(a) (b)

Figure 29.40 Egg-laying mammals. (a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme, with long hairs modified into spines. (credit b: modification of work by Barry Thomas)

Over 2/3 of the approximately 330 living species of marsupials are found in Australia, with the rest, nearly all various types of opossum, found in the Americas, especially South America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure 29.41), and several other species. Like monotremes, the embryos of marsupials are nourished during a short gestational period (about a month in kangaroos) by a yolk-sac placenta, but with no intervening egg shell. Some marsupial embryos can enter an embryonic diapause, and delay implantation, suspending development until implantation is completed. Marsupial young are also effectively fetal at birth. Most, but not all, species of marsupials possess a pouch in which the very premature young reside, receiving milk and continuing their development. In kangaroos, the young joeys continue to nurse for about a year and a half.

Figure 29.41 A marsupial mammal. The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians (placentals) are the most widespread and numerous of the mammals, occurring throughout the world. Eutherian mammals are sometimes called "placental mammals" because all species possess a complex **chorioallantoic placenta** that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. There are about 4,000 species of placental mammals in 18 to 20 orders with various adaptations for burrowing, flying, swimming, hunting, running, and climbing. In the evolutionary sense, they have been incredibly successful in form, diversity, and abundance. The eutherian mammals are classified in two major clades, the Atlantogenata and the Boreoeutheria. The Atlantogeneta include the Afrotheria (e.g., elephants, hyraxes, and manatees) and the Xenarthra (anteaters, armadillos, and sloths). The Boreoeutheria contain two large groups, the Euarchontoglires and the Laurasiatheria. Familiar orders in the Euarchontoglires are the Scandentia (tree shrews), Rodentia (rats, mice, squirrels, porcupines), Lagomorpha (rabbits and hares), and the Primates (including humans). Major Laurasiatherian orders include the Perissodactyla (e.g., horses and rhinos), the Cetartiodactyla (e.g., cows, giraffes, pigs, hippos, and whales), the Carnivora (e.g., cats, dogs, and bears), and the Chiroptera (bats and flying foxes). The two largest orders are the rodents (2,000 species) and bats (about 1,000 species), which together constitute approximately 60 percent of all eutherian species.

29.7 The Evolution of Primates

By the end of this section, you will be able to do the following:

- Describe the derived features that distinguish primates from other animals
- Describe the defining features of the major groups of primates
- Identify the major hominin precursors to modern humans
- Explain why scientists are having difficulty determining the true lines of descent in hominids

Order Primates of class Mammalia includes lemurs, tarsiers, monkeys, apes, and humans. Non-human primates live primarily in the tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates are of particular interest to us as they allow us to understand the evolution of our own species.

Characteristics of Primates

All primate species possess adaptations for climbing trees, as they all descended from tree-dwellers. This arboreal heritage of primates has resulted in hands and feet that are adapted for climbing, or brachiation (swinging through trees using the arms). These adaptations include, but are not limited to: 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes (except humans) and thumbs sufficiently separated from fingers to allow for gripping branches, and 3) **stereoscopic vision**, two overlapping fields of vision from the eyes, which allows for the perception of depth and gauging distance. Other characteristics of primates are brains that are larger than those of most other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: Strepsirrhini ("turned-nosed") and Haplorhini ("simple-nosed") primates. Strepsirrhines, also called the wet-nosed primates, include prosimians like the bush babies and pottos of Africa, the lemurs of Madagascar, and the lorises of Southeast Asia. Haplorhines, or dry-nosed primates, include tarsiers (Figure 29.42) and simians (New World monkeys, Old World monkeys, apes, and humans). In general, strepsirrhines tend to be nocturnal, have larger olfactory centers in the brain, and exhibit a smaller size and smaller brain than anthropoids. Haplorhines, with a few exceptions, are diurnal, and depend more on their vision. Another interesting difference between the strepsirrhines and haplorhines is that strepsirrhines have the enzymes for making vitamin C, while haplorhines have to get it from their food.

Figure 29.42 A Philippine tarsier. This tarsier, *Carlito syrichta*, is one of the smallest primates—about 5 inches long, from nose to the base of the tail. The tail is not shown, but is about twice the length of the body. Note the large eyes, each of which is about the same size as the animal's brain, and the long hind legs. (credit: mtoz (http://creativecommons.org/licenses/by-sa/2.0 (http://openstax.org/l/CCSA_2)), via Wikimedia Commons)

Evolution of Primates

The first primate-like mammals are referred to as proto-primates. They were roughly similar to squirrels and tree shrews in size and appearance. The existing fossil evidence (mostly from North Africa) is very fragmented. These proto-primates remain largely mysterious creatures until more fossil evidence becomes available. Although genetic evidence suggests that primates diverged from other mammals about 85 MYA, the oldest known primate-like mammals with a relatively robust fossil record date to about 65 MYA. Fossils like the proto-primate *Plesiadapis* (although some researchers do not agree that *Plesiadapis* was a proto-primate) had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic and went extinct by the end of the Eocene.

