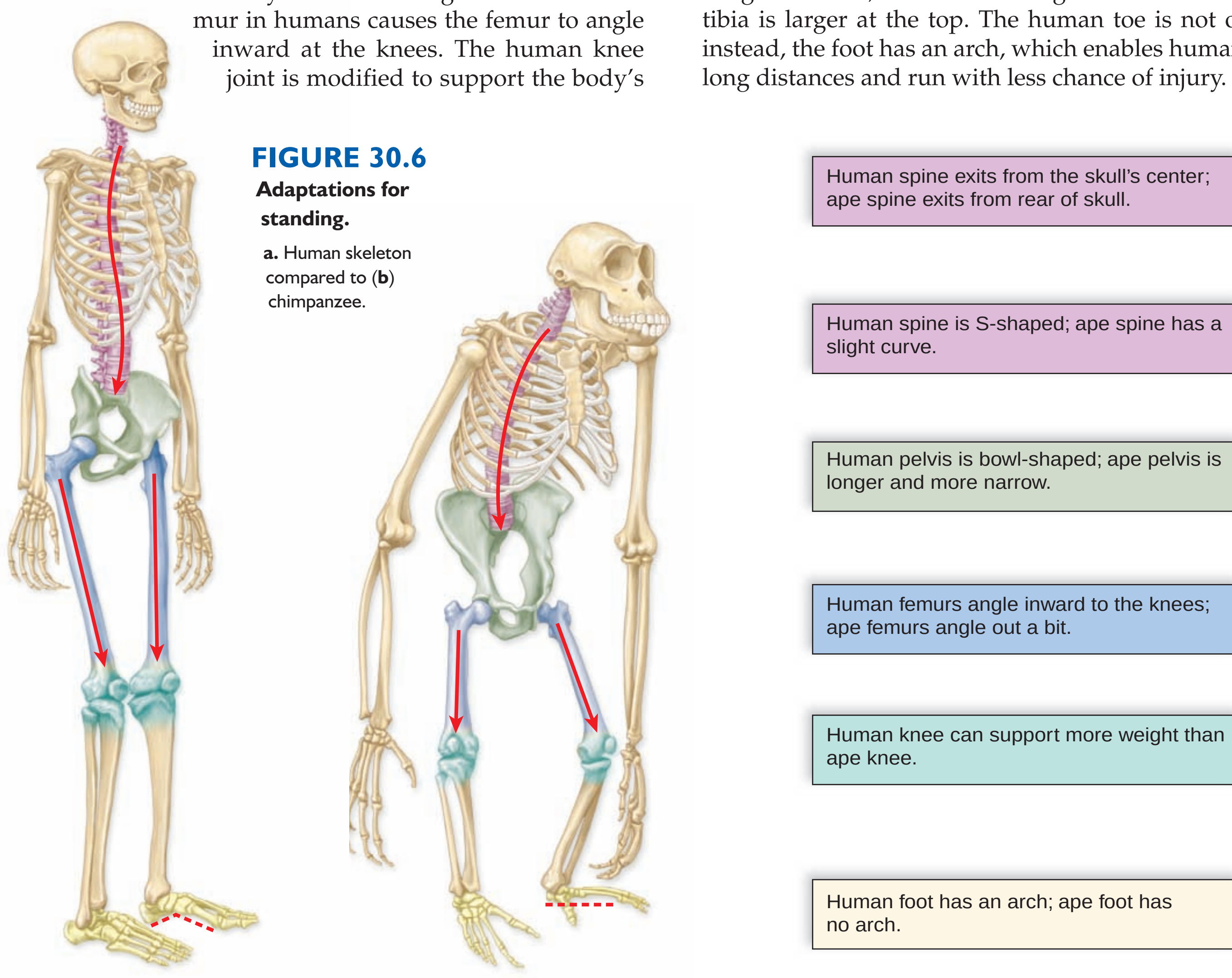


FIGURE 30.6 **Adaptations for standing.**
a. Human skeleton compared to (**b**) chimpanzee.

The Early Humanlike Hominins

Paleontologists use evidence of bipedalism to identify the early humanlike hominins. Until recently, many scientists thought that hominins began to stand upright in response to a dramatic change in climate that caused forests to be replaced by grassland. Now, some biologists suggest that the first humanlike hominins evolved even while they lived in trees, because they see no evidence of a dramatic shift in vegetation about 7 MYA. Their environment is now thought to have included some forest, some woodland, and some grassland. While still living in trees, the first humanlike hominins may have walked upright on large branches as they collected fruit from overhead. Then, when they began to forage on the ground, an upright stance would have made it easier for them to travel from woodland to woodland and/or to forage among bushes. Bipedalism may have had the added advantage of making it easier for males to carry food back to females. Or, bipedalism may be associated with the need to carry a helpless infant from place to place.

In Figure 30.7, early humanlike hominins are represented by orange-colored bars. The bars extend from the date of a species' appearance in the fossil record to the date it became extinct. Paleontologists have now found several fossils dated around the time the ape lineage and the human lineage are believed to have split, and one of these is *Sahelanthropus tchadensis*. Only the braincase has been found and dated at 7 MYA. Although the braincase is very apelike, the location of the opening for the spine at the back of the skull suggests bipedalism. Also, the canines are smaller and the tooth enamel is thicker than those of an ape.

Another early humanlike hominin, *Ardipithecus ramidus*, is representative of the ardipithecines of 4.5 MYA. So far, only skull fragments of *A. ramidus* have been described. Indirect evidence suggests that the species was possibly bipedal, and that some individuals may have been 122 cm tall. The teeth seem intermediate between those of earlier apes and later humanlike hominins, which are discussed next. Recently, fossils dated 4 MYA show a direct link between *A. ramidus* and the australopiths, discussed next.

Check Your Progress 30.2

1. What environmental influence may have caused bipedalism to evolve?
2. What is the strongest evidence that humanlike hominin evolution began around 7 MYA?

