

23

How Humans Evolved

Concept Outline

23.1 The evolutionary path to humans starts with the advent of primates.

The Evolutionary Path to Apes. Primates first evolved 65 million years ago, giving rise first to prosimians and then to monkeys.

How the Apes Evolved. Apes, including our closest relatives, the chimpanzees, arose from an ancestor common to Old World monkeys.

23.2 The first hominids to evolve were australopithecines.

An Evolutionary Tree with Many Branches. The first hominids were australopithecines, of which there were several different kinds.

The Beginning of Hominid Evolution. The ability to walk upright on two legs marks the beginning of hominid evolution. One can draw the hominid family tree in two very different ways, either lumping variants together or splitting them into separate species.

23.3 The genus *Homo* evolved in Africa.

African Origin: Early *Homo*. There may have been several species of early *Homo*, with brains significantly larger than those of australopithecines.

Out of Africa: *Homo erectus*. The first hominid species to leave Africa was the relatively large-brained *H. erectus*, the longest lived species of *Homo*.

23.4 Modern humans evolved quite recently.

The Last Stage of Hominid Evolution. Modern humans evolved within the last 600,000 years, our own species within the last 200,000 years.

Our Own Species: *Homo sapiens*. Our species appears to have evolved in Africa, and then migrated to Europe and Asia.

Human Races. Our species is unique in evolving culturally. Differences in populations in skin color reflect adaptation to different environments, rather than genetic differentiation among populations.



FIGURE 23.1

The trail of our ancestors. These fossil footprints, made in Africa 3.7 million years ago, look as if they might have been left by a mother and child walking on the beach. But these tracks, preserved in volcanic ash, are not human. They record the passage of two individuals of the genus *Australopithecus*, the group from which our genus, *Homo*, evolved.

In 1871 Charles Darwin published another groundbreaking book, *The Descent of Man*. In this book, he suggested that humans evolved from the same African ape ancestors that gave rise to the gorilla and the chimpanzee. Although little fossil evidence existed at that time to support Darwin's case, numerous fossil discoveries made since then strongly support his hypothesis (figure 23.1). Human evolution is the part of the evolution story that often interests people most, and it is also the part about which we know the most. In this chapter we follow the evolutionary journey that has led to humans, telling the story chronologically. It is an exciting story, replete with controversy.

23.1 The evolutionary path to humans starts with the advent of primates.

The Evolutionary Path to Apes

The story of human evolution begins around 65 million years ago, with the explosive radiation of a group of small, arboreal mammals called the Archonta. These primarily insectivorous mammals had large eyes and were most likely nocturnal (active at night). Their radiation gave rise to different types of mammals, including bats, tree shrews, and primates, the order of mammals that contains humans.

The Earliest Primates

Primates are mammals with two distinct features that allowed them to succeed in the arboreal, insect-eating environment:

- 1. Grasping fingers and toes.** Unlike the clawed feet of tree shrews and squirrels, primates have grasping hands and feet that let them grip limbs, hang from branches, seize food, and, in some primates, use tools. The first digit in many primates is opposable and at least some, if not all, of the digits have nails.
- 2. Binocular vision.** Unlike the eyes of shrews and squirrels, which sit on each side of the head so that the two fields of vision do not overlap, the eyes of primates are shifted forward to the front of the face. This produces overlapping binocular vision that lets the brain judge distance precisely—important to an animal moving through the trees.

Other mammals have binocular vision, but only primates have both binocular vision and grasping hands, making them particularly well adapted to their environment. While early primates were mostly insectivorous, their dentition began to change from the shearing, triangular-shaped molars specialized for insect eating to the more flattened, square-shaped molars and rodentlike incisors specialized for plant eating. Primates that evolved later also show a continuous reduction in snout length and number of teeth.

The Evolution of Prosimians

About 40 million years ago, the earliest primates split into two groups: the prosimians and the anthropoids. The prosimians (“before monkeys”) looked something like a cross between a squirrel and a cat and were common in North America, Europe, Asia, and Africa. Only a few prosimians survive today, lemurs, lorises and tarsiers (figure 23.2). In addition to having grasping digits and binocular vision, prosimians have large eyes with increased visual acuity. Most prosimians are nocturnal, feeding on fruits, leaves, and flowers, and many lemurs have long tails for balancing.



FIGURE 23.2

A prosimian. This tarsier, a prosimian native to tropical Asia, shows the characteristic features of primates: grasping fingers and toes and binocular vision.

Origin of the Anthropoids

The anthropoids, or higher primates, include monkeys, apes, and humans (figure 23.3). Anthropoids are almost all diurnal—that is, active during the day—feeding mainly on fruits and leaves. Evolution favored many changes in eye design, including color vision, that were adaptations to daytime foraging. An expanded brain governs the improved senses, with the braincase forming a larger portion of the head. Anthropoids, like the relatively few diurnal prosimians, live in groups with complex social interactions. In addition, the anthropoids tend to care for their young for prolonged periods, allowing for a long childhood of learning and brain development.

The early anthropoids, now extinct, are thought to have evolved in Africa. Their direct descendants are a very successful group of primates, the monkeys.

New World Monkeys. About 30 million years ago, some anthropoids migrated to South America, where they evolved in isolation. Their descendants, known as the **New World monkeys**, are easy to identify: all are arboreal, they have flat spreading noses, and many of them grasp objects with long prehensile tails (figure 23.4a).

