109 Human Evolution

Human evolution is marked by advances in cognitive function and global migration.



East Africans.
Comparing the genomes of human populations distributed across the world provides an unprecedented ability to study human evolution and migration out of Africa.
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Topics Covered in this Module

- Human Evolution

Major Objectives of this Module

- Describe adaptations of major hominid lineages.
- Explain how hominin evolution is characterized by diversification and the concurrent existence of multiple hominin species.
- Describe the major features of human evolution, including bipedalism, migration, technology, and culture.

Human Evolution

The advent of the molecular age has transformed the study of human evolution. Molecular tools enable scientists to compare the DNA of populations in different areas as well as the DNA sequences of species (including some extinct ones!), providing unprecedented insight into evolutionary relationships and migration patterns.

Starting in the 1970s, scientists using these tools began to realize the remarkable genetic similarity between humans (*Homo sapiens*) and our closest living relatives in the genus *Pan*, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). We share between 95–99% of our genetic material with these two species, depending on how exactly genetic similarity is quantified. In fact, humans and the two Pan species are more closely related to each other than any are to the next most similar species, the gorilla (*Gorilla gorilla*), and many scientists believe the three species technically should be placed in the same genus.

Despite the anatomical and behavioral similarities between humans and the *Pan* species (Figure 1), there are key differences. Humans regularly stand upright and walk on two legs. They have larger brains, weaker jaws, and smaller teeth. Although *Pan* species have complex cultures and have rudimentary communication and tool usage, humans have taken these and other behaviors to the extreme. What can account for this apparent discrepancy?



Figure 1: *Pan* relatives.
Chimpanzees (*Pan troglodytes*, above) and bonobos (*Pan paniscus*, not shown) are the closest living human relatives. Compared with humans, they have smaller brains, longer arms, fingers and toes that can better grasp tree branches, larger canine teeth, and more prominent jaws.
Connie Bransilver/Science Source.

In a landmark study published in 1975, Mary-Claire King and Allan Wilson suggested a radical explanation: that changes in just a few critical regulatory genes might account for the many observed differences in humans and chimpanzees. Regulatory genes are "master" genes. They turn other genes on and off in complex developmental orchestrations. Since King and Wilson first published their study, much supportive evidence has accumulated. For

example, a study in 2006 by Gilad and colleagues found that within the last five million years, the genes for transcription factors (which control the expression of other genes) were four times as likely to have changed in the human genome than the genes they regulated.

In addition to humans and the two *Pan* species, the family Hominidae includes gorillas (*Gorilla gorilla*) and the two species of orangutans (*Pongo* spp.); all members of the Hominidae family share a common ancestor, who lived around 12–16 million years ago. Figure 2 shows the evolutionary relationships among the hominid apes and their primate relatives as well as their estimated times of divergence. Each point of divergence represents a shared ancestor.