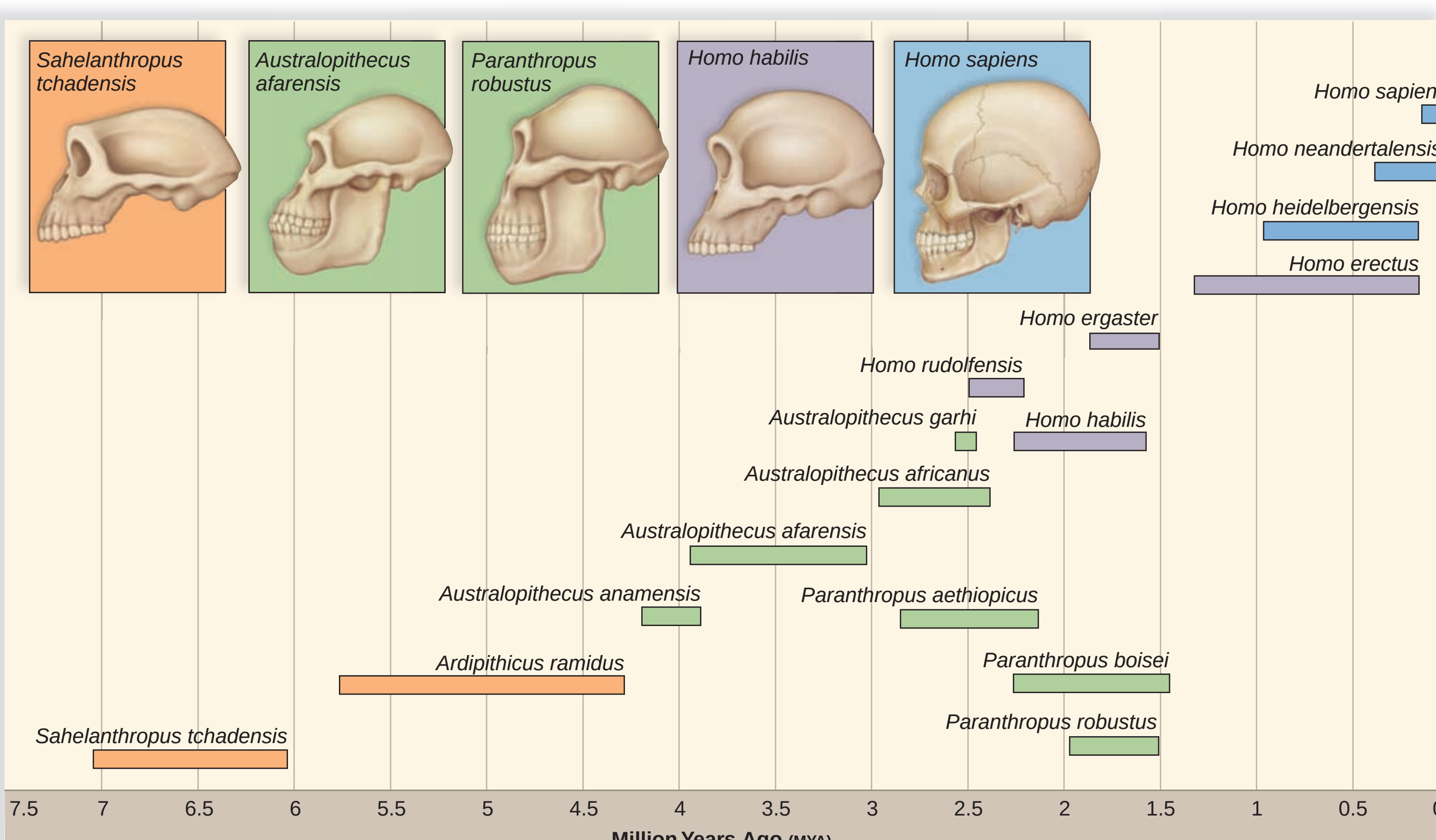


FIGURE 30.7 Human Evolution.

Several groups of extinct hominins preceded the evolution of modern humans. These groups have been divided into the early humanlike hominins (orange), later humanlike hominins (green), early *Homo* species (lavender), and finally the later *Homo* species (blue). Only modern humans are classified as *Homo sapiens*.

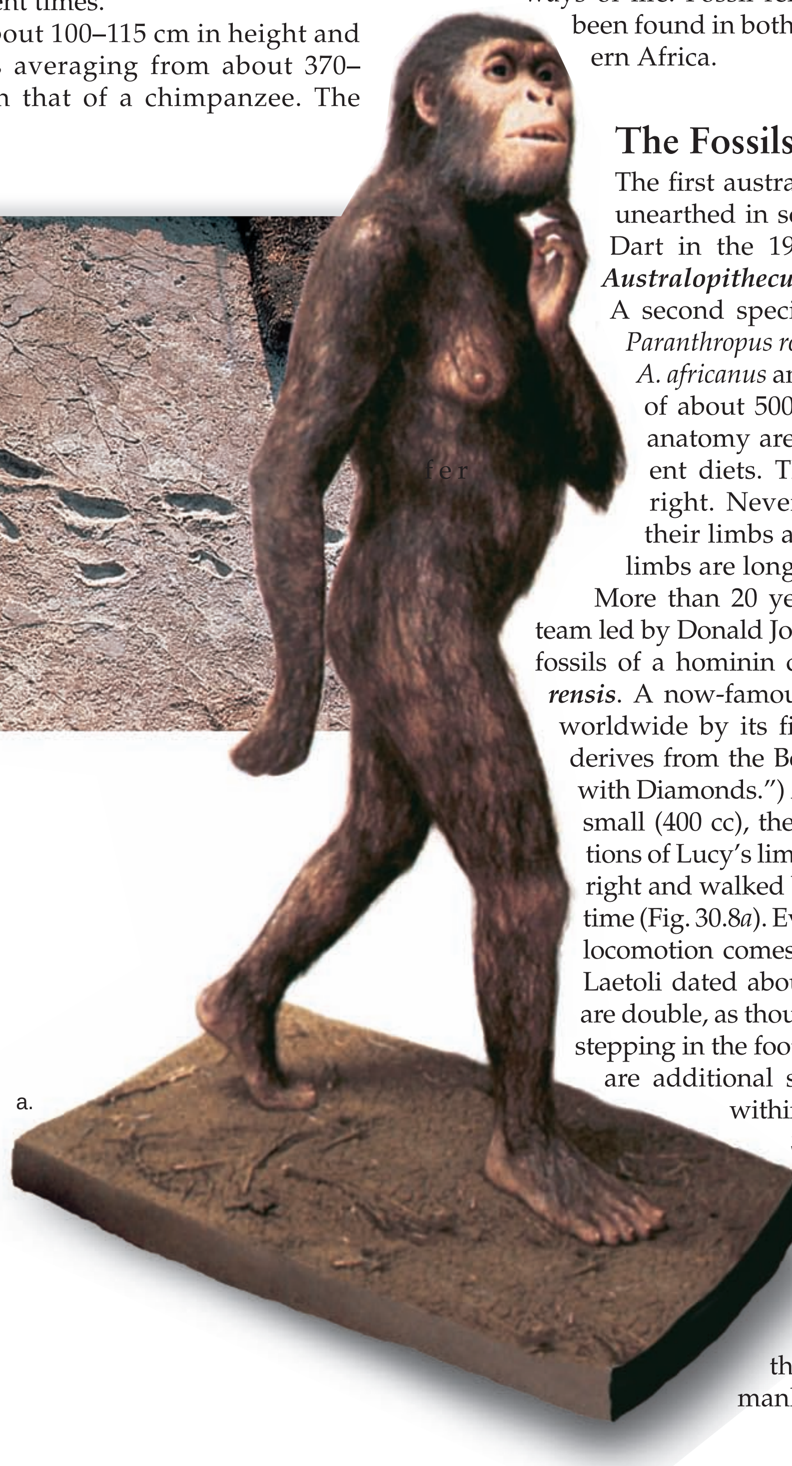
30.3 Evolution of Later Humanlike Hominins

The **australopithecines** (called **australopiths** for short) are a group of hominins that evolved and diversified in Africa from 4 MYA until about 1 MYA. In Figure 30.7, the australopiths are represented by green-colored bars. The australopiths had a small brain (an apelike characteristic) and walked erect (a humanlike characteristic). Therefore, it seems that human characteristics did not evolve all together at the same time. Australopiths give evidence of **mosaic evolution,** meaning that different body parts change at different rates and, therefore, at different times.

Australopiths stood about 100–115 cm in height and had relatively small brains averaging from about 370–515 cc—slightly larger than that of a chimpanzee. The forehead was low and the face projected forward (Fig. 30.8). Tool use is not in evidence except for later appearing *A. garhi*.