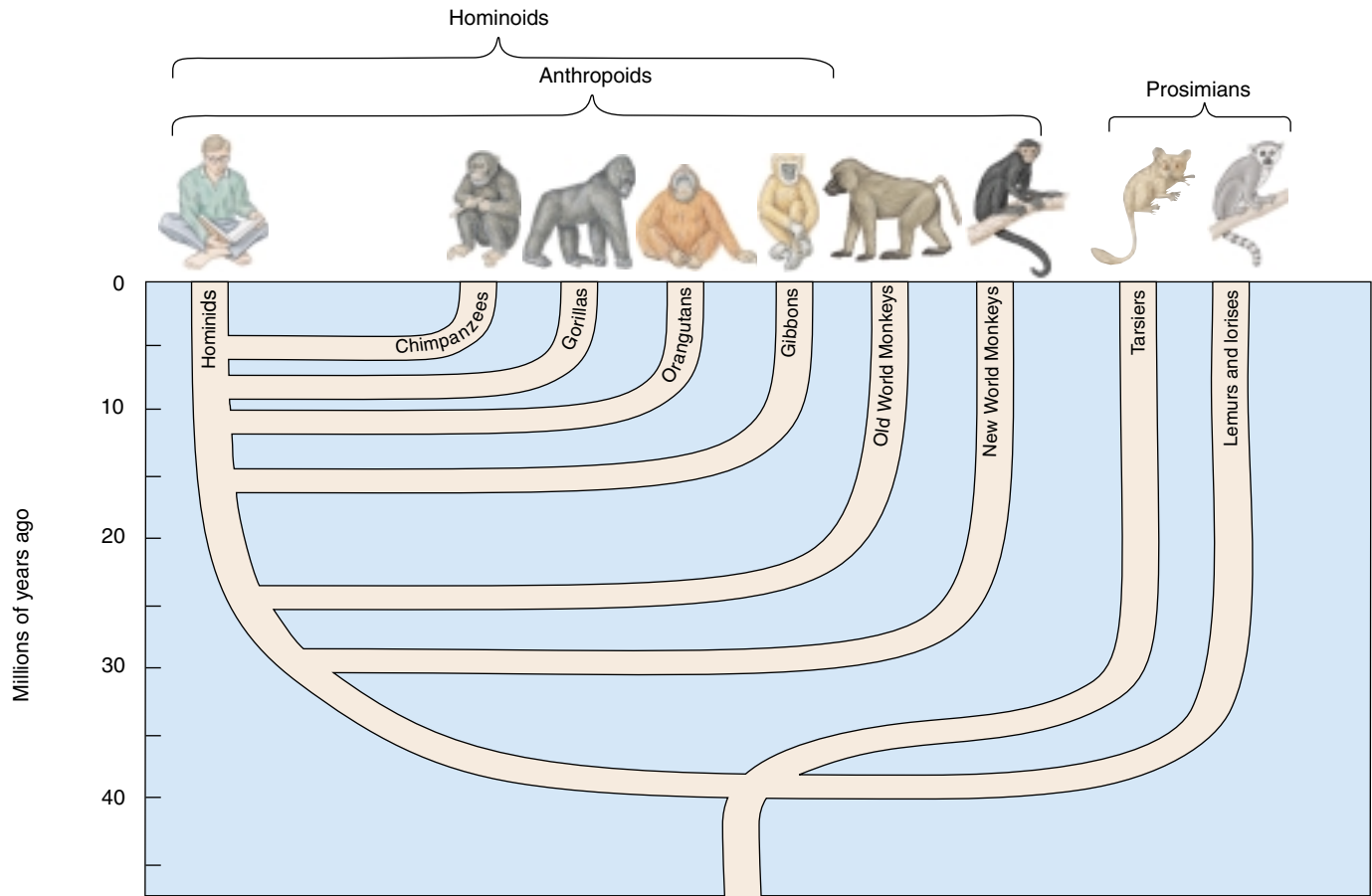


FIGURE 23.3
A primate evolutionary tree. The most ancient of the primates are the prosimians, while the hominids were the most recent to evolve.

Old World Monkeys. Around 25 million years ago, anthropoids that remained in Africa split into two lineages: one gave rise to the **Old World monkeys** and one gave rise to the hominoids (see page 480). Old World monkeys include ground-dwelling as well as arboreal species. None of the Old World monkeys have prehensile tails. Their nostrils are close together, their noses point downward, and some have toughened pads of skin for prolonged sitting (figure 23.4*b*).

The earliest primates arose from small, tree-dwelling, insect-eaters and gave rise to prosimians and then anthropoids. Early anthropoids gave rise to New World monkeys and Old World monkeys.



(a)



(b)

FIGURE 23.4
New and Old World monkeys. (a) New World monkeys, such as this golden lion tamarin, are arboreal, and many have prehensile tails. (b) Old World monkeys lack prehensile tails, and many are ground dwellers.

How the Apes Evolved

The other African anthropoid lineage is the **hominoids**, which includes the **apes** and the **hominids** (humans and their direct ancestors). The living apes consist of the gibbon (genus *Hylobates*), orangutan (*Pongo*), gorilla (*Gorilla*), and chimpanzee (*Pan*) (figure 23.5). Apes have larger brains than monkeys, and they lack tails. With the exception of the gibbon, which is small, all living apes are larger than any monkey. Apes exhibit the most adaptable behavior of any mammal except human beings. Once widespread in Africa and Asia, apes are rare today, living in relatively small areas. No apes ever occurred in North or South America.

The First Hominoid

Considerable controversy exists about the identity of the first hominoid. During the 1980s it was commonly believed that the common ancestor of apes and hominids was a late Miocene ape living 5 to 10 million years ago. In 1932, a candidate fossil, an 8-million-year-old jaw with teeth, was unearthed in India. It was called *Ramapithecus* (after the Hindi deity Rama). However, these fossils have never been found in Africa, and more complete fossils discovered in 1981 made it clear that *Ramapithecus* is in fact closely related to the orangutan. Attention has now shifted to an earlier Miocene ape, *Proconsul*, which has many of the characteristics of Old World monkeys but lacks a tail and has apelike hands, feet, and pelvis. However, because very few fossils have been recovered from the period 5 to 10 million years ago, it is not yet possible to identify with certainty the first hominoid ancestor.



(a)



(b)



(c)



(d)

FIGURE 23.5

The living apes. (a) Mueller gibbon, *Hylobates muelleri*. (b) Orangutan, *Pongo pygmaeus*. (c) Gorilla, *Gorilla gorilla*. (d) Chimpanzee, *Pan troglodytes*.

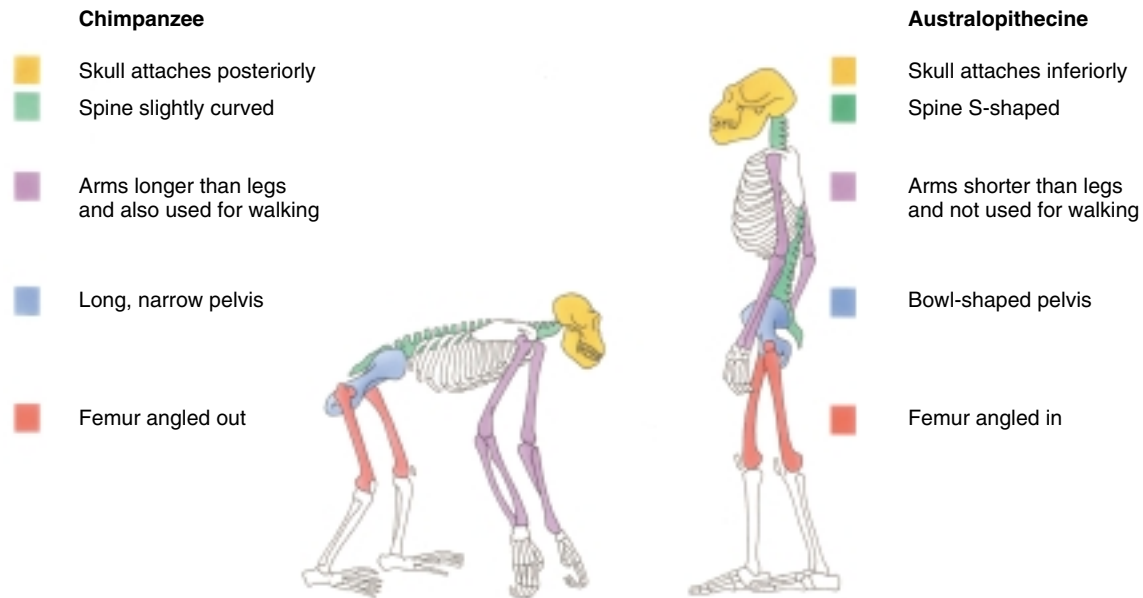


FIGURE 23.6

A comparison of ape and hominid skeletons. Early humans, such as australopithecines, were able to walk upright because their arms were shorter, their spinal cord exited from the bottom of the skull, their pelvis was bowl-shaped and centered the body weight over the legs, and their femurs angled inward, directly below the body, to carry its weight.