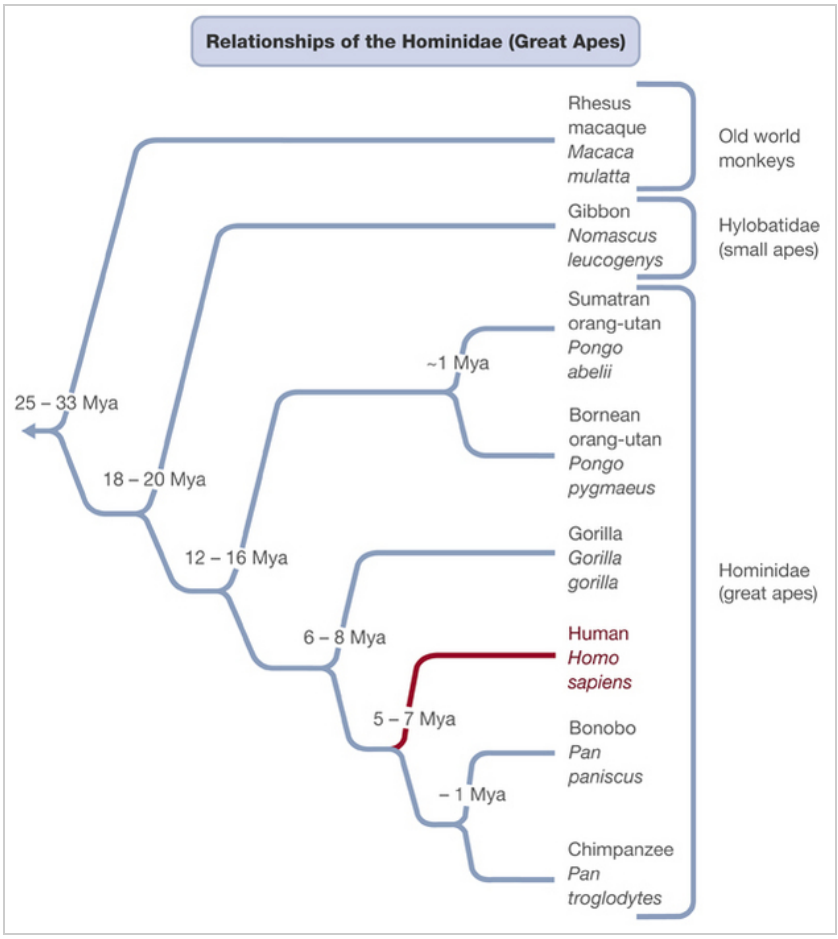


Figure 2: The hominid clade.
Orangutans, gorillas, chimps, bonobos, and humans are considered hominids — the great apes. Hominins (represented by the red line) diverged from the common ancestor of humans and chimpanzees/bonobos 5–7 million years ago (MYA). This line is anything but direct as several species evolved and went extinct before modern humans emerged as the only surviving hominin.
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Articles about human evolution often use the terms *hominid* and *hominin*, sometimes interchangeably, to refer to human ancestors and other apes. What is the difference? *Hominid* is the older term. It refers to humans and their human-like ancestors, and it is still used by some scientists in this manner. However, **hominids** is a taxonomic grouping that refers to any member of the great apes (the family Hominidae), including humans (and their extinct relatives) as well as chimpanzees, bonobos, gorillas, and the two orangutan species. A **hominin**, on the other hand, refers to a species that evolved after the lineage that led to modern humans split from chimpanzees and bonobos.

In Figure 2, the hominins are represented by the line that splits from the chimp-human divergence, some 5–7 million years ago. The only extant (living) hominin is *Homo sapiens*, the anatomically modern human, although we know of many extinct species from the fossil record.

Hominins diverged from other great apes about 5–7 million years ago.

The earliest known hominin fossils are skull fragments that are ~6.5 million years old. Skull fragments are the only part of this individual that exists, but they were detailed enough for scientists to determine that they belonged to an ancient hominin that they named *Sahelanthropus tchadensis*, which had many similarities to, but also important differences with, modern humans. The skull of *S. tchadensis* was smaller than a modern human's, and it had a brain about the size of a non-human hominid (e.g., chimpanzee or orangutan). However, it differed from a non-human hominid in having smaller canine teeth and a flatter face, more similar to a human skull.

The *S. tchadensis* skull also suggested that the body had a more upright stance than non-human apes, judging by the position of the foramen magnum, the hole through which the spinal cord passes. The foramen magnum is located more centrally under the brain in humans than in other apes (Figure 3), as a result of upright walking.

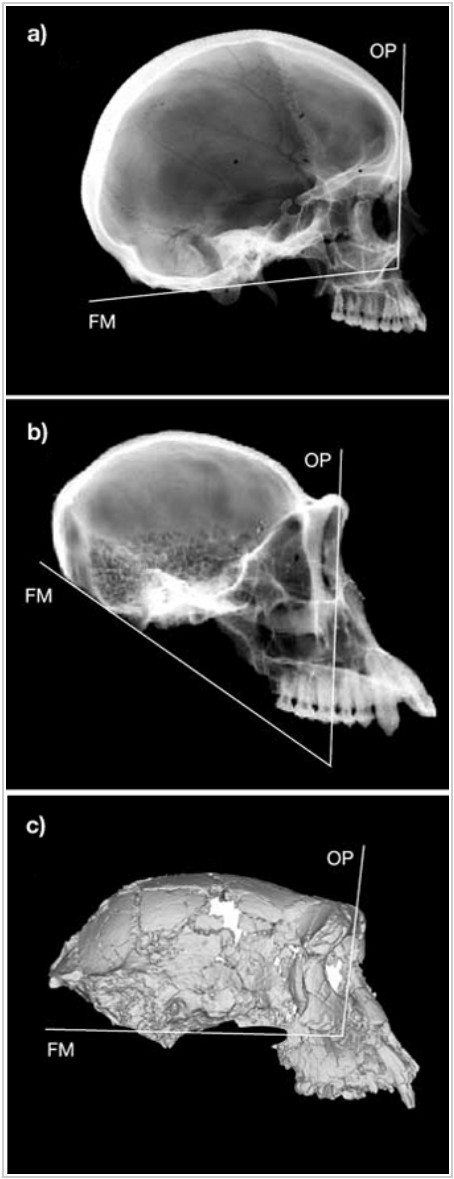


Figure 3: Comparing foramen

magnum placement.
The angled lines on each skull mark the orbital plane (OP), where the eyes are, and the plane of the foramen magnum (FM), the hole that the spinal cord passes through. The foramen magnum is more directly under the skull in a hominid that walks upright. (a) Modern human (*Homo sapiens*), (b) Chimpanzee (*Pan troglodytes*), (c) *Sahelanthropus tchadensis* (reconstructed).
© 2005 Nature Publishing Group
Zollikofer, C. *et al.* Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 434, 755–759 (2005) doi:10.1038/nature03397. Used with permission.