Some australopiths were slight of frame and termed *gracile* (slender). Others were *robust* (powerful) and tended to have massive jaws because of their large grinding teeth. The larger species, now placed in the genus *Paranthropus*, had well-developed chewing muscles that were anchored to a prominent bony crest along the top of the skull. Their diet included seeds and roots. The gracile types of genus *Australopithecus* most likely fed on soft fruits and leaves. Therefore, the australopiths show an adaptation to different ways of life. Fossil remains of australopiths have been found in both southern Africa and in eastern Africa.

b.



a.

FIGURE 30.8

Australopithecus afarensis.

a. A reconstruction of Lucy on display at the St. Louis Zoo. **b.** These fossilized footprints occur in ash from a volcanic eruption some 3.7 MYA. The larger footprints are double, and a third, smaller individual was walking to the side. (A female holding the hand of a youngster may have been walking in the footprints of a male.) The footprints suggest that *A. afarensis* walked bipedally.

The Fossils

The first australopith to be discovered was unearthed in southern Africa by Raymond Dart in the 1920s. This hominin, named ***Australopithecus africanus,*** is a gracile type. A second specimen from southern Africa, *Paranthropus robustus,* is a robust type. Both *A. africanus* and *P. robustus* had a brain size of about 500 cc; variations in their skull anatomy are essentially due to their different diets. These hominins walked upright. Nevertheless, the proportions of their limbs are apelike—that is, the forelimbs are longer than the hindlimbs.

More than 20 years ago in eastern Africa, a team led by Donald Johanson unearthed nearly 250 fossils of a hominin called ***Australopithecus afarensis***. A now-famous female skeleton is known worldwide by its field name, Lucy. (The name derives from the Beatles song "Lucy in the Sky with Diamonds.") Although her brain was quite small (400 cc), the shapes and relative proportions of Lucy's limbs indicate that she stood upright and walked bipedally at least some of the time (Fig. 30.8*a*). Even better evidence of bipedal locomotion comes from a trail of footprints in Laetoli dated about 3.7 MYA. The larger prints are double, as though a smaller-sized being was stepping in the footprints of another—and there are additional small prints off to the side, within hand-holding distance (Fig. 30.8*b*). *A. afarensis,* a gracile type, is believed to be ancestral to the robust types found in eastern Africa, including *P. aethiopicus* and *P. boisei*. *P. boisei* had a powerful upper body and the largest molars of any humanlike hominin.

In 2000, a team of scientists from the Max Planck Institute unearthed the fossilized remains of a 3.3-million-year-old juvenile *A. afarensis* just 4 km from where Lucy had been discovered. Dubbed Salem by her discoverer, she is often called "Lucy's baby," even though she is tens of thousands of years older than Lucy. Not only is this fossil exceptional because the remains of infants and juveniles rarely fossilize, but it represents the most complete *A. afarensis* fossil to date.

An earlier find called *A. garhi* may be the transitional link between the australopiths and the next group of fossils we will be discussing, namely, the early *Homo* species, represented in Figure 30.7 by lavender-colored bars. *A garhi* is an australopith, but it made tools.

Check Your Progress 30.3

1. In general terms, compare the gracile australopith species with the robust species. What accounts for the differences in their anatomies?
2. Is a southern or eastern australopith fossil likely to be an ancestor of early *Homo*? Explain.

science focus

Origins of the Genus *Homo*

Remains of australopiths indicate that they spent part of their time climbing trees and that they retained many apelike traits. Most likely, the australopiths climbed trees for the same reason that chimpanzees do today: to gather fruits and nuts in trees and to sleep aboveground at night so as to avoid predatory animals, such as lions and hyenas.

Whereas our brain is about the size of a grapefruit, that of the australopiths was about the size of an orange. Their brain was only slightly larger than that of a chimpanzee.

We know that the genus *Homo* evolved from the genus *Australopithecus*, but it seemed to me [Stephen Stanley] they could not have done so as long as the australopiths climbed trees every day. The obstacle relates to the way we, members of *Homo*, develop our large brain. Unlike other primates, we retain the high rate of fetal brain growth through the first year after birth. (That is why a one-year-old child has a very large head in proportion to the rest of its body.) The brain of other primates, including monkeys and apes, grows rapidly before birth, but immediately after birth, their brain grows more slowly. As a result, an adult human brain is more than three times as large as that of an adult chimpanzee.

A continuation of the high rate of fetal brain growth eventually allowed the genus *Homo* to evolve from the genus *Australopithecus*. But there was a problem in that continued brain growth is linked to underdevelopment of the entire body. Although the human brain becomes much larger, human babies are remarkably weak and uncoordinated. Such helpless infants must be carried about and tended. Human babies are unable to cling to their mothers the way chimpanzee babies can (Fig. 30A).

The origin of the *Homo* genus entailed a great evolutionary compromise. Humans gained a large brain, but they were saddled with the largest interval of infantile helplessness of all the mammals. The positive value of a large brain must have outweighed the negative aspects of infantile helplessness, such as the inability of adults to climb trees while holding a helpless infant, or else genus *Homo* would not have evolved. Having a larger brain meant that humans were able to outsmart or ward off predators with weapons they were clever enough to manufacture.

Probably very few genetic changes were required to delay the maturation of *Australopithecus* and produce the large brain of *Homo*. The mutation of a *Hox* developmental gene could have delayed early maturation, allowing the brain to enlarge under the selection forces resulting from the increased social nature of *Homo*. As we learn more about the human genome, we will eventually uncover the particular gene or gene combinations that cause us to have a large brain, and this will be a very exciting discovery.

Steven Stanley
Johns Hopkins University

FIGURE 30A Human infant.
A human infant is often cradled and has no means to cling to its mother when she goes about her daily routine.

30.4 Evolution of Early *Homo*

Early *Homo* species appear in the fossil record somewhat earlier or later than 2 MYA. They all have a brain size that is 600 cc or greater, their jaw and teeth resemble those of humans, and tool use is in evidence.