Which Ape Is Our Closest Relative?

Studies of ape DNA have explained a great deal about how the living apes evolved. The Asian apes evolved first. The line of apes leading to gibbons diverged from other apes about 15 million years ago, while orangutans split off about 10 million years ago (see figure 23.3). Neither are closely related to humans.

The African apes evolved more recently, between 6 and 10 million years ago. These apes are the closest living relatives to humans; some taxonomists have even advocated placing humans and the African apes in the same zoological family, the Hominidae. Fossils of the earliest hominids, described later in the chapter, suggest that the common ancestor of the hominids was more like a chimpanzee than a gorilla. Based on genetic differences, scientists estimate that gorillas diverged from the line leading to chimpanzees and humans some 8 million years ago.

Sometime after the gorilla lineage diverged, the common ancestor of all hominids split off from chimpanzee line to begin the evolutionary journey leading to humans. Because this split was so recent, the genes of humans and chimpanzees have not had time to evolve many genetic differences. For example, a human hemoglobin molecule differs from its chimpanzee counterpart in only a single amino acid. In general, humans and chimpanzees exhibit a level of genetic similarity normally found between closely related sibling species of the same genus!

Comparing Apes to Hominids

The common ancestor of apes and hominids is thought to have been an arboreal climber. Much of the subsequent evolution of the hominoids reflected different approaches to locomotion. Hominids became **bipedal**, walking upright, while the apes evolved knuckle-walking, supporting their weight on the back sides of their fingers (monkeys, by contrast, use the palms of their hands).

Humans depart from apes in several areas of anatomy related to bipedal locomotion (figure 23.6). Because humans walk on two legs, their vertebral column is more curved than an ape's, and the human spinal cord exits from the bottom rather than the back of the skull. The human pelvis has become broader and more bowl-shaped, with the bones curving forward to center the weight of the body over the legs. The hip, knee, and foot (in which the human big toe no longer splays sideways) have all changed proportions. Being bipedal, humans carry much of the body's weight on the lower limbs, which comprise 32 to 38% of the body's weight and are longer than the upper limbs; human upper limbs do not bear the body's weight and make up only 7 to 9% of human body weight. African apes walk on all fours, with the upper and lower limbs both bearing the body's weight; in gorillas, the longer upper limbs account for 14 to 16% of body weight, the somewhat shorter lower limbs for about 18%.

Hominoids, the apes and hominids, arose from Old World monkeys. Among living apes, chimpanzees seem the most closely related to humans.

23.2 The first hominids to evolve were australopithecines.

An Evolutionary Tree with Many Branches

Five to 10 million years ago, the world's climate began to get cooler, and the great forests of Africa were largely replaced with savannas and open woodland. In response to these changes, a new kind of hominoid was evolving, one that was bipedal. These new hominoids are classified as hominids—that is, of the human line.

There are two major groups of hominids: three to seven species of the genus *Homo* (depending how you count them) and seven species of the older, smaller-brained genus *Australopithecus*. In every case where the fossils allow a determination to be made, the hominids are bipedal, walking upright. Bipedal locomotion is the hallmark of hominid evolution. We will first discuss *Australopithecus*, and then *Homo*.

Discovery of *Australopithecus*

The first hominid was discovered in 1924 by Raymond Dart, an anatomy professor at Johannesburg in South Africa. One day, a mine worker brought him an unusual chunk of rock—actually, a rock-hard mixture of sand and soil. Picking away at it, Professor Dart uncovered a skull unlike that of any ape he had ever seen. Beautifully pre-

served, the skull was of a five-year-old individual, still with its milk teeth. While the skull had many apelike features such as a projecting face and a small brain, it had distinctly human features as well—for example, a rounded jaw unlike the pointed jaw of apes. The ventral position of the foramen magnum (the hole at the base of the skull from which the spinal cord emerges) suggested that the creature had walked upright. Dart concluded it was a human ancestor.

What riveted Dart's attention was that the rock in which the skull was embedded had been collected near other fossils that suggested that the rocks and their fossils were several million years old! At that time, the oldest reported fossils of hominids were less than 500,000 years old, so the antiquity of this skull was unexpected and exciting. Scientists now estimate Dart's skull to be 2.8 million years old. Dart called his find *Australopithecus africanus* (from the Latin *australo*, meaning “southern” and the Greek *pithecus*, meaning “ape”), the ape from the south of Africa.

Today, fossils are dated by the relatively new process of single-crystal laser-fusion dating. A laser beam melts a single potassium feldspar crystal, releasing argon gas, which is measured in a gas mass spectrometer. Because the argon in the crystal has accumulated at a known rate, the amount released reveals the age of the rock and thus of nearby fossils. The margin of error is less than 1%.



FIGURE 23.7

Nearly human. These four skulls, all photographed from the same angle, are among the best specimens available of the key *Australopithecus* species.

Other Kinds of *Australopithecus*

In 1938, a second, stockier kind of *Australopithecus* was unearthed in South Africa. Called *A. robustus*, it had massive teeth and jaws. In 1959, in East Africa, Mary Leakey discovered a third kind of *Australopithecus*—*A. boisei* (after Charles Boise, an American-born businessman who contributed to the Leakeys' projects)—who was even more stockily built. Like the other australopithecines, *A. boisei* was very old—almost 2 million years. Nicknamed “Nutcracker man,” *A. boisei* had a great bony ridge—a Mohawk haircut of bone—on the crest of the head to anchor its immense jaw muscles (figure 23.7).

In 1974, anthropologist Don Johanson went to the remote Afar Desert of Ethiopia in search of early human fossils and hit the jackpot. He found the most complete, best preserved australopithecine skeleton known. Nicknamed “Lucy,” the skeleton was 40% complete and over 3 million years old. The skeleton and other similar fossils have been assigned the scientific name *Australopithecus afarensis* (from the Afar Desert). The shape of the pelvis indicated that Lucy was a female, and her leg bones proved she walked upright. Her teeth were distinctly hominid, but her head was shaped like an ape's, and her brain was no larger than that of a chimpanzee, about 400 cubic centimeters, about the size of a large orange. More than 300 specimens of *A. afarensis* have since been discovered.

In the last 10 years, three additional kinds of australopithecines have been reported. These seven species provide ample evidence that australopithecines were a diverse group, and additional species will undoubtedly be described by future investigators. The evolution of hominids seems to have begun with an initial radiation of numerous species.

Early Australopithecines Were Bipedal

We now know australopithecines from hundreds of fossils. The structure of these fossils clearly indicates that australopithecines walked upright. These early hominids weighed about 18 kilograms and were about 1 meter tall. Their dentition was distinctly hominid, but their brains were not any larger than those of apes, generally 500 cc or less. *Homo* brains, by comparison, are usually larger than 600 cc; *modern H. sapiens* brains average 1350 cc. Australopithecine fossils have been found only in Africa. Although all the fossils to date come from sites in South and East Africa (except for one specimen from Chad), it is probable that they lived over a much broader area of Africa. Only in South and East Africa, however, are sediments of the proper age exposed to fossil hunters.

The australopithecines were hominids that walked upright and lived in Africa over 3 million years ago.



FIGURE 23.7 (continued).