The first true primates date to about 55 MYA in the Eocene epoch. They were found in North America, Europe, Asia, and Africa. These early primates resembled present-day prosimians such as lemurs. Evolutionary changes continued in these early primates, with larger brains and eyes, and smaller muzzles being the trend. By the end of the Eocene epoch, many of the early prosimian species went extinct due either to cooler temperatures or competition from the first monkeys.

Anthropoid monkeys evolved from prosimians during the Oligocene epoch. By 40 million years ago, evidence indicates that monkeys were present in the New World (South America) and the Old World (Africa and Asia). New World monkeys are also called Platyrrhini—a reference to their broad noses (Figure 29.43). Old World monkeys are called Catarrhini—a reference to their narrow, downward-pointed noses. There is still quite a bit of uncertainty about the origins of the New World monkeys. At the time the platyrrhines arose, the continents of South American and Africa had drifted apart. Therefore, it is thought that monkeys arose in the Old World and reached the New World either by drifting on log rafts or by crossing land bridges. Due to this reproductive isolation, New World monkeys and Old World monkeys underwent separate adaptive radiations over millions of years. The New World monkeys are all arboreal, whereas Old World monkeys include both arboreal and ground-dwelling species. The arboreal habits of the New World monkeys are reflected in the possession of prehensile or grasping tails by most species. The tails of Old World monkeys are never prehensile and are often reduced, and some species have ischial callosities—thickened patches of skin on their seats.

Figure 29.43 A New World monkey. The howler monkey is native to Central and South America. It makes a call that sounds like a lion roaring. (credit: Xavi Talleda)

Apes evolved from the catarrhines in Africa midway through the Cenozoic, approximately 25 million years ago. Apes are generally larger than monkeys and they do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. When walking quadrupedally, monkeys walk on their palms, while apes support the upper body on their knuckles. Apes are more intelligent than monkeys, and they have larger brains relative to body size. The apes are divided into two groups. The lesser apes comprise the family **Hylobatidae**, including gibbons and siamangs. The great apes include the genera ***Pan*** (chimpanzees and bonobos) ***Gorilla*** (gorillas), ***Pongo*** (orangutans), and ***Homo*** (humans) (Figure 29.44).

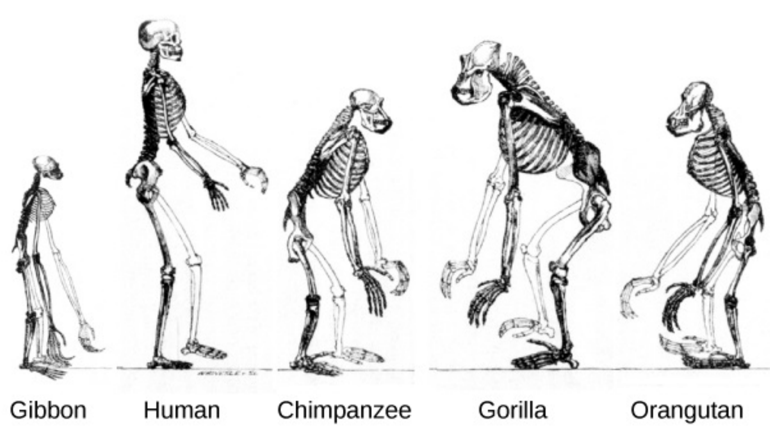

Figure 29.44 Primate skeletons. All great apes have a similar skeletal structure. (credit: modification of work by Tim Vickers)

The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the sexes are not markedly different in size), although in some species, the sexes differ in color; and they have relatively longer arms used for swinging through trees (Figure 29.45a). Two species of orangutan are native to different islands in Indonesia: Borneo (*P. pygmaeus*) and Sumatra (*P. abelii*). A third orangutan species, *Pongo tapanuliensis*, was reported in 2017 from the Batang Toru forest in Sumatra. Orangutans are arboreal and solitary. Males are much larger than females and have cheek and throat pouches when mature. Gorillas all live in Central Africa. The eastern and western populations are recognized as separate species, *G. berengei* and *G. gorilla*. Gorillas are strongly sexually dimorphic, with males about twice the size of females. In older males, called silverbacks, the hair on the back turns white or gray. Chimpanzees (Figure 29.45b) are the species considered to be most closely related to humans. However, the species most closely related to the chimpanzee is the bonobo. Genetic evidence suggests that chimpanzee and human lineages separated 5 to 7 MYA, while chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) lineages separated about 2 MYA. Chimpanzees and bonobos both live in Central Africa, but the two species are separated by the Congo River, a significant geographic barrier. Bonobos are slighter than chimpanzees, but have longer legs and more hair on their heads. In chimpanzees, white tail tufts identify juveniles, while bonobos keep their white tail tufts for life. Bonobos also have higher-pitched voices than chimpanzees. Chimpanzees are more aggressive and sometimes kill animals from other groups, while bonobos are not known to do so. Both chimpanzees and bonobos are omnivorous. Orangutan and gorilla diets also include foods from multiple sources, although the predominant food items are fruits for orangutans and foliage for gorillas.