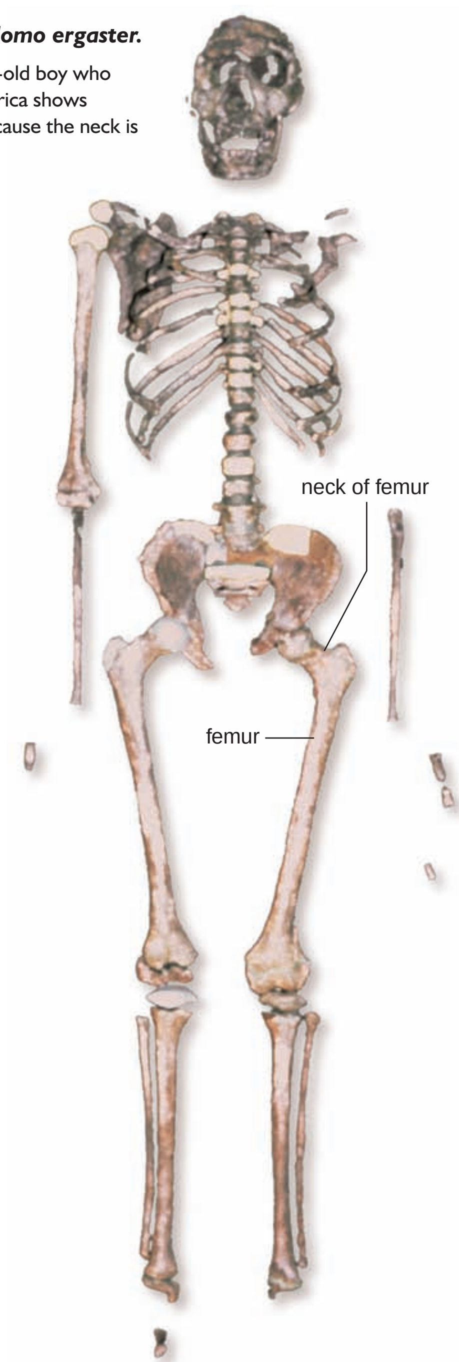
Homo habilis and *Homo rudolfensis*

Homo habilis and *Homo rudolfensis* are closely related and will be considered together. *Homo habilis* means handyman, and these two species are credited by some as being the first peoples to use stone tools, as discussed in the Ecology Focus on page 569. Most believe that while they were socially organized, they were probably scavengers rather than hunters. The cheek teeth of these hominins tend to be smaller than even those of the gracile australopiths. This is also evidence that they were omnivorous and ate meat, in addition to plant material.

Compared to australopiths, the protrusion of the face was less, and the brain was larger. Although the height of *H. rudolfensis* did not exceed that of the australopiths, some of this species' fossils have a brain size as large as 800 cc, which is considerably larger than that of *A. afarensis*.

FIGURE 30.9 ***Homo ergaster.***

This skeleton of a 10-year-old boy who lived 1.6 MYA in eastern Africa shows femurs that are angled because the neck is quite long.



Homo ergaster and *Homo erectus*

Homo ergaster evolved in Africa perhaps from *H. rudolfensis.* Similar fossils found in Asia are different enough to be classified as ***Homo erectus*** [L. *homo,* man, and *erectus,* upright]. These fossils span the dates between 1.9 and 0.3 MYA, and many other fossils belonging to both species have been found in Africa and Asia.

Compared to *H. habilis, H. ergaster* had a larger brain (about 1,000 cc) and a flatter face with a projecting nose. This type of nose is adaptive for a hot, dry climate because it permits water to be removed before air leaves the body. The recovery of an almost complete skeleton of a 10-year-old boy indicates that *H. ergaster* was much taller than the hominins discussed thus far (Fig. 30.9). Males were 1.8 m tall, and females were 1.55 m tall. Indeed, these hominins stood erect and, most likely, had a *striding gait* like that of modern humans. The robust and most likely heavily muscled skeleton still retained some australopithecine features. Even so, the size of the birth canal indicates that infants were born in an immature state that required an extended period of care.

H. ergaster first appeared in Africa but then migrated into Europe and Asia sometime between 2 MYA and 1 MYA. Most likely, *H. erectus* evolved from *H. ergaster* after *H. ergaster* arrived in Asia. In any case, such an extensive population movement is a first in the history of humankind and a tribute to the intellectual and physical skills of these peoples. They also had a knowledge of fire and may have been the first to cook meat.

Homo floresiensis

In 2004, scientists announced the discovery of the fossil remains of *Homo floresiensis.* The 18,000-year-old fossil of a 1 m tall, 25 kg adult female was discovered on the island of Flores in the South Pacific. The specimen was the size of a three-year-old *Homo sapien* but possessed a braincase only one-third the size of modern humans. A 2007 study supports the hypothesis that this diminutive hominin and her peers evolved from normal-sized, island hopping *Homo erectus* populations that reached Flores about 840,000 years ago. Apparently, *H. floresiensis* used tools and fire.

Check Your Progress 30.4

1. What is significant about the migration of *H. ergaster* out of Africa?
2. What are the cultural advancements that early *Homo* made over the australopiths?

ecology focus

Biocultural Evolution Began with *Homo*

Culture encompasses human activities and products that are passed on from one generation to another outside of direct biological inheritance. *Homo habilis* (and *Homo rudolfensis*) could make the simplest of stone tools, called Oldowan tools after a location in Africa where the tools were first found. The main tool could have been used for hammering, chopping, and digging. A flake tool was a type of knife sharp enough to scrape away hide and remove meat from bones. The diet of *H. habilis* most likely consisted of collected plants. But they probably had the opportunity to eat meat scavenged from kills abandoned by lions, leopards, and other large predators in Africa.

Homo erectus, who lived in Eurasia, also made stone tools, but the flakes were sharper and had straighter edges. They are called Acheulian tools for a location in France where they were first found. Their so-called multipurpose hand axes were large flakes with an elongated oval shape, a pointed end, and sharp edges on the sides. Supposedly they were handheld, but no one knows for sure. *H. erectus* also made the same core and flake tools as *H. habilis.* In addition, *H. erectus* could have also made many other implements out of wood or bone, and even grass, which can be twisted together to make string and rope. Excavation of *H. erectus* campsites dated 400,000 years ago have uncovered literally tens of thousands of tools.

H. erectus, like *H. habilis,* also gathered plants as food. However, *H. erectus* may have also harvested large fields of wild plants. The members of this species were not master hunters, but they gained some meat through scavenging and hunting. The bones of all sorts of animals litter the areas where they lived. Apparently, they ate pigs, sheep, rhinoceroses, buffalo, deer, and many other smaller animals. *H. erectus* lived during the last Ice Age, but even so, moved northward. No wonder *H. erectus* is believed to have used fire. A campfire would have protected them from wild beasts and kept them warm at night. And the ability to cook would have made meat easier to eat. In order for the humans to survive during the winter in northern climates, meat must have become a substantial part of the diet since plant sources are not available in the dead of winter. It is even possible that the campsites of *H. erectus* were "home bases" where the women stayed behind with the children while the men went out to hunt. If so, these people may have been the first **hunter-gatherers** (Fig. 30B)—that is, they hunted animals and gathered plants. This was a successful way of life that allowed the hominin populations to increase from a few thousand australopiths in Africa 2 MYA to hundreds of thousands of *H. erectus* by 300,000 years ago.

Hunting most likely encourages the development and spread of culture between individuals and generations. Those who could speak a language would have been able to cooperate better as they hunted and even as they sought places to gather food. Among animals, only humans have a complex language that allows them to communicate their experiences symbolically. Words stand for objects and events that can be pictured in the mind. The cultural achievements of *H. erectus* essentially began a new phase of human evolution, called **biocultural evolution,** in which natural selection is influenced by cultural achievements rather than by anatomic phenotype. *H. erectus* succeeded in new, colder environments because these individuals occupied caves, used fire, and became more capable of obtaining and eating meat as a substantial part of their diet.