The Beginning of Hominid Evolution

The Origins of Bipedalism

For much of this century, biologists have debated the sequence of events that led to the evolution of hominids. A key element may have been bipedalism. Bipedalism seems to have evolved as our ancestors left dense forests for grasslands and open woodland (figure 23.8). One school of thought proposes that hominid brains enlarged first, and then hominids became bipedal. Another school sees bipedalism as a precursor to bigger brains. Those who favor the brain-first hypothesis speculate that human intelligence was necessary to make the decision to walk upright and move out of the forests and onto the grassland. Those who favor the bipedalism-first hypothesis argue that bipedalism freed the forelimbs to manufacture and use tools, favoring the subsequent evolution of bigger brains.

A treasure trove of fossils unearthed in Africa has settled the debate. These fossils demonstrate that bipedalism extended back 4 million years ago; knee joints, pelvis, and leg bones all exhibit the hallmarks of an upright stance. Substantial brain expansion, on the other hand, did not appear until roughly 2 million years ago. In hominid evolution, upright walking clearly preceded large brains.

Remarkable evidence that early hominids were bipedal is a set of some 69 hominid footprints found at Laetoli, East Africa. Two individuals, one larger than the other, walked upright side-by-side for 27 meters, their footprints preserved in 3.7-million-year-old volcanic ash (see figure 23.1). Importantly, the big toe is not splayed out to the side as in a monkey or ape—the footprints were clearly made by a hominid.

The evolution of bipedalism marks the beginning of the hominids. The reason why bipedalism evolved in hominids remains a matter of controversy. No tools appeared until 2.5 million years ago, so toolmaking seems an unlikely cause. Alternative ideas suggest that walking upright is faster and uses less energy than walking on four legs; that an upright posture permits hominids to pick fruit from trees and see over tall grass; that being upright reduces the body surface exposed to the sun's rays; that an upright stance aided the wading of aquatic hominids, and that bipedalism frees the forelimbs of males to carry food back to females, encouraging pair-bonding. All of these suggestions have their proponents, and none are universally accepted. The origin of bipedalism, the key event in the evolution of hominids, remains a mystery.

The Root of the Hominid Tree

The Oldest Known Hominid. In 1994, a remarkable, nearly complete fossil skeleton was unearthed in Ethiopia. The skeleton is still being painstakingly assembled, but it seems almost certainly to have been bipedal; the foramen magnum, for example, is situated far forward, as in other bipedal hominids. Some 4.4 million years old, it is the most ancient hominid yet discovered. It is significantly more apelike than any australopithecine and so has been assigned to a new genus, *Ardipithecus* from the local Afar language *ardi* for “ground” and the Greek *pithecus* for “ape” (figure 23.9a).

The First Australopithecine. In 1995, hominid fossils of nearly the same age, 4.2 million years old, were found in the Rift Valley in Kenya. The fossils are fragmentary, but they include complete upper and lower jaws, a piece of the

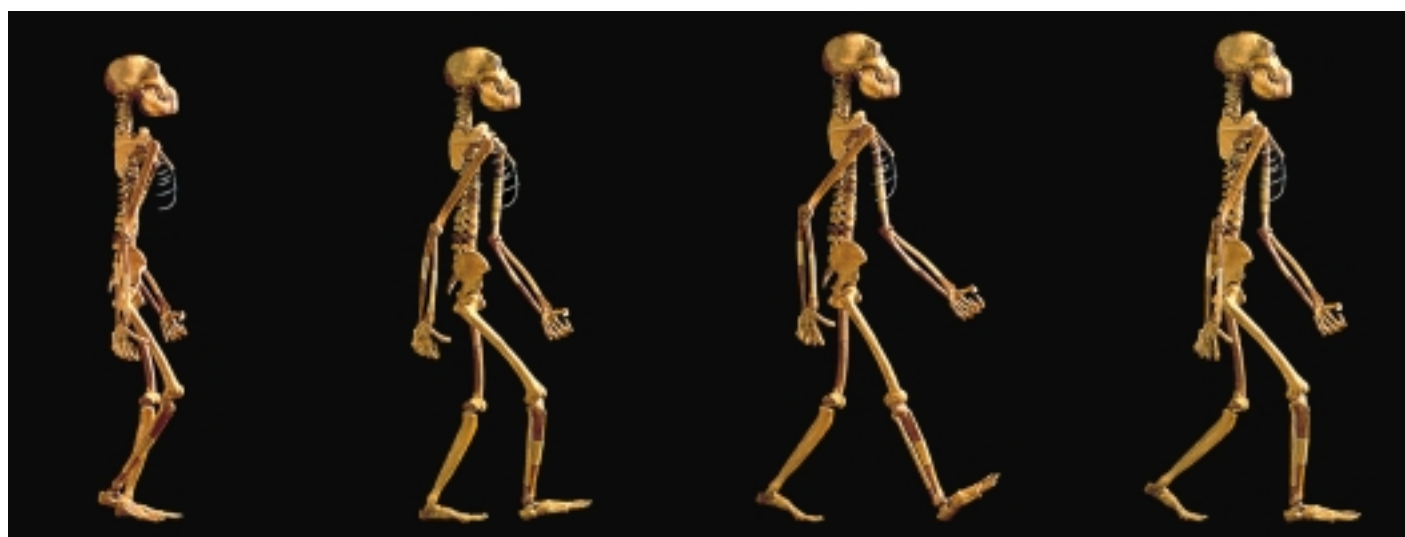
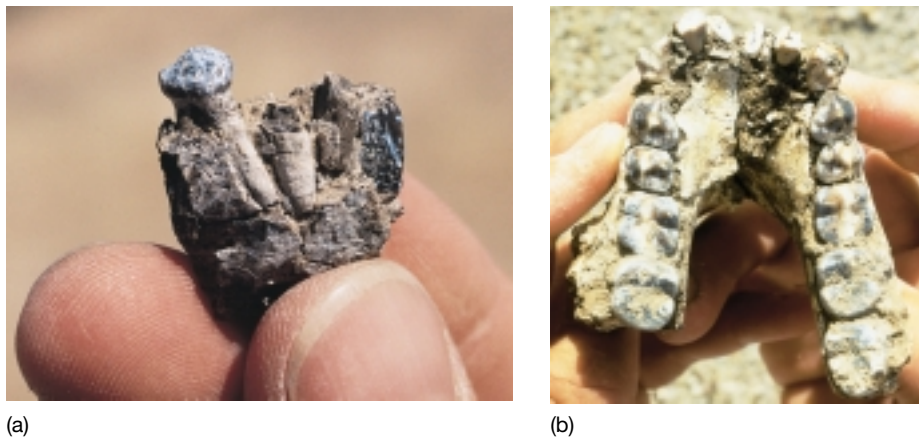


FIGURE 23.8

A reconstruction of an early hominid walking upright. These articulated plaster skeletons, made by Owen Lovejoy and his students at Kent State University, depict an early hominid (*Australopithecus afarensis*) walking upright.