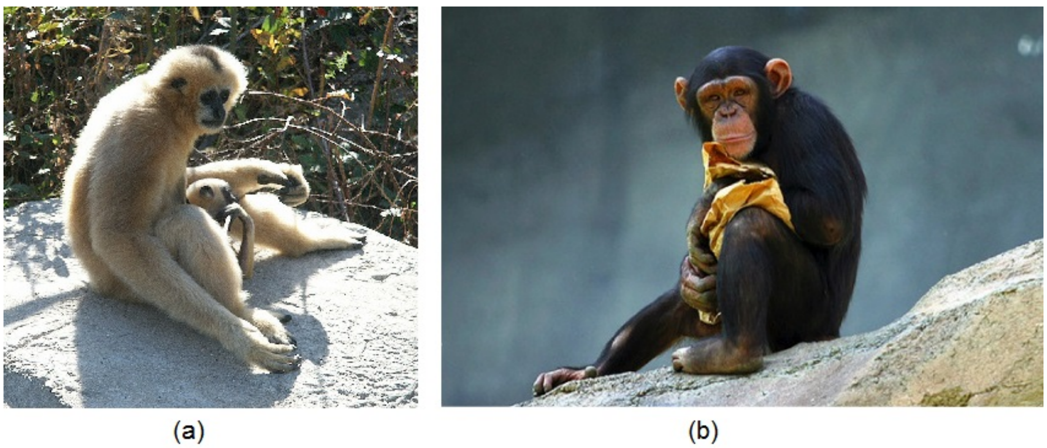

Figure 29.45 Lesser and great apes. This white-cheeked gibbon (a) is a lesser ape. In gibbons of this species, females and infants are buff and males are black. This young chimpanzee (b) is one of the great apes. It possesses a relatively large brain and has no tail. (credit a: MAC. credit b: modification of work by Aaron Logan)

Human Evolution

The family Hominidae of order Primates includes the hominoids: the great apes and humans (Figure 29.46). Evidence from the fossil record and from a comparison of human and chimpanzee DNA suggests that humans and chimpanzees diverged from a common hominoid ancestor approximately six million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term hominin is used to refer to those species that evolved after this split of the primate line, thereby designating species that are more closely related to humans than to chimpanzees. A number of marker features differentiate humans from the other hominoids, including bipedalism or upright posture, increase in the size of the brain, and a fully opposable thumb that can touch the little finger. Bipedal hominins include several groups that were probably part of the modern human lineage—*Australopithecus*, *Homo habilis*, and *Homo erectus*—and several non-ancestral groups that can be considered "cousins" of modern humans, such as Neanderthals and Denisovans.

Determining the true lines of descent in hominins is difficult. In years past, when relatively few hominin fossils had been recovered, some scientists believed that considering them in order, from oldest to youngest, would demonstrate the course of evolution from early hominins to modern humans. In the past several years, however, many new fossils have been found, and it is clear that there was often more than one species alive at any one time and that many of the fossils found (and species named) represent hominin species that died out and are not ancestral to modern humans.