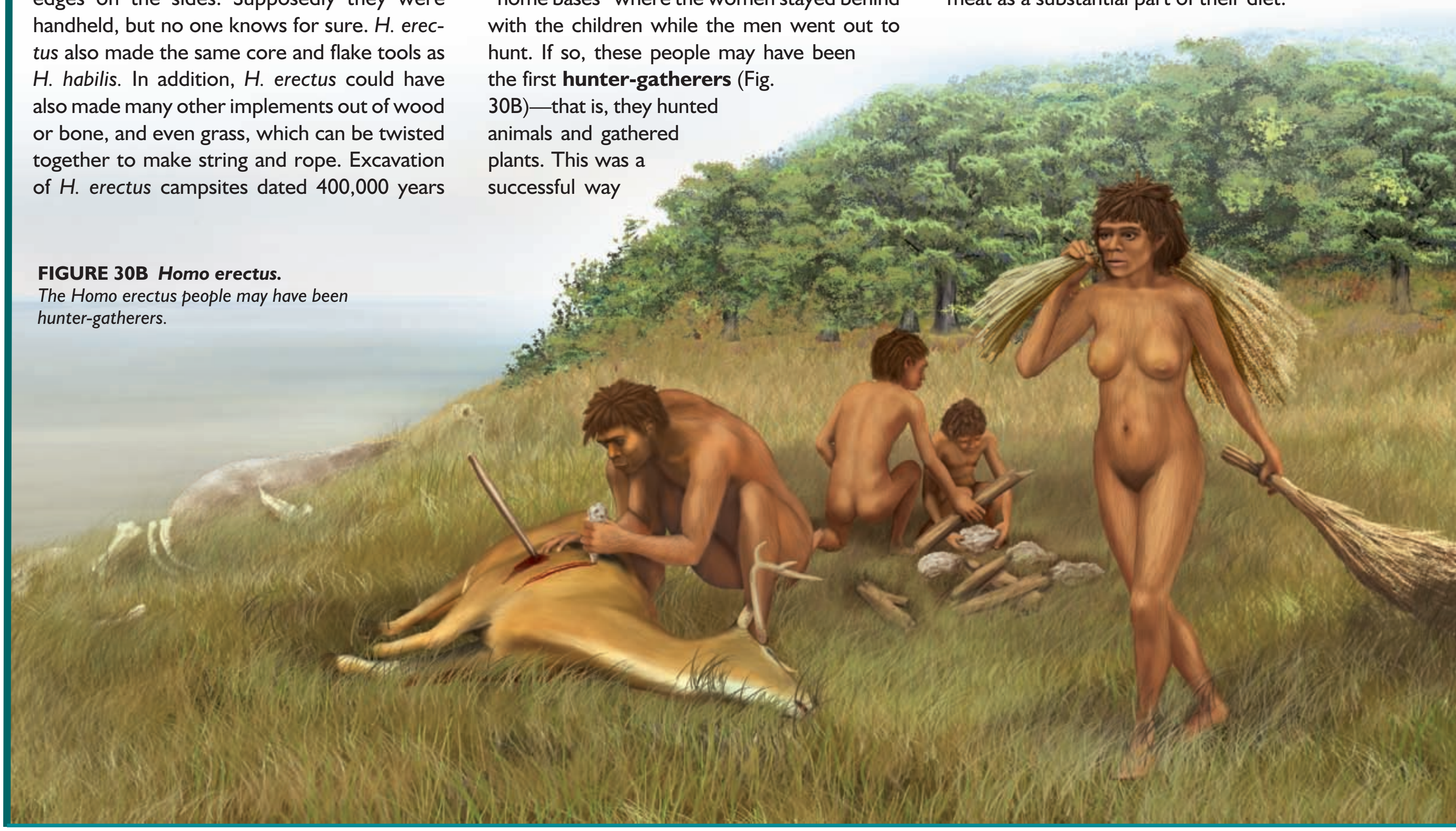


FIGURE 30B *Homo erectus.*
The Homo erectus people may have been hunter-gatherers.

30.5 Evolution of Later *Homo*

Later *Homo* species are represented by blue-colored bars in Figure 30.7. The evolution of these species from older *Homo* species has been the subject of much debate. Most researchers believe that modern humans (*Homo sapiens*) evolved from *H. ergaster,* but they differ as to the details. Many disparate early *Homo* species in Europe are now classified as *Homo heidelbergensis.* Just as *H. erectus* is believed to have evolved from *H. ergaster* in Asia, so *H. heidelbergensis* is believed to have evolved from *H. ergaster* in Europe. Further, for the sake of discussion, *H. ergaster* in Africa, *H. erectus* in Asia, and *H. heidelbergensis* (and *H. neandertalensis*) in Europe can be grouped together as archaic humans who lived as long as a million years ago. The most widely accepted hypothesis for the evolution of modern humans from archaic humans is referred to as the **replacement model** or **out-of-Africa hypothesis,** which proposes that modern humans evolved from archaic humans only in Africa, and then modern humans migrated to Asia and Europe, where it replaced the archaic species about 100,000 years BP (before the present) (Fig. 30.10).

The replacement model is supported by the fossil record. The earliest remains of modern humans (Cro-Magnon), dating at least 130,000 years BP, have been found only in Africa. Modern humans are found in Asia until 100,000 years BP and not in Europe until 60,000 years BP. Until earlier modern human fossils are found in Asia and Europe, the replacement model is supported.

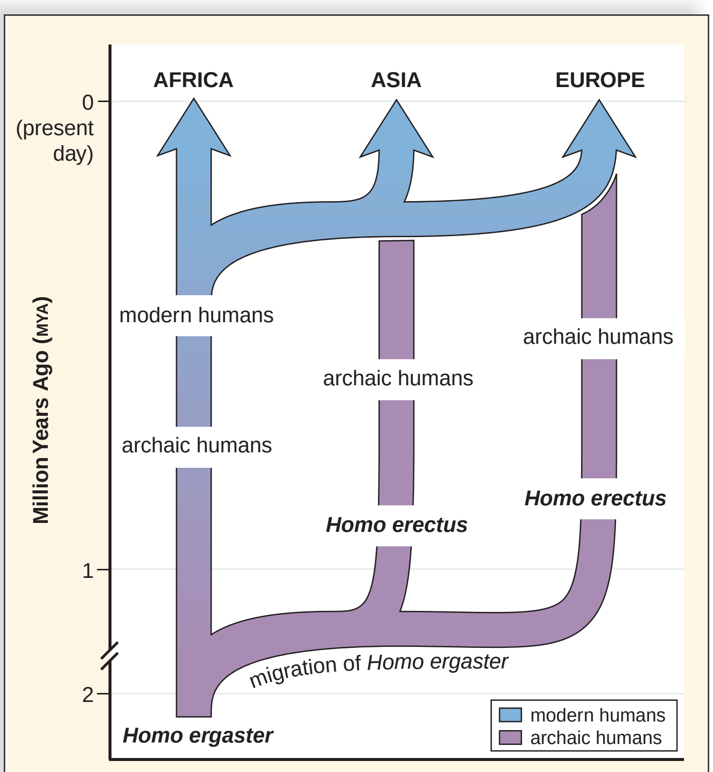


FIGURE 30.10 Replacement model.

Modern humans evolved in Africa and then replaced archaic humans in Asia and Europe.

The replacement model is also supported by DNA data. Several years ago, a study showed that the mitochondrial DNA of Africans is more diverse that the DNA of the people in Europe (and the world). This is significant because if mitochondrial DNA has a constant rate of mutation, Africans should show the greatest diversity, since modern humans have existed the longest in Africa. Called the "mitochondrial Eve" hypothesis by the press (note that this is a misnomer because no single ancestor is proposed), the statistics that calculated the date of the African migration were found to be flawed. Still, the raw data—which indicate a close genetic relationship among all Europeans—support the replacement model.