FIGURE 23.9

Hominid fossils. (a) Our earliest known ancestor. A tooth from *Ardipithecus ramidus*, discovered in 1994. The name *ramidus* is from the Latin word for “root,” as this is thought to be the root of the hominid family tree. The earliest known hominid, at 4.4 million years old, *A. ramidus* was about the size of a chimpanzee and apparently could walk upright. (b) The earliest australopithecine. This fossil jaw of *Australopithecus* is about 4.2 million years old, making *A. anamensis* the oldest known australopithecine.



skull, arm bones, and a partial leg bone. The fossils were assigned to the species *Australopithecus anamensis* (figure 23.9b); *anam* is the Turkana word for lake. They were categorized in the genus *Australopithecus* rather than *Ardipithecus* because the fossils have bipedal characteristics and are much less apelike than *A. ramidus*. Although clearly australopithecine, the fossils are intermediate in many ways between apes and *A. afarensis*. Numerous fragmentary specimens of *A. anamensis* have since been found. Most researchers agree that these slightly built *A. anamensis* individuals represent the true base of our family tree, the first members of the genus *Australopithecus*, and thus ancestor to *A. afarensis* and all other australopithecines.

Differing Views of the Hominid Family Tree

Investigators take two different philosophical approaches to characterizing the diverse group of African hominid fossils. One group focuses on common elements in different fossils, and tends to lump together fossils that share key characters. Differences between the fossils are attributed to diversity within the group. Other investigators focus more pointedly on the differences between hominid fossils. They are more inclined to assign fossils that exhibit differences to different species. The hominid phylogenetic tree in figure 23.10 presents such a view. Where the “lumpers” tree presents three species of *Homo*, for example, the “splitters” tree presents no fewer than seven! At this point, it is not possible to decide which view is correct; more fossils are needed to determine how much

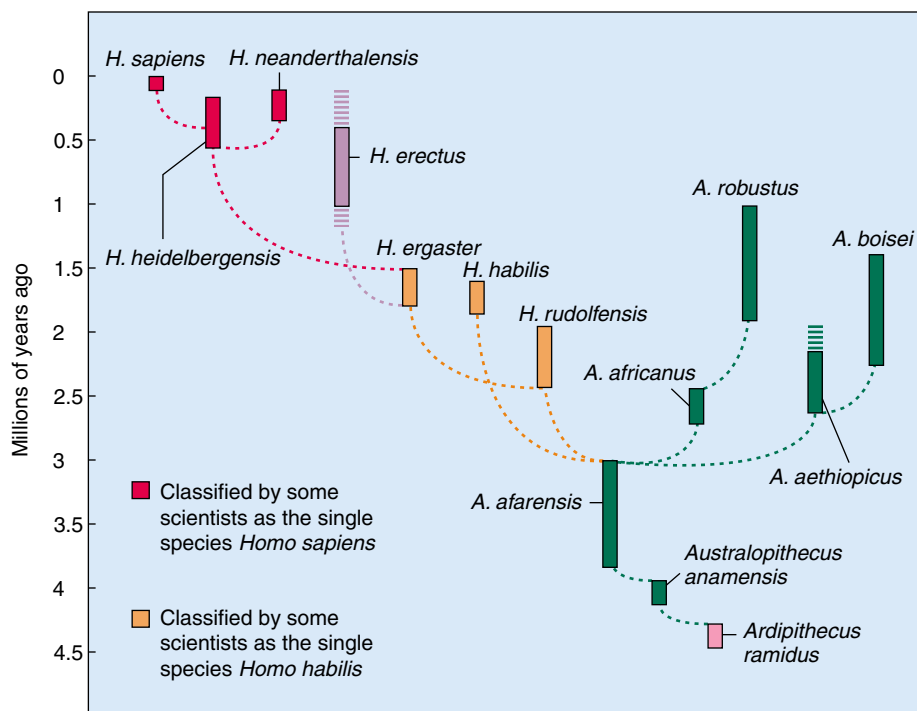


FIGURE 23.10
A hominid evolutionary tree. In this tree, the most widely accepted, the vertical bars show the known dates of first and last appearances of proposed species; bars are broken where dates are uncertain. Six species of *Australopithecus* and seven of *Homo* are included.

of the differences between fossils represents within-species variation and how much characterizes between-species differences.

The evolution of bipedalism—walking upright—marks the beginning of hominid evolution, although no one is quite sure why bipedalism evolved. The root of the hominid evolutionary tree is only imperfectly known. The earliest australopithecine yet described is *A. anamensis*, over 4 million years old.

23.3 The genus *Homo* evolved in Africa.

African Origin: Early *Homo*

The first humans evolved from australopithecine ancestors about 2 million years ago. The exact ancestor has not been clearly defined, but is commonly thought to be *A. afarensis*. Only within the last 30 years have a significant number of fossils of early *Homo* been uncovered. An explosion of interest has fueled intensive field exploration in the last few years, and new finds are announced regularly; every year, our picture of the base of the human evolutionary tree grows clearer. The account given here will undoubtedly be outdated by future discoveries, but it provides a good example of science at work.

Homo habilis

In the early 1960s, stone tools were found scattered among hominid bones close to the site where *A. boisei* had been unearthed. Although the fossils were badly crushed, painstaking reconstruction of the many pieces suggested a skull with a brain volume of about 680 cubic centimeters, larger than the australopithecine range of 400 to 550 cubic centimeters. Because of its association with tools, this early human was called *Homo habilis*, meaning “handy man.” Partial skeletons discovered in 1986 indicate that *H. habilis* was small in stature, with arms longer than legs and a skeleton much like *Australopithecus*. Because of its general similarity to australopithecines, many researchers at first questioned whether this fossil was human.

Homo rudolfensis

In 1972, Richard Leakey, working east of Lake Rudolf in northern Kenya, discovered a virtually complete skull about the same age as *H. habilis*. The skull, 1.9 million years old, had a brain volume of 750 cubic centimeters and many of the characteristics of human skulls—it was clearly human and not australopithecine. Some anthropologists assign this skull to *H. habilis*, arguing it is a large male. Other anthropologists assign it to a separate species, *H. rudolfensis*, because of its substantial brain expansion.

Homo ergaster

Some of the early *Homo* fossils being discovered do not easily fit into either of these species (figure 23.11). They tend to have even larger brains than *H. rudolfensis*, with skeletons less like an australopithecine and more like a modern human in both size and proportion. Interestingly, they also have small cheek teeth, as modern humans do. Some anthropologists have placed these specimens in a third species of early *Homo*, *H. ergaster* (*ergaster* is from the Greek for “workman”).



FIGURE 23.11

Early *Homo*. This skull of a boy, who apparently died in early adolescence, is 1.6 million years old and has been assigned to the species *Homo ergaster* (a form of *Homo habilis* recognized by some as a separate species). Much larger than earlier hominids, he was about 1.5 meters in height and weighed approximately 47 kilograms.

How Diverse Was Early *Homo*?

Because so few fossils have been found of early *Homo*, there is lively debate about whether they should all be lumped into *H. habilis* or split into the three species *H. rudolfensis*, *H. habilis*, and *H. ergaster*. If the three species designations are accepted, as increasing numbers of researchers are doing, then it would appear that *Homo* underwent an adaptive radiation (as described in chapter 22) with *H. rudolfensis* the most ancient species, followed by *H. habilis* and then *H. ergaster*. Because of its modern skeleton, *H. ergaster* is thought the most likely ancestor to later species of *Homo* (see figure 23.10).