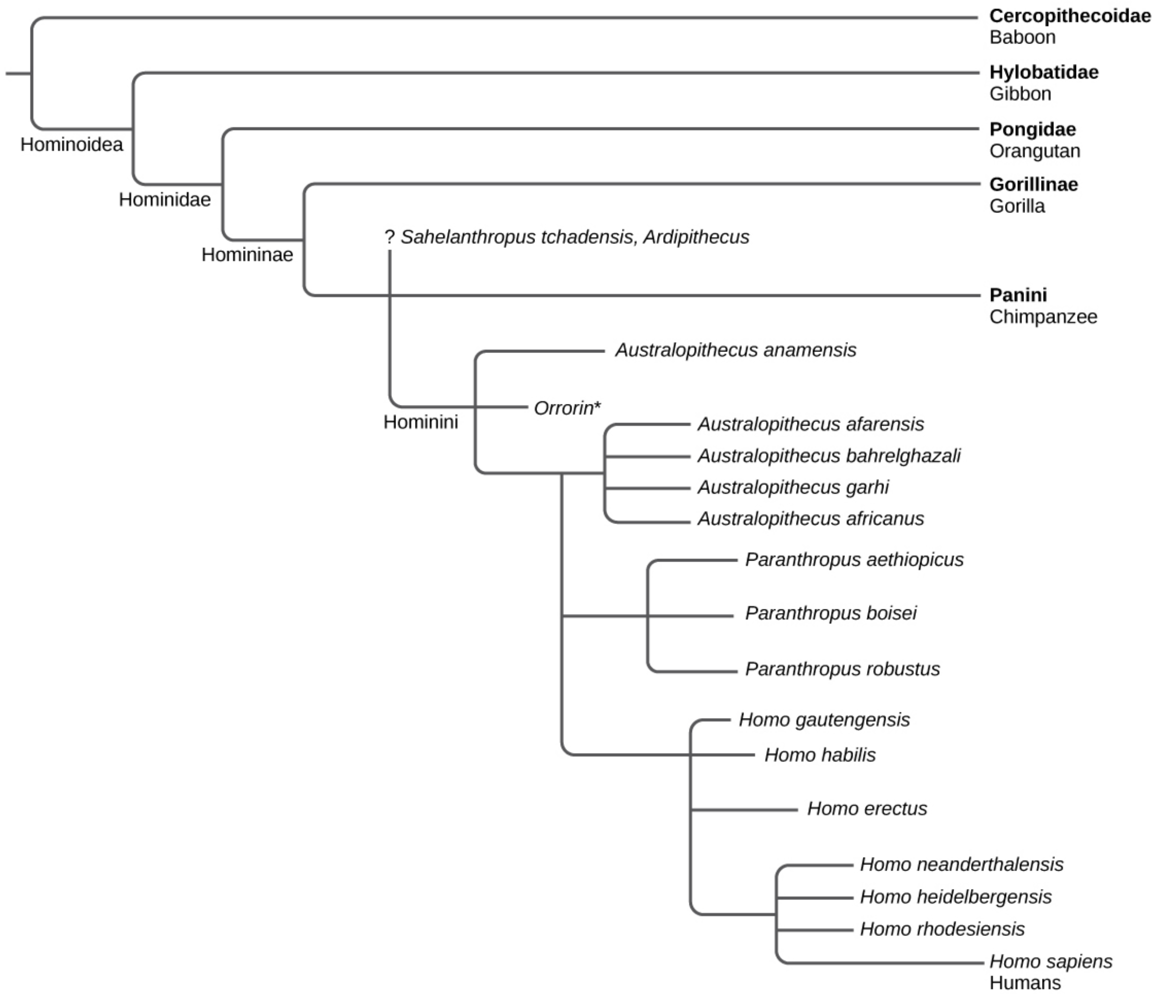

Figure 29.46 Hominin phylogeny. This chart shows evolutionary relationship among Hominins and hypothesized relation to modern humans. (*still debated phylogeny position).

Very Early Hominins

Three species of very early hominids have made news in the late 20th and early 21st centuries: *Ardipithecus*, *Sahelanthropus*, and *Orrorin*. The youngest of the three species, *Ardipithecus*, was discovered in the 1990s, and dates to about 4.4 MYA. Although the bipedality of the early specimens was uncertain, several more specimens of *Ardipithecus* were discovered in the intervening years and demonstrated that the organism was bipedal. Two different species of *Ardipithecus* have been identified, *A. ramidus* and *A. kadabba*, whose specimens are older, dating to 5.6 MYA. However, the status of this genus as a human ancestor is uncertain.

The oldest of the three, *Sahelanthropus tchadensis*, was discovered in 2001-2002 and has been dated to nearly seven million years ago. There is a single specimen of this genus, a skull that was a surface find in Chad. The fossil, informally called "Toumai," is a mosaic of primitive and evolved characteristics, and it is unclear how this fossil fits with the picture given by molecular data, namely that the line leading to modern humans and modern chimpanzees apparently bifurcated about six million years ago. It is not thought at this time that this species was an ancestor of modern humans.

A younger (c. 6 MYA) species, *Orrorin tugenensis*, is also a relatively recent discovery, found in 2000. There are several specimens of *Orrorin*. Some features of *Orrorin* are more similar to those of modern humans than are the australopithicenes, although *Orrorin* is much older. If *Orrorin* is a human ancestor, then the australopithicenes may not be in the direct human lineage. Additional specimens of these species may help to clarify their role.

Early Hominins: Genus *Australopithecus*

Australopithecus ("southern ape") is a genus of hominin that evolved in eastern Africa approximately four million years ago and went extinct about two million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from a common ancestor shared with *Australopithecus* about two million years ago (after likely passing through some transitional states). *Australopithecus* had a number of characteristics that were more similar to the great apes than to modern humans. For example, sexual dimorphism was more exaggerated than in modern humans. Males were up to 50 percent larger than females, a ratio that is similar to that seen in modern gorillas and orangutans. In contrast, modern human males are approximately 15 to 20 percent larger than females. The brain size of *Australopithecus* relative to its body mass was also smaller than in modern humans and more similar to that seen in the great apes. A key feature that *Australopithecus* had in common with modern humans was bipedalism, although it is likely that *Australopithecus* also spent time in trees. Hominin footprints, similar to those of modern humans, were found in Laetoli, Tanzania and dated to 3.6 million years ago. They showed that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, which are often referred to as *australopiths*. *Australopithecus anamensis* lived about 4.2 million years ago. More is known about another early species, *Australopithecus afarensis*, which lived between 3.9 and 2.9 million years ago. This species demonstrates a trend in human evolution: the reduction of the dentition and jaw in size. *A. afarensis* (Figure 29.47a) had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380 to 450 cubic centimeters, approximately the size of a modern chimpanzee brain. It also had prognathic jaws, which is a relatively longer jaw than that of modern humans. In the mid-1970s, the fossil of an adult female *A. afarensis* was found in the Afar region of Ethiopia and dated to 3.24 million years ago (Figure 29.48). The fossil, which is informally called “Lucy,” is significant because it was the most complete australopith fossil found, with 40 percent of the skeleton recovered.

(a) (b)

Figure 29.47 Australopithicene and modern human skulls. The skull of (a) *Australopithecus afarensis*, an early hominid that lived between two and three million years ago, resembled that of (b) modern humans but was smaller with a sloped forehead, larger teeth, and a prominent jaw.