An opposing hypothesis to the out-of-Africa hypothesis does exist. This hypothesis, called the multiregional continuity hypothesis, proposes that modern humans arose from archaic humans in essentially the same manner in Africa, Asia, and Europe. The hypothesis is multiregional because it applies equally to Africa, Asia, and Europe, and it supposes that in these regions, genetic continuity will be found between modern populations and archaic populations. This hypothesis has sparked many innovative studies to test which hypothesis is correct.

Neandertals

The **Neandertals,** *Homo neandertalensis,* are an intriguing species of archaic humans that lived between 200,000 and 28,000 years ago. Neandertal fossils are known from the Middle East and throughout Europe. Neandertals take their name from Germany's Neander Valley, where one of the first Neandertal skeletons, dated some 200,000 years ago, was discovered.

According to the replacement model, the Neandertals were also supplanted by modern humans. Surprisingly, however, the Neandertal brain was, on the average, slightly larger than that of *Homo sapiens* (1,400 cc, compared with 1,360 cc in most modern humans). The Neandertals had massive brow ridges and wide, flat noses. They also had a forward-sloping forehead and a receding lower jaw. Their nose, jaws, and teeth protruded far forward. Physically, the Neandertals were powerful and heavily muscled, especially in the shoulders and neck (Fig. 30.11). The bones of Neandertals were shorter and thicker than those of modern humans. New fossils show that the pubic bone was long compared to that of modern humans. The Neandertals lived in Europe and Asia during the last Ice Age, and their sturdy build could have helped conserve heat.

Archaeological evidence suggests that Neandertals were culturally advanced. Some Neandertals lived in caves; however, others probably constructed shelters. They manufactured a variety of stone tools, including spear points, which could have been used for hunting, and scrapers and knives, which would have helped in food preparation. They most likely successfully hunted bears, woolly mammoths, rhinoceroses, reindeer, and other contemporary animals. They used and could control fire, which probably helped in cooking frozen meat and in keeping warm. They even buried their dead with flowers and tools and may have had a religion.

FIGURE 30.11 Neandertals.

This drawing shows that the nose and the mouth of the Neandertals protruded from their faces, and their muscles were massive. They made stone tools and were most likely excellent hunters.

FIGURE 30.12 Cro-Magnons.

Cro-Magnon people are the first to be designated *Homo sapiens*. Their tool-making ability and other cultural attributes, such as their artistic talents, are legendary.

Cro-Magnons

Cro-Magnons are the oldest fossils to be designated *Homo sapiens*. In keeping with the replacement model, the Cro-Magnons, who are named after a fossil location in France, were the modern humans who entered Asia from Africa about 100,000 years BP and then spread to Europe. They probably reached western Europe about 40,000 years ago. Cro-Magnons had a thoroughly modern appearance (Fig. 30.12). They had lighter bones, flat high foreheads, domed skulls housing brains of 1,590 cc, small teeth, and a distinct chin. They were hunter-gatherers, as was *H. erectus,* but they hunted more efficiently.

Tool Use in Cro-Magnons

During the last Ice Age, *Homo sapiens* had colonized all of the continents except Antarctica. Glaciation had caused a significant drop in sea level and, as a result, land bridges to the New World and Australia were available. No doubt, colonization was fostered by the combination of a larger brain and free hands with opposable thumbs that made it possible for Cro-Magnons to draft and manipulate tools and weapons of increasing sophistication. They made advanced stone tools, including compound tools, as when stone flakes were fitted to a wooden handle. They may have been the first to make knifelike blades and to throw spears, enabling them to kill animals from a distance. They were such accomplished hunters that some researchers believe they may have been responsible for the extinction of many larger mammals, such as the giant sloth, the mammoth, the saber-toothed tiger, and the giant ox, during the late Pleistocene epoch. This event is known as the Pleistocene overkill.

Language and Cro-Magnons

A more highly developed brain may have also allowed Cro-Magnons to perfect a language composed of patterned sounds. Language greatly enhanced the possibilities for cooperation and a sense of cohesion within the small bands that were the predominant form of human social organization, even for the Cro-Magnons. They combined hunting and fishing with the gathering of fruits, berries, grains, and root crops that grew in the wild.

The Cro-Magnons were extremely creative. They sculpted small figurines and jewelry out of reindeer bones and antlers. These sculptures could have had religious significance or been seen as a way to increase fertility. The most impressive artistic achievements of the Cro-Magnons were cave paintings, realistic and colorful depictions of a variety of animals, from woolly mammoths to horses, that have been discovered deep in caverns in southern France and Spain. These paintings suggest that Cro-Magnons had the ability to think symbolically, as would be needed in order to speak.

Check Your Progress 30.5A

1. What evidence is there to support the replacement model (out-of-Africa hypothesis) for the evolution of modern humans from archaic humans?
2. Describe the tools of Cro-Magnons. How are they advanced over those seen in archaic humans?
3. What is the significance of the development of art by Cro-Magnons?

Human Variation

Human beings have been widely distributed about the globe ever since they evolved. As with any other species that has a wide geographic distribution, phenotypic and genotypic variations are noticeable between populations. Today, we say that people have different ethnicities (Fig. 30.13*a*).

It has been hypothesized that human variations evolved as adaptations to local environmental conditions. One obvious difference among people is skin color. A darker skin is protective against the high UV intensity of bright sunlight. On the other hand, a white skin ensures vitamin D production in the skin when the UV intensity is low. Harvard University geneticist Richard Lewontin points out, however, that this hypothesis concerning the survival value of dark and light skin has never been tested.

FIGURE 30.13 Ethnic groups.

a. Some of the differences between the various prevalent ethnic groups in the United States may be due to adaptations to the original environment. **b.** The Massai live in East Africa. **c.** Eskimos live near the Arctic Circle.

Two correlations between body shape and environmental conditions have been noted since the nineteenth century. The first, known as Bergmann's rule, states that animals in colder regions of their range have a bulkier body build. The second, known as Allen's rule, states that animals in colder regions of their range have shorter limbs, digits, and ears. Both of these effects help regulate body temperature by increasing the surface-area-to-volume ratio in hot climates and decreasing the ratio in cold climates. For example, Figure 30.13*b*, *c* shows that the Massai of East Africa tend to be slightly built with elongated limbs, while the Eskimos, who live in northern regions, are bulky and have short limbs.

Other anatomic differences among ethnic groups, such as hair texture, a fold on the upper eyelid (common in Asian peoples), or the shape of lips, cannot be explained as adaptations to the environment. Perhaps these features became fixed in different populations due simply to genetic drift. As far as intelligence is concerned, no significant disparities have been found among different ethnic groups.

Genetic Evidence for a Common Ancestry

The replacement model for the evolution of humans, discussed on page 570, pertains to the origin of ethnic groups. This hypothesis proposes that all modern humans have a relatively recent common ancestor, that is, Cro-Magnon, who evolved in Africa and then spread into other regions. Paleontologists tell us that the variation among modern populations is considerably less than among archaic human populations some 250,000 years ago. If so, all ethnic groups evolved from the same single, ancestral population.

A comparative study of mitochondrial DNA shows that the differences among human populations are consistent with their having a common ancestor no more than a million years ago. Lewontin has also found that the genotypes of different modern populations are extremely similar. He examined variations in 17 genes, including blood groups and various enzymes, among seven major geographic groups: Caucasians, black Africans, mongoloids, south Asian Aborigines, Amerinids, Oceanians, and Australian Aborigines. He found that the great majority of genetic variation—85%—occurs within ethnic groups, not among them. In other words, the amount of genetic variation between individuals of the same ethnic group is greater than the variation between ethnic groups.