Early species of *Homo*, the oldest members of our genus, had a distinctly larger brain than australopithecines and most likely used tools. There may have been several different species.

Out of Africa: *Homo erectus*

Our picture of what early *Homo* was like lacks detail, because it is based on only a few specimens. We have much more information about the species that replaced it, *Homo erectus*.

Java Man

After the publication of Darwin's book *On the Origin of Species* in 1859, there was much public discussion about "the missing link," the fossil ancestor common to both humans and apes. Puzzling over the question, a Dutch doctor and anatomist named Eugene Dubois decided to seek fossil evidence of the missing link in the home country of the orangutan, Java. Dubois set up practice in a river village in eastern Java. Digging into a hill that villagers claimed had "dragon bones," he unearthed a skull cap and a thighbone in 1891. He was very excited by his find, informally called Java man, for three reasons:

1. The structure of the thigh bone clearly indicated that the individual had long, straight legs and was an excellent walker.
2. The size of the skull cap suggested a very large brain, about 1000 cubic centimeters.
3. Most surprisingly, the bones seemed as much as 500,000 years old, judged by other fossils Dubois unearthed with them.

The fossil hominid that Dubois had found was far older than any discovered up to that time, and few scientists were willing to accept that it was an ancient species of human.

Peking Man

Another generation passed before scientists were forced to admit that Dubois had been right all along. In the 1920s a skull was discovered near Peking (now Beijing), China, that closely resembled Java man. Continued excavation at the site eventually revealed 14 skulls, many excellently preserved. Crude tools were also found, and most important of all, the ashes of campfires. Casts of these fossils were distributed for study to laboratories around the world. The originals were loaded onto a truck and evacuated from Peking at the beginning of World War II, only to disappear into the confusion of history. No one knows what happened to the truck or its priceless cargo. Fortunately, Chinese scientists have excavated numerous additional skulls of Peking man since 1949.

A Very Successful Species

Java man and Peking man are now recognized as belonging to the same species, *Homo erectus*. *Homo erectus* was a lot larger than *Homo habilis*—about 1.5 meters tall. It had a large brain, about 1000 cubic centimeters (figure 23.12),

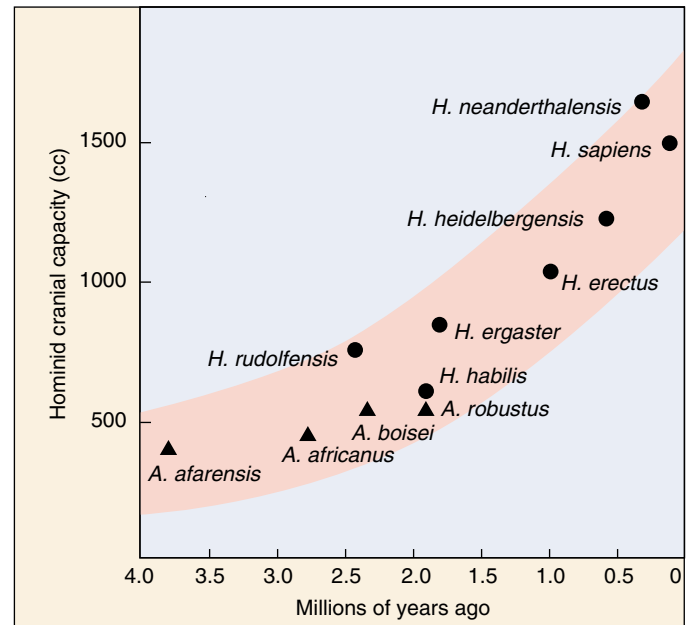


FIGURE 23.12

Brain size increased as hominids evolved. *Homo erectus* had a larger brain than early *Homo*, which in turn had larger brains than those of the australopithecines with which they shared East African grasslands. Maximum brain size (and apparently body size) was attained by *H. neanderthalensis*. Both brain and body size appear to have declined some 10% in recent millennia.

and walked erect. Its skull had prominent brow ridges and, like modern humans, a rounded jaw. Most interesting of all, the shape of the skull interior suggests that *H. erectus* was able to talk.

Where did *H. erectus* come from? It should come as no surprise to you that it came out of Africa. In 1976 a complete *H. erectus* skull was discovered in East Africa. It was 1.5 million years old, a million years older than the Java and Peking finds. Far more successful than *H. habilis*, *H. erectus* quickly became widespread and abundant in Africa, and within 1 million years had migrated into Asia and Europe. A social species, *H. erectus* lived in tribes of 20 to 50 people, often dwelling in caves. They successfully hunted large animals, butchered them using flint and bone tools, and cooked them over fires—the site in China contains the remains of horses, bears, elephants, deer, and rhinoceroses.

Homo erectus survived for over a million years, longer than any other species of human. These very adaptable humans only disappeared in Africa about 500,000 years ago, as modern humans were emerging. Interestingly, they survived even longer in Asia, until about 250,000 years ago.

Homo erectus evolved in Africa, and migrated from there to Europe and Asia.

23.4 Modern humans evolved quite recently.

The Last Stage of Hominid Evolution

The evolutionary journey to modern humans entered its final phase when modern humans first appeared in Africa about 600,000 years ago. Investigators who focus on human diversity consider there to have been three species of modern humans: *Homo heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* (see figure 23.10). Other investigators lump the three species into one, *H. sapiens* (“wise man”). The oldest modern human, *Homo heidelbergensis*, is known from a 600,000-year-old fossil from Ethiopia. Although it coexisted with *H. erectus* in Africa, *H. heidelbergensis* has more advanced anatomical features, such as a bony keel running along the midline of the skull, a thick ridge over the eye sockets, and a large brain. Also, its forehead and nasal bones are very like those of *H. sapiens*.

As *H. erectus* was becoming rarer, about 130,000 years ago, a new species of human arrived in Europe from Africa. *Homo neanderthalensis* likely branched off from the ancestral line leading to modern humans as long as 500,000 years ago. Compared with modern humans, Neanderthals were short, stocky, and powerfully built. Their skulls were massive, with protruding faces, heavy, bony ridges over the brows (figure 23.13), and larger brain-cases.

Out of Africa—Again?

The oldest fossil known of *Homo sapiens*, our own species, is from Ethiopia and is about 130,000 years old. Other fossils from Israel appear to be between 100,000 and 120,000 years old. Outside of Africa and the Middle East, there are no clearly dated *H. sapiens* fossils older than roughly 40,000 years of age. The implication is that *H. sapiens* evolved in Africa, then migrated to Europe and Asia, the Out-of-Africa model. An opposing view, the Multiregional model, argues that the human races independently evolved from *H. erectus* in different parts of the world.

Recently, scientists studying human mitochondrial DNA have added fuel to the fire of this controversy. Because DNA accumulates mutations over time, the oldest populations should show the greatest genetic diversity. It turns out that the greatest number of different mitochondrial DNA sequences occur among modern Africans. This result is consistent with the hypothesis that humans have been living in Africa longer than on any other continent, and from there spread to all parts of the world, retracing the path taken by *H. erectus* half a million years before (figure 23.14).



FIGURE 23.13

Our own genus. These four skulls illustrate the changes that have occurred during the evolution of the genus *Homo*. The *Homo sapiens* is essentially the same as human skulls today. The skulls were photographed from the same angle.