Figure 29.48 Lucy. This adult female *Australopithecus afarensis* skeleton, nicknamed Lucy, was discovered in the mid-1970s. (credit: "120"/Wikimedia Commons)

Australopithecus africanus lived between two and three million years ago. It had a slender build and was bipedal, but had robust arm bones and, like other early hominids, may have spent significant time in trees. Its brain was larger than that of *A. afarensis* at 500 cubic centimeters, which is slightly less than one-third the size of modern human brains. Two other species, *Australopithecus bahrelghazali* and *Australopithecus garhi*, have been added to the roster of australopiths in recent years. A. *bahrelghazali* is unusual in being the only australopith found in Central Africa.

A Dead End: Genus *Paranthropus*

The australopiths had a relatively slender build and teeth that were suited for soft food. In the past several years, fossils of hominids of a different body type have been found and dated to approximately 2.5 million years ago. These hominids, of the genus *Paranthropus*, were muscular, stood 1.3 to 1.4 meters tall, and had large grinding teeth. Their molars showed heavy wear, suggesting that they had a coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the australopiths. *Paranthropus* includes *Paranthropus robustus* of South Africa, and *Paranthropus aethiopicus* and *Paranthropus boisei* of East Africa. The hominids in this genus went extinct more than one million years ago and are not thought to be ancestral to modern humans, but rather members of an evolutionary branch on the hominin tree that left no descendants.

Early Hominins: Genus *Homo*

The human genus, *Homo*, first appeared between 2.5 and three million years ago. For many years, fossils of a species called *H. habilis* were the oldest examples in the genus *Homo*, but in 2010, a new species called *Homo gautengensis* was discovered and may be older. Compared to *A. africanus*, *H. habilis* had a number of features more similar to modern humans. *H. habilis* had a jaw that was less prognathic than the australopiths and a larger brain, at 600 to 750 cubic centimeters. However, *H. habilis* retained some features of older hominin species, such as long arms. The name *H. habilis* means "handy man," which is a reference to the stone tools that have been found with its remains.

LINK TO LEARNING

Watch this video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.

[Click to view content (https://www.openstax.org/l/diet_detective)](https://www.openstax.org/l/diet_detective)

H. erectus appeared approximately 1.8 million years ago (Figure 29.49). It is believed to have originated in East Africa and was the first hominin species to migrate out of Africa. Fossils of *H. erectus* have been found in India, China, Java, and Europe, and were known in the past as "Java Man" or "Peking Man." *H. erectus* had a number of features that were more similar to modern humans than those of *H. habilis*. *H. erectus* was larger in size than earlier hominins, reaching heights up to 1.85 meters and weighing up to 65 kilograms, which are sizes similar to those of modern humans. Its degree of sexual dimorphism was less than in earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our own species. *H. erectus* had a larger brain than earlier species at 775 to 1,100 cubic centimeters, which compares to the 1,130 to 1,260 cubic centimeters seen in modern human brains. *H. erectus* also had a nose with downward-facing nostrils similar to modern humans, rather than the forward-facing nostrils found in other primates. Longer, downward-facing nostrils allow for the warming of cold air before it enters the lungs and may have been an adaptation to colder climates. Artifacts found with fossils of *H. erectus* suggest that it was the first hominin to use fire, hunt, and have a home base. *H. erectus* is generally thought to have lived until about 50,000 years ago.

Figure 29.49 *Homo erectus. Homo erectus* had a prominent brow and a nose that pointed downward rather than forward.

Humans: *Homo sapiens*

A number of species, sometimes called archaic *Homo sapiens*, apparently evolved from *H. erectus* starting about 500,000 years ago. These species include *Homo heidelbergensis*, *Homo rhodesiensis*, and *Homo neanderthalensis*. These archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200 to 1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these species survived until 30,000 to 10,000 years ago, overlapping with modern humans (Figure 29.50).

Figure 29.50 Neanderthal. The *Homo neanderthalensis* used tools and may have worn clothing.

There is considerable debate about the origins of anatomically modern humans or ***Homo sapiens sapiens***. As discussed earlier, *H. erectus* migrated out of Africa and into Asia and Europe in the first major wave of migration about 1.5 million years ago. It is thought that modern humans arose in Africa from *H. erectus* and migrated out of Africa about 100,000 years ago in a second major migration wave. Then, modern humans replaced *H. erectus* species that had migrated into Asia and Europe in the first wave.

This evolutionary timeline is supported by molecular evidence. One approach to studying the origins of modern humans is to examine mitochondrial DNA (mtDNA) from populations around the world. Because a fetus develops from an egg containing its mother's mitochondria (which have their own, non-nuclear DNA), mtDNA is passed entirely through the maternal line. Mutations in mtDNA can now be used to estimate the timeline of genetic divergence. The resulting evidence suggests that all modern humans have mtDNA inherited from a common ancestor that lived in Africa about 160,000 years ago. Another approach to the molecular understanding of human evolution is to examine the Y chromosome, which is passed from father to son. This evidence suggests that all men today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.