Check Your Progress 30.5B

1. What data support the hypothesis that humans are one species?
2. Where is the greater amount of variability in modern human populations, within ethnic groups or between them?

Connecting the Concepts

Aside from various anatomical differences related to human bipedalism and intelligence, a cultural evolution separates us from the apes. A hunter-gatherer society evolved when humans became able to make and use tools. That society then gave way to an agricultural economy about 12,000 to 15,000 years ago, perhaps because we were too efficient at killing big game so that a food shortage arose. The agricultural period extended from that time to about 200 years ago, when the Industrial Revolution began. Now most people live in urban areas. Perhaps as a result, modern humans are for the most part divorced from nature and often endowed with the philosophy of exploiting and controlling nature.

Our cultural evolution has had far-reaching effects on the biosphere, especially since the human population has expanded to the point that it is crowding out many other species. Our degradation and disruption of the environment threaten the continued existence of many species, including our own. As discussed in Chapter 47, however, we have recently begun to realize that we must work with, rather than against, nature if biodiversity is to be maintained and our own species is to continue to exist.

Before we examine the environment and the role of humans in ecosystems, we will study the various organ systems of the human body. Humans need to keep themselves and the environment fit so that they and their species can endure.

summary

30.1 Evolution of Primates

Primates, in contrast to other types of mammals, are adapted for an arboreal life. The evolution of primates is characterized by trends toward mobile limbs; grasping hands; a flattened face; stereoscopic vision; a large, complex brain; and one birth at a time. These traits are particularly useful for living in trees.

The term hominin is now used for chimpanzees, humans, and their closely related, but extinct, relatives. A hominin is a member of the group hominines that also includes the gorilla, which are the apes most closely related to hominins on the basis of molecular data. There follows ever increasing sized groups.

Proconsul is a transitional link between monkeys and the hominoids, which include the gibbons, organgutans, and the hominines.

30.2 Evolution of Humanlike Hominins

Fossil and molecular data tell us humanlike hominins shared a common ancestor with chimpanzees until about 5 MYA, and the split between their lineage and the human lineage occurred around this time.

Humans walk erect, and this causes our anatomy to differ from the apes. In humans, the spinal cord curves and exits from the center of the skull, rather than from the rear of the skull. The human pelvis is broader and more bowl-shaped to place the weight of the body over the legs. Humans use only the longer, heavier lower limbs for walking; in apes, all four limbs are used for walking, and the upper limbs are longer than the lower limbs.

To be a humanlike hominin, a fossil must have an anatomy suitable to standing erect. Perhaps bipedalism developed when humanlike hominins stood on branches to reach fruit overhead, and then they continued to use this stance when foraging among bushes. An upright posture reduces exposure of the body to the sun's rays, and leaves the hands free to carry food, perhaps as a gift to receptive females.

Several early humanlike hominin fossils, such as *Sahelanthropus tchadensis,* have been dated around the time of a shared ancestor for apes and humans (7 MYA). The ardipithecines appeared about 4.5 MYA. All the early humanlike hominins have a chimp-sized braincase but are believed to have walked erect.

30.3 Evolution of Later Humanlike Hominins

It is possible that an australopith (4 MYA–1 MYA) is a direct ancestor for humans. These hominins walked upright and had a brain size of 370–515 cc. In southern Africa, hominins classified as australopiths include *Australopithecus africanus,* a gracile form, and *Paranthropus robustus,* a robust form. In eastern Africa, hominins classified as australopiths include, *A. afarensis* (Lucy), a gracile form, and also robust forms. Many of the australopiths coexisted, and the species *A. garhi* is the probable ancestor to the genus *Homo.*

30.4 Evolution of Early *Homo*

Early *Homo,* such as *Homo habilis* and *Homo rudolfensis,* dated around 2 MYA, is characterized by a brain size of at least 600 cc, a jaw with teeth that resembled those of modern humans, and the use of tools.

Homo ergaster and *Homo erectus* (1.9–0.3 MYA) had a striding gait, made well-fashioned tools, and could control fire. *Homo ergaster* migrated into Asia and Europe from Africa between 2 and 1 MYA. *Homo erectus* evolved in Asia and gave rise to *H. floresiensis.*

30.5 Evolution of Later *Homo*

The replacement model of human evolution says that modern humans originated only in Africa and, after migrating into Europe and Asia, replaced the archaic *Homo* species found there.

The Neandertals, a group of archaic humans, lived in Europe and Asia. Their chinless faces, squat frames, and heavy muscles are apparently adaptations to the cold. Cro-Magnon is a name often given to modern humans. Their tools were sophisticated, and they definitely had a culture, as witnessed by the paintings on the walls of caves. The human ethnic groups of today differ in ways that can be explained in part by adaptation to the environment. Genetic studies tell us that there are more genetic differences between people of the same ethnic group than between ethnic groups. We are one species.

understanding the terms

Match the terms to these definitions:

a. ______________ Group of primates that includes monkeys, apes, and humans.
b. ______________ The common name for the first fossils generally accepted as being modern humans.
c. ______________ Hominin with a sturdy build who lived during the last Ice Age in Eurasia; hunted large game and lived together in a kind of society.
d. ______________ Type of early *Homo* to first have a striding gait similar to that of modern humans.
e. ______________ Member of a group that does not include prosiminans nor monkeys, nor gibbons.

reviewing this chapter

1. List and discuss various evolutionary trends among primates, and state how they would be beneficial to animals with an arboreal life. 560–61
2. What is the significance of the fossils known as *Proconsul?* 563
3. How does an upright stance cause human anatomy to differ from that of chimpanzees? 564–65
4. Discuss the possible benefits of bipedalism in early hominins. 565
5. Why does the term *mosaic evolution* apply to the australopiths? 566
6. Why are the early *Homo* species classified as humans? If these hominins did make tools, what does this say about their probable way of life? 568–69
7. What role might *H. ergaster* have played in the evolution of modern humans according to the replacement model? 570
8. Who were the Neandertals and the Cro-Magnons, and what is their place in the evolution of humans according to the replacement model mentioned in question 7? 570–71

testing yourself

Choose the best answer for each question.