A clearer analysis is possible using chromosomal DNA, segments of which are far more variable than mitochondrial DNA, providing more “markers” to compare. When a variable segment of DNA from human chromosome 12 was analyzed in 1996, a clear picture emerged. A total of 24 different versions of this segment were found. Fully 21 of them were present in human populations in Africa, while three were found in Europeans and only two in Asians and in Americans. This result argues strongly that chromosome 12 has existed in Africa far longer than among non-African humans, strongly supporting an African origin of *H. sapiens*. Recently discovered fossils of early *H. sapiens* from Africa also lend strong support to this hypothesis.

Homo sapiens, our species, seems to have evolved in Africa and then, like *H. erectus* before it, migrated to Europe and Asia.

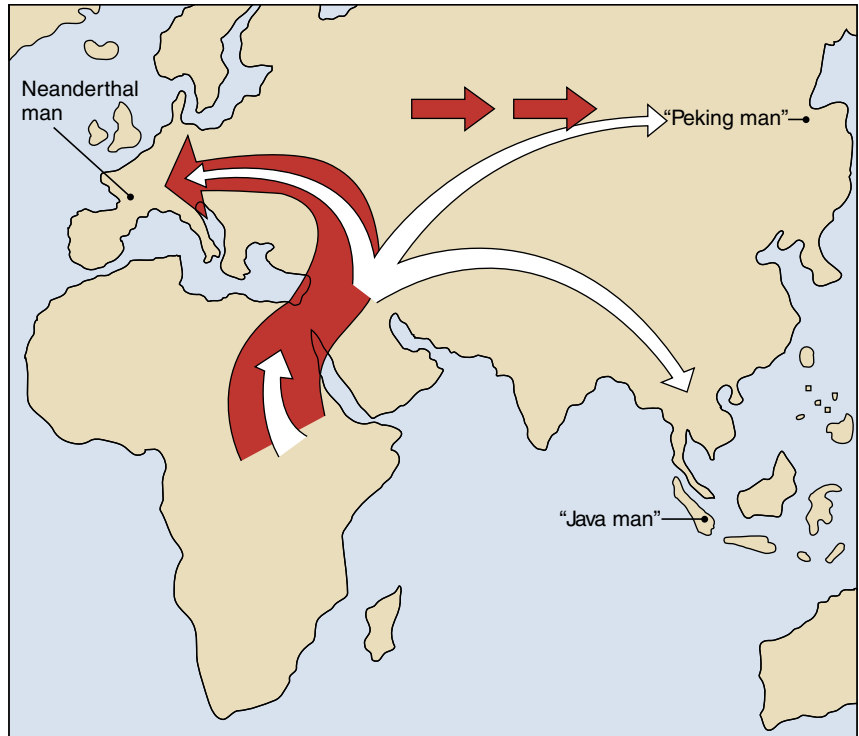


FIGURE 23.14

Out of Africa—many times. A still-controversial theory suggests that *Homo* spread from Africa to Europe and Asia repeatedly. First, *Homo erectus* (white arrow) spread as far as Java and China. Later, *H. erectus* was followed and replaced by *Homo neanderthalensis*, a pattern repeated again still later by *Homo sapiens* (red arrow).



FIGURE 23.13 (continued)

Our Own Species: *Homo sapiens*

H. sapiens is the only surviving species of the genus *Homo*, and indeed is the only surviving hominid. Some of the best fossils of *Homo sapiens* are 20 well-preserved skeletons with skulls found in a cave near Nazareth in Israel. Modern dating techniques date these humans to between 90,000 and 100,000 years old. The skulls are modern in appearance, with high, short braincases, vertical foreheads with only slight brow ridges, and a cranial capacity of roughly 1550 cc, well within the range of modern humans.

Cro-Magnons Replace the Neanderthals

The Neanderthals (classified by many paleontologists as a separate species *Homo neanderthalensis*) were named after the Neander Valley of Germany where their fossils were first discovered in 1856. Rare at first outside of Africa, they became progressively more abundant in Europe and Asia, and by 70,000 years ago had become common. The Neanderthals made diverse tools, including scrapers, spearheads, and handaxes. They lived in huts or caves. Neanderthals took care of their injured and sick and commonly buried their dead, often placing food, weapons, and even flowers with the bodies. Such attention to the dead strongly suggests that they believed in a life after death. This is the first evidence of the symbolic thinking characteristic of modern humans.

Fossils of *H. neanderthalensis* abruptly disappear from the fossil record about 34,000 years ago and are replaced by fossils of *H. sapiens* called the Cro-Magnons (named after the valley in France where their fossils were first discovered). We can only speculate why this sudden replacement occurred, but it was complete all over Europe in a short period. There is some evidence that the Cro-Magnons came from Africa—fossils of essentially modern aspect but as much as 100,000 years old have been found there. Cro-Magnons seem to have replaced the Neanderthals completely in the Middle East by 40,000 years ago, and then spread across Europe, coexisting and possibly even interbreeding with the Neanderthals for several thousand years. The Cro-Magnons had a complex social organization and are thought to have had full language capabilities. They lived by hunting. The world was cooler than it is now—the time of the last great ice age—and Europe was covered with grasslands inhabited by large herds of grazing animals. Pictures of them can be seen in elaborate and often beautiful cave paintings made by Cro-Magnons throughout Europe (figure 23.15).

Humans of modern appearance eventually spread across Siberia to North America, which they reached at least 13,000 years ago, after the ice had begun to retreat and a land bridge still connected Siberia and Alaska. By 10,000 years ago, about 5 million people inhabited the entire world (compared with more than 6 billion today).



FIGURE 23.15
Cro-Magnon art. Rhinoceroses are among the animals depicted in this remarkable cave painting found in 1995 near Vallon-Pont d'Arc, France.

Homo sapiens Are Unique

We humans are animals and the product of evolution. Our evolution has been marked by a progressive increase in brain size, distinguishing us from other animals in several ways. First, humans are able to make and use tools effectively—a capability that, more than any other factor, has been responsible for our dominant position in the animal kingdom. Second, although not the only animal capable of conceptual thought, we have refined and extended this ability until it has become the hallmark of our species. Lastly, we use symbolic language and can with words shape concepts out of experience. Our language capability has allowed the accumulation of experience, which can be transmitted from one generation to another. Thus, we have what no other animal has ever had: extensive cultural evolution. Through culture, we have found ways to change and mold our environment, rather than changing evolutionarily in response to the demands of the environment. We control our biological future in a way never before possible—an exciting potential and frightening responsibility.

Our species, *Homo sapiens*, is good at conceptual thought and tool use, and is the only animal that uses symbolic language.

Human Races

Human beings, like all other species, have differentiated in their characteristics as they have spread throughout the world. Local populations in one area often appear significantly different from those that live elsewhere. For example, northern Europeans often have blond hair, fair skin, and blue eyes, whereas Africans often have black hair, dark skin, and brown eyes. These traits may play a role in adapting the particular populations to their environments. Blood groups may be associated with immunity to diseases more common in certain geographical areas, and dark skin shields the body from the damaging effects of ultraviolet radiation, which is much stronger in the tropics than in temperate regions.