The study of mitochondrial DNA led to the identification of another human species or subspecies, the Denisovans. DNA from teeth and finger bones suggested two things. First, the mitochondrial DNA was different from that of both modern humans and Neanderthals. Second, the genomic DNA suggested that the Denisovans shared a common ancestor with the Neanderthals. Genes from both Neanderthals and Denisovans have been identified in modern human populations, indicating that interbreeding among the three groups occurred over part of their range.

KEY TERMS

Acanthostega one of the earliest known tetrapods

Actinopterygii ray-finned fishes

allantois membrane of the egg that stores nitrogenous wastes produced by the embryo; also facilitates respiration

amnion membrane of the egg that protects the embryo from mechanical shock and prevents dehydration

amniote animal that produces a terrestrially adapted egg protected by amniotic membranes

Amphibia frogs, salamanders, and caecilians

ampulla of Lorenzini sensory organ that allows sharks to detect electromagnetic fields produced by living things

anapsid animal having no temporal fenestrae in the cranium

anthropoid monkeys, apes, and humans

Anura frogs

apocrine gland scent gland that secretes substances that are used for chemical communication

Apoda caecilians

Archaeopteryx transition species from dinosaur to bird from the Jurassic period

archosaur modern crocodilian or bird, or an extinct pterosaur or dinosaur

Australopithecus genus of hominins that evolved in eastern Africa approximately four million years ago

brachiation movement through trees branches via suspension from the arms

brumation period of much reduced metabolism and torpor that occurs in any ectotherm in cold weather

caecilian legless amphibian that belongs to the clade Apoda

Casineria one of the oldest known amniotes; had both amphibian and reptilian characteristics

Catarrhini clade of Old World monkeys

Cephalochordata chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chondrichthyes jawed fish with paired fins and a skeleton made of cartilage

Chordata phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

chorion membrane of the egg that surrounds the embryo and yolk sac

contour feather feather that creates an aerodynamic surface for efficient flight

Craniata clade composed of chordates that possess a cranium; includes Vertebrata together with hagfishes

cranium bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones

Crocodilia crocodiles and alligators

cutaneous respiration gas exchange through the skin

dentary single bone that comprises the lower jaw of mammals

diapsid animal having two temporal fenestrae in the cranium

diphyodont refers to the possession of two sets of teeth in a lifetime

dorsal hollow nerve cord hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

down feather feather specialized for insulation

eccrine gland sweat gland

Enantiornithes dominant bird group during the Cretaceous period

eutherian mammal mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

flight feather feather specialized for flight

frog tail-less amphibian that belongs to the clade Anura

furcula wishbone formed by the fusing of the clavicles

gnathostome jawed fish

Gorilla genus of gorillas

hagfish eel-like jawless fish that live on the ocean floor and are scavengers

heterodont tooth different types of teeth that are modified for different purposes

hominin species that are more closely related to humans than chimpanzees

hominoid pertaining to great apes and humans

Homo genus of humans

Homo sapiens sapiens anatomically modern humans

Hylobatidae family of gibbons

Hylonomus one of the earliest reptiles

lamprey jawless fish characterized by a toothed, funnel-like, sucking mouth

lancelet member of Cephalochordata; named for its blade-like shape

lateral line sense organ that runs the length of a fish's body; used to detect vibration in the water

lepidosaur modern lizards, snakes, and tuataras

mammal one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland in female mammals, a gland that produces milk for newborns

marsupial one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme egg-laying mammal

Myxini hagfishes

Neognathae birds other than the Paleognathae

Neornithes modern birds

notochord flexible, rod-shaped support structure that is found in the embryonic stage of all chordates and in the

adult stage of some chordates
Ornithorhynchidae clade that includes the duck-billed platypus
Osteichthyes bony fish
ostracoderm one of the earliest jawless fish covered in bone
Paleognathae ratites; flightless birds, including ostriches and emus
Pan genus of chimpanzees and bonobos
Petromyzontidae clade of lampreys
pharyngeal slit opening in the pharynx
Platyrrhini clade of New World monkeys
Plesiadapis oldest known primate-like mammal
pneumatic bone air-filled bone
Pongo genus of orangutans
post-anal tail muscular, posterior elongation of the body extending beyond the anus in chordates
primary feather feather located at the tip of the wing that provides thrust
Primates order of lemurs, tarsiers, monkeys, apes, and humans
prognathic jaw long jaw
prosimian division of primates that includes bush babies and pottos of Africa, lemurs of Madagascar, and lorises of Southeast Asia
salamander tailed amphibian that belongs to the clade Urodela
Sarcopterygii lobe-finned fish
sauropsid reptile or bird
sebaceous gland in mammals, a skin gland that produce a lipid mixture called *sebum*
secondary feather feather located at the base of the wing that provides lift
Sphenodontia clade of tuataras
Squamata clade of lizards and snakes
stereoscopic vision two overlapping fields of vision from the eyes that produces depth perception
swim bladder in fishes, a gas filled organ that helps to control the buoyancy of the fish
synapsid mammal having one temporal fenestra
Tachyglossidae clade that includes the echidna or spiny anteater
tadpole larval stage of a frog
temporal fenestra non-orbital opening in the skull that may allow muscles to expand and lengthen
Testudines order of turtles
tetrapod phylogenetic reference to an organism with a four-footed evolutionary history; includes amphibians, reptiles, birds, and mammals
theropod dinosaur group ancestral to birds
tunicate sessile chordate that is a member of Urochordata
Urochordata clade composed of tunicates
Urodela salamanders
vertebral column series of separate bones joined together as a backbone
Vertebrata members of the phylum Chordata that possess a backbone