1. Which of these gives the correct order of divergence from the main primate line of descent?
   a. prosimians, monkeys, gibbons, orangutans, African apes, humanlike hominins
   b. gibbons, orangutans, prosimians, monkeys, African apes, humanlike hominins
   c. monkeys, gibbons, prosimians, African apes, orangutans, humanlike hominins
   d. African apes, gibbons, monkeys, orangutans, prosimians, humanlike hominins
   e. *H. habilis, H. ergaster, H. neandertalensis,* Cro-Magnon
2. Lucy is a(n)
   a. early *Homo.*
   b. australopith.
   c. ardipithecine.
   d. modern human.
3. What possibly influenced the evolution of bipedalism?
   a. Humans wanted to stand erect in order to use tools.
   b. With bipedalism, it's possible to reach food overhead.
   c. With bipedalism, sexual intercourse is facilitated.
   d. An upright stance exposes more of the body to the sun, and vitamin D production requires sunlight.
   e. All of these are correct.
4. Which of these is an incorrect association with robust types?
   a. massive chewing muscles attached to bony skull crest
   b. some australopiths
   c. diet included fibrous foods
   d. lived during an Ice Age
   e. Both a and c are incorrect associations.
5. *H. ergaster* could have been the first to
   a. use and control fire.
   b. migrate out of Africa.
   c. make axes and cleavers.
   d. have a brain of about 1,000 cc.
   e. All of these are correct.
6. Which of these characteristics is not consistent with the others?
   a. brow ridges
   b. small cheek teeth (molars)
   c. high forehead
   d. projecting face
   e. stereoscopic vision
7. Which of these statements is correct? The last common ancestor for chimpanzees and hominins
   a. has been found, and it resembles a gibbon.
   b. was probably alive around 5 MYA.
   c. has been found, and it has been dated at 30 MYA.
   d. is not expected to be found because there was no such common ancestor.
   e. is now believed to have lived in Asia, not Africa.
8. Which of these pairs is incorrectly matched?
   a. gibbon—hominoid
   b. *A. africanus*—hominin
   c. tarsier—anthropoid
   d. *H. erectus—H. ergaster*
   e. early *Homo—H. habilis*
9. If the out-of Africa hypothesis is correct, then
   a. human fossils in China after 100,000 years BP would not be expected to resemble earlier fossils.
   b. human fossils in China after 100,000 years BP would be expected to resemble earlier fossils.
   c. humans did not migrate out of Africa.
   d. Both b and c are correct.
   e. Both a and c are correct.
10. Which of these pairs is incorrectly matched?
    a. *H. erectus*—made tools
    b. Neandertal—good hunter
    c. *H. habilis*—controlled fire
    d. Cro-Magnon—good artist
    e. *A. robustus*—fibrous diet
11. Which hominins could have inhabited the Earth at the same time?
    a. australopiths and Cro-Magnons
    b. *Paranthropus robustus* and *Homo habilis*
    c. *Homo habilis* and *Homo sapiens*
    d. gibbons and humans
12. Which of these is an incorrect statement?
    a. *H. habilis* and *H. rudolfensis* were omnivores with a brain size of about 800 cc.
    b. *H. ergaster* had a brain size larger than that of *H. erectus.*
    c. *H. floresiensis,* discovered in 2004, used tools and fire.
    d. All of these are correct.

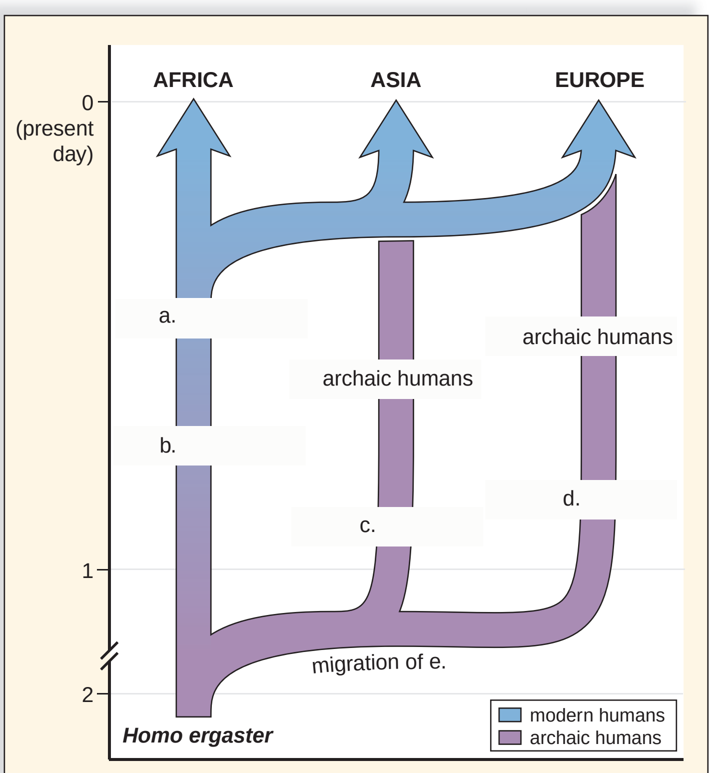
For questions 13–17, indicate whether the statement is true (T) or false (F).

13. Australopiths were adapted to different diets. ______________

14. *Homo habilis* made stone tools. ________________
15. The human pelvis is bowl-shaped, and the ape pelvis is long and narrow. ________________
16. The gibbon is an Asian ape, while the chimpanzee is an African ape. ________________
17. Mitochondrial DNA differences are inconsistent with the existence of a recent human common ancestor for all ethnic groups. ________________

For questions 18–22, fill in the blanks.

18. Along with monkeys and all apes, humans are ________________.
19. The out-of-Africa hypothesis proposes that modern humans evolved in ________________ only.
20. The australopiths could probably walk ________________, but they had a ________________ brain.
21. The only fossil rightly called *Homo sapien* is that of ________________.
22. Modern humans evolved ________________ (choose billions, millions, thousands) of years ago.
23. Which human characteristic is not thought to be an adaptation to the environment?
    a. bulky bodies of Eskimos
    b. long limbs of Africans
    c. light skin of northern Europeans
    d. hair texture of Asians
    e. Both a and b are correct.
24. Complete this diagram of the replacement model by filling in the blanks.



Replacement Model

thinking scientifically

1. Bipedalism has many selective advantages. However, there is one particular disadvantage to walking on two feet: Giving birth to an offspring with a large head through the smaller pelvic opening that is necessitated by upright posture is very difficult. This situation results in a high percentage of deaths (of both mother and child) during birth compared to other primates. How do you explain the selection of a trait that is both positive and negative?
2. How might you use biotechnology to show that humans today have Neandertal genes, and therefore, Cro-Magnons and Neandertals interbred with one another?

bioethical issue

Manipulation of Evolution

Since the dawn of civilization, humans have carried out cross-breeding programs to develop plants and animals of use to them. With the advent of DNA technology, we have entered a new era in which even greater control can be exerted over the evolutionary process. We can manipulate genes and give organisms traits that they would not ordinarily possess. Some plants today produce human proteins that can be extracted from their seeds, and some animals grow larger because we have supplied them with an extra gene for growth hormone. Does this type of manipulation seem justifiable?

What about the possibility that we are manipulating our own evolution? Should doctors increase the fitness of certain couples by providing them with a means to reproduce that they cannot achieve on their own? Is the use of alternate means of reproduction bioethically justifiable? In the near future, it may be possible for parents to choose the phenotypic traits of their offspring; in effect, this might enable humans to ensure that their offspring are stronger and brighter than their parents. Does this choosing of "designer babies" seem ethical to you?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

part VII

Comparative Animal Biology

In contrast to plants, which are autotrophic and make their own organic food, animals are heterotrophic and feed on organic molecules made by other organisms. Their mobility, which is dependent upon nerve and muscle fibers, is essential to escaping predators, finding a mate, and acquiring food. Food is then digested, and the nutrients are distributed to the body's cells. Finally, waste products are expelled.

In complex animals, a distinct division of labor exists, and each of the organ systems is specialized to carry out specific functions. A cardiovascular system transports materials from one body part to another; a respiratory system carries out gas exchange; and a urinary system filters the blood and removes its wastes. The lymphatic system, along with the immune system, protects the body from infectious diseases. The nervous system and endocrine system coordinate the activities of the other systems.

Our comparative study will show how the systems evolved and how they function to maintain homeostasis, the relative constancy of the internal environment.