All human beings are capable of mating with one another and producing fertile offspring. The reasons that they do or do not choose to associate with one another are purely psychological and behavioral (cultural). The number of groups into which the human species might logically be divided has long been a point of contention. Some contemporary anthropologists divide people into as many as 30 “races,” others as few as three: Caucasoid, Negroid, and Oriental. American Indians, Bushmen, and Aborigines are examples of particularly distinctive subunits that are sometimes regarded as distinct groups.

The problem with classifying people or other organisms into races in this fashion is that the characteristics used to define the races are usually not well correlated with one another, and so the determination of race is always somewhat arbitrary. Humans are visually oriented; consequently, we have relied on visual cues—primarily skin color—to define races. However, when other types of characters, such as blood groups, are examined, patterns of variation correspond very poorly with visually determined racial classes. Indeed, if one were to break the human species into subunits based on overall genetic similarity, the groupings would be very different than those based on skin color or other visual features (figure 23.16).

In human beings, it is simply not possible to delimit clearly defined races that reflect biologically differentiated and well-defined groupings. The reason is simple: different groups of people have constantly intermingled and interbred with one another during the entire course of history. This constant gene flow has prevented the human species from fragmenting in highly differentiated subspecies. Those characteristics that are differentiated among populations, such as skin color, represent classic examples of the antagonism between gene flow and natural selection. As we saw in chapter 20, when selection is strong enough, as it is for dark coloration in tropical regions, populations can differentiate even in the presence of gene flow. However, even in cases such as this, gene flow will still ensure that populations are relatively homogeneous for genetic variation at other loci.

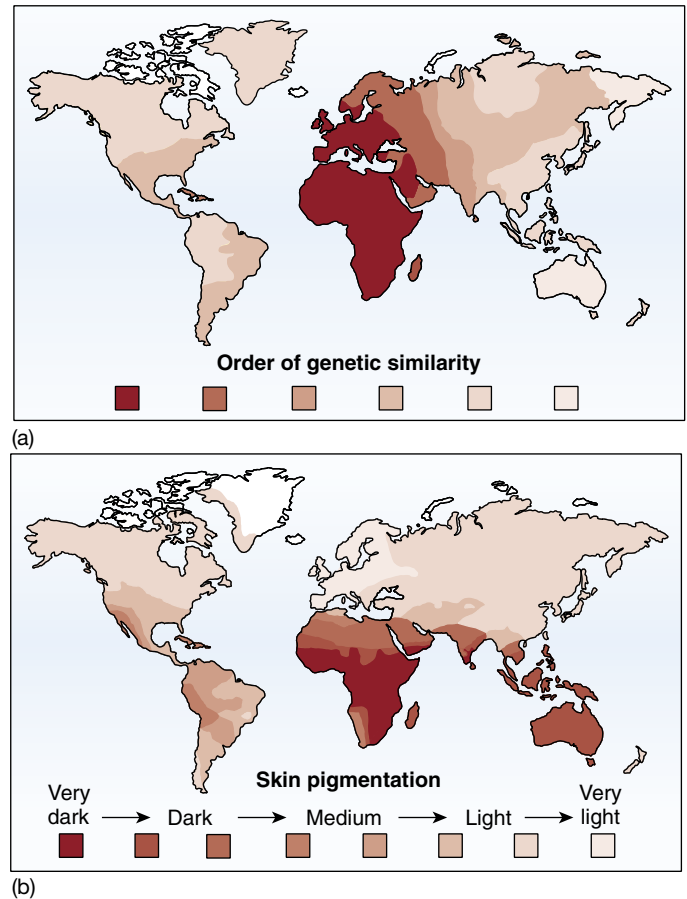


FIGURE 23.16
Patterns of genetic variation in human populations differ from patterns of skin color variation. (a) Genetic variation among *Homo sapiens*. Eight categories of humans were recognized based on overall similarity at many enzyme and blood group genetic loci. The code below the figure is arranged in order of similarity. (b) Similarity among *Homo sapiens* based on skin color. The categories are arranged by amount of pigmentation in the skin.

For this reason, relatively little of the variation in the human species represents differences between the described races. Indeed, one study calculated that only 8% of all genetic variation among humans could be accounted for as differences that exist among racial groups; in other words, the human racial categories do a very poor job in describing the vast majority of genetic variation that exists in humans. For this reason, most modern biologists reject human racial classifications as reflecting patterns of biological differentiation in the human species. This is a sound biological basis for dealing with each human being on his or her own merits and not as a member of a particular “race.”

Human races do not reflect significant patterns of underlying biological differentiation.



Summary

Questions

Media Resources

23.1 The evolutionary path to humans starts with the advent of primates.

- Prehensile (grasping) fingers and toes and binocular vision were distinct adaptations that allowed early primates to be successful in their particular environments.
- Mainly diurnal (day-active) anthropoids and mainly nocturnal (night-active) prosimians diverged about 40 million years ago. Anthropoids include monkeys, apes, and humans, and all exhibit complex social interactions and enlarged brains.
- The hominoids evolved from anthropoid ancestors about 25 million years ago. Hominoids consist of the apes (gibbons, orangutans, gorillas, and chimpanzees) and upright-walking hominids (human beings and their direct ancestors).

1. Which characteristics were selected for in the earliest primates to allow them to become successful in their environment?
2. How do monkeys differ from prosimians?
3. How are apes distinguished from monkeys?
4. What is the best explanation for why humans and chimpanzees are so similar genetically?



• Evolution of Primates

23.2 The first hominids to evolve were australopithecines.

- Early hominids belonging to the genus *Australopithecus* were ancestral to humans. They exhibited bipedalism (walking upright on two feet) and lived in Africa over 4 million years ago.

5. When did the first hominids appear? What were they called? What distinguished them from the apes?

23.3 The genus *Homo* evolved in Africa.

- Hominids with an enlarged brain and the ability to use tools belong to the genus *Homo*. Species of early *Homo* appeared in Africa about 2 million years ago and became extinct about 1.5 million years ago.
- *Homo erectus* appeared in Africa at least 1.5 million years ago and had a much larger brain than early species of *Homo*. *Homo erectus* also walked erect and presumably was able to talk. Within a million years, *Homo erectus* migrated from Africa to Europe and Asia.

6. Why is there some doubt in the scientific community that *Homo habilis* was a true human?

7. How did *Homo erectus* differ from *Homo habilis*?

• On Science Article:
Human Evolution**23.4 Modern humans evolved quite recently.**

- The modern species of *Homo* appeared about 600,000 years ago in Africa and about 350,000 years ago in Eurasia.
- The Neanderthals appeared in Europe about 130,000 years ago. They made diverse tools and showed evidence of symbolic thinking.
- Studies of mitochondrial DNA suggest (but do not yet prove) that all of today's human races originated from Africa.
- Categorization of humans into races does not adequately reflect patterns of genetic differentiation among people in different parts of the world.

8. The greatest number of different mitochondrial DNA sequences in humans occurs in Africa. What does this tell us about human evolution?

9. How did Cro-Magnons differ from Neanderthals? Is there any evidence that they coexisted with Neanderthals? If so, where and when?

10. Are the commonly recognized human races equivalent to subspecies of other plant and animal species?



• Hominid History