CHAPTER SUMMARY

29.1 Chordates

The five characteristic features of chordates present during some time of their life cycles are a notochord, a dorsal hollow tubular nerve cord, pharyngeal slits, endostyle/thyroid gland, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in the Vertebrata/Craniata. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Most tunicates live on the ocean floor and are suspension feeders. Which of the two invertebrate chordate clades is more closely related to the vertebrates continues to be debated. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade. The name Craniata (organisms with a cranium) is considered to be synonymous with Vertebrata.

29.2 Fishes

The earliest vertebrates that diverged from the invertebrate chordates were the agnathan jawless fishes, whose extant members include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic or predaceous on other fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources.

Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods (amphibians, reptiles, mammals). Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes (Osteichthyes) can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species, but form the sister group of the tetrapods).

29.3 Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration, although lungs are found in the adults of many species.

All amphibians are carnivores and possess many small teeth. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Living Amphibia can be divided into three classes: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). In the majority of amphibians, development occurs in two distinct stages: a gilled aquatic larval stage that metamorphoses into an adult stage, acquiring lungs and legs, and losing the tail in Anurans. A few species in all three clades bypass a free-living larval stage. Various levels of parental care are seen in the amphibians.

29.4 Reptiles

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by four extra-embryonic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids and diapsids (crocodiles, dinosaurs, birds, and modern reptiles).

Reptiles are tetrapods that ancestrally had four limbs; however, a number of extant species have secondarily lost them or greatly reduced them over evolutionary time. For example, limbless reptiles (e.g., snakes) are classified as tetrapods, because they descended from ancestors with four limbs. One of the key adaptations that permitted reptiles to live on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades of nonavian organisms: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles). Currently, this classification is paraphyletic, leaving out the birds, which are now classified as avian reptiles in the class Reptilia.

29.5 Birds

Birds are the most speciose group of land vertebrates and display a number of adaptations related to their ability to fly, which were first present in their theropod (maniraptoran) ancestors. Birds are endothermic (and homeothermic), meaning they have a very high metabolism that produces a considerable amount of heat, as well as structures such as feathers that allow them to retain their own body heat. These adaptations are used to regulate their internal temperature, making it largely independent of ambient thermal conditions.

Birds have feathers, which allow for insulation and flight, as well as for mating and warning signals. Flight feathers have a broad and continuously curved vane that produces lift. Some birds have pneumatic bones containing air spaces that are sometimes connected to air sacs in the body cavity. Airflow through bird lungs travels in one direction, creating a counter-current gas exchange with the blood.

Birds are highly modified diapsids and belong to a group called the archosaurs. Within the archosaurs, birds are most likely evolved from theropod (maniraptoran) dinosaurs. One of the oldest known fossils (and best known) of a “dinosaur-bird” is that of *Archaeopteryx*, which is dated from the Jurassic period. Modern birds are now classified into three groups: Paleognathae, Galloanserae, and Neoaves.

29.6 Mammals

Mammals are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands.

Mammals are synapsids, meaning that they have a single opening in the skull behind the eye. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. A key characteristic of synapsids is endothermy, and most mammals are homeothermic.

There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Marsupials give birth to very immature young, which typically complete their development in a pouch. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. All mammals nourish their young with milk, which is derived from modified sweat or sebaceous glands.

29.7 The Evolution of Primates

All primate species possess adaptations for climbing trees and probably descended from arboreal ancestors, although not all living species are arboreal. Other characteristics of primates are brains that are larger, relative to body size, than those of other mammals, claws that have been modified into flattened nails, typically only one young per pregnancy, stereoscopic vision, and a trend toward holding the body upright. Primates are divided into two groups: strepsirrhines, which include most prosimians, and haplorhines, which include simians. Monkeys evolved from prosimians during the Oligocene epoch. The simian line includes both platyrrhine and catarrhine branches. Apes evolved from catarrhines in Africa during the Miocene epoch. Apes are divided into the lesser apes and the greater apes. Hominins include those groups that gave rise to our own species, such as *Australopithecus* and *H. erectus*, and those groups that can be considered "cousins" of humans, such as Neanderthals and Denisovans. Fossil evidence shows that hominins at the time of *Australopithecus* were walking upright, the first evidence of bipedal hominins. A number of species, sometimes called archaic *H. sapiens*, evolved from *H. erectus* approximately 500,000 years ago. There is considerable debate about the origins of anatomically modern humans or *H. sapiens sapiens*, and the discussion will continue, as new evidence from fossil finds and genetic analysis emerges.

VISUAL CONNECTION QUESTIONS

1. Figure 29.3 Which of the following statements about common features of chordates is true?
   a. The dorsal hollow nerve cord is part of the chordate central nervous system.
   b. In vertebrate fishes, the pharyngeal slits become the gills.
   c. Humans are not chordates because humans do not have a tail.
   d. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

2. Figure 29.22 Which of the following statements about the parts of an amniotic egg are false?
   a. The allantois stores nitrogenous waste and facilitates respiration.
   b. The chorion facilitates gas exchange.
   c. The yolk provides food for the growing embryo.
   d. The amniotic cavity is filled with albumen.

3. Figure 29.24 Members of the order Testudines have an anapsid-like skull without obvious temporal fenestrae. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

REVIEW QUESTIONS

4. Which of the following is *not* contained in phylum Chordata?
   a. Cephalochordata
   b. Echinodermata
   c. Urochordata
   d. Vertebrata

5. Which group of invertebrates is most closely related to vertebrates?
   a. cephalochordates
   b. echinoderms
   c. arthropods
   d. urochordates

6. Hagfish, lampreys, sharks, and tuna are all chordates that can also be classified into which group?
   a. Craniates
   b. Vertebrates
   c. Cartilaginous fish
   d. Cephalocordata

7. Members of Chondrichthyes differ from members of Osteichthyes by having (a) ________.
   a. jaw
   b. bony skeleton
   c. cartilaginous skeleton
   d. two sets of paired fins

8. Members of Chondrichthyes are thought to be descended from fishes that had ________.
   a. a cartilaginous skeleton
   b. a bony skeleton
   c. mucus glands
   d. slime glands

9. A marine biologist catches a species of fish she has never seen before. Upon examination, she determines that the species has a predominantly cartilaginous skeleton and a swim bladder. If its pectoral fins are not fused with its head, to which category of fish does the specimen belong?
   a. Rays
   b. Osteichthyes
   c. Sharks
   d. Hagfish

10. Which of the following is *not* true of *Acanthostega*?
    a. It was aquatic.
    b. It had gills.
    c. It had four limbs.
    d. It laid shelled eggs.

11. Frogs belong to which order?
    a. Anura
    b. Urodela
    c. Caudata
    d. Apoda

12. During the Mesozoic period, diapsids diverged into_______.
    a. pterosaurs and dinosaurs
    b. mammals and reptiles
    c. lepidosaurs and archosaurs
    d. Testudines and Sphenodontia
13. Squamata includes_______.
    a. crocodiles and alligators
    b. turtles
    c. tuataras
    d. lizards and snakes
14. Which of the following reptile groups gave rise to modern birds?
    a. Lepidosaurs
    b. Pterosaurs
    c. Anapsids
    d. Archosaurs
15. A bird or feathered dinosaur is ________.
    a. Neornithes
    b. *Archaeopteryx*
    c. Enantiornithes
    d. Paleognathae
16. Which of the following feather types helps to reduce drag produced by wind resistance during flight?
    a. Flight feathers
    b. Primary feathers
    c. Secondary feathers
    d. Contour feathers
17. Eccrine glands produce ________.
    a. sweat
    b. lipids
    c. scents
    d. milk
18. Monotremes include:
    a. kangaroos.
    b. koalas.
    c. bandicoots.
    d. platypuses.
19. The evolution of which of the following features of mammals is hardest to trace through the fossil record?
    a. Jaw structure
    b. Mammary glands
    c. Middle ear structure
    d. Development of hair
20. Which of the following is *not* an anthropoid?
    a. Lemurs
    b. Monkeys
    c. Apes
    d. Humans
21. Which of the following is part of a clade believed to have died out, leaving no descendants?
    a. *Paranthropus robustus*
    b. *Australopithecus africanus*
    c. *Homo erectus*
    d. *Homo sapiens sapiens*
22. Which of the following human traits is not a shared characteristic of primates?
    a. Hip structure supporting bipedalism
    b. Detection and processing of three-color vision
    c. Nails at the end of each digit
    d. Enlarged brain area associated with vision, and reduced area associated with smell

CRITICAL THINKING QUESTIONS

23. What are the characteristic features of the chordates?
24. What is the structural advantage of the notochord in the human embryo? Be sure to compare the notochord with the corresponding structure in adults.
25. What can be inferred about the evolution of the cranium and vertebral column from examining hagfishes and lampreys?
26. Why did gnathostomes replace most agnathans?
27. Explain why frogs are restricted to a moist environment.
28. Describe the differences between the larval and adult stages of frogs.
29. Describe how metamorphosis changes the structures involved in gas exchange over the life cycle of animals in the clade Anura, and what evolutionary advantage this change provides.
30. Describe the functions of the three extra-embryonic membranes present in amniotic eggs.
31. What characteristics differentiate lizards and snakes?
32. Based on how reptiles thermoregulate, which climates would you predict to have the highest reptile population density, and why?
33. Explain why birds are thought to have evolved from theropod dinosaurs.

34. Describe three skeletal adaptations that allow for flight in birds.

35. How would the chest structure differ between ostriches, penguins, and terns?

36. Describe three unique features of the mammalian skeletal system.

37. Describe three characteristics of the mammalian brain that differ from other vertebrates.

38. How did the evolution of jaw musculature allow mammals to spread?

39. How did archaic *Homo sapiens* differ from anatomically modern humans?

40. Why is it so difficult to determine the sequence of hominin ancestors that have led to modern *Homo sapiens*?