Bipedalism, derived from the Latin word *biped* (*bi* for "two" and *ped* for "foot"), or walking upright on two legs, is a hominin characteristic. Why did hominins evolve bipedalism? Most scientists think that a change in climate was at least partly responsible. About 10 million years ago, the climate in Africa and Asia became drier. Forests began to shrink and grasslands expanded. Scientists rigorously debate exactly what advantages bipedalism conferred in a changing climate. It is possible that individuals who could walk or run more easily in these wide-open spaces might have had better access to food sources separated by grassy savannas. Likewise, walking bipedally freed up the early hominins' forelimbs (which we call arms) for carrying large items across these long distances, which is difficult to do when the arms are used for locomotion. Whatever the reason, hominins did not evolve complete bipedalism rapidly, and fossils indicate that early hominins could probably walk on all four legs, swing through trees, and walk upright.

When did hominins start to walk upright? Wrist bones of all hominin fossils older than about 3 million years indicate that these hominins practiced knuckle-walking, with their knuckles bearing some of their weight while they walked on the backs of their fingers and feet (such as the chimpanzee shown in Figure 4). Wrist bones of hominins that lived more recent (or less) than 3 million years ago are more similar to those of modern humans. This suggests that the origin of bipedalism was around 3 million years ago. However, the first hominins who likely walked or ran long distances, judging from their long legs and human-like hip joints, probably did not emerge until about 1.9 million years ago. There have been no wrist fragments recovered from *Sahelanthropus tchadensis*, so it is not possible to determine if they were knuckle-walkers, but skull evidence indicates they may have been bipedal. Gaps in the fossil record, such as the absent *S. tchadensis* wrist bones, make it difficult to determine the origin of behaviors of our extinct ancestors.



Figure 4: Four on the ground.
Wrist fossils indicate that the earliest hominins were probably knuckle-walkers, like these chimpanzees (*Pan troglodytes*).
Connie Bransilver/Science Source.

Complex tool making and use is another distinguishing feature of hominins. Many apes use sticks as tools to forage for insects or for other purposes. Chimpanzees will cushion their feet with leaves to walk in comfort over thorns. But these are not the kinds of tools that typically survive as fossil evidence. The earliest widely accepted signs of tool use by hominins are cut marks on animal bones, which indicate that hominins used stones to cut meat off bones (Figure 5). The oldest confirmed cut marks have been found on bones about 2.5 million years old, but there is also some evidence that tools were in use as early as 3.4 million years ago.



Figure 5: Hand axes.
Hand axes are just one of the many tools that have been discovered and associated with hominins.
Courtesy of the National Park Service.

When did human brains reach their current size? The average modern human brain is 1300–1350 cm^3. Chimp brains, in contrast, average 280–450 cm^3. The fossil record indicates that some early hominins had braincases as small as 300 cm^3. Brain size in hominins appears to have increased stepwise over time, with many new species exhibiting jumps in size. About 4 million years ago, *Australopithecus africanus* had a brain slightly larger than that of a chimpanzee but still only one-third the size of a human brain. By about 2 million years ago, *Homo habilis* had a brain of 600–750 cm^3, and 200,000 years after that, *Homo erectus* had a brain of about 900 cm^3. One hypothesized reason that might account for these stepwise increases in brain size could be changes in regulatory genes.

Australopithecus africanus, H. habilis, and *H. ergaster* are only three of many hominins

known to have existed over the past several million years. How many hominins were there? There were probably dozens of species. Figure 6 illustrates some of the hominin species that scientists have described based on fossil evidence and one interpretation of their evolutionary relationships. Note that some hominin species co-existed, and all but one — *Homo sapiens* — are now extinct. Notice how recent some important fossil discoveries are. New hominin fossils are discovered all the time. How many other species await description?

Figure 6: Representative hominin phylogeny and timeline.
Many fossils have been found that represent members of the hominin phylogeny, some of which are shown here. Although the exact placement of species in the phylogeny continues to be debated, one can get a sense from the number of species and their possible relationships of the complex evolutionary history of our lineage. This phylogenetic tree shows one of several interpretations.

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Test Yourself

On what continent were all but the most recent hominin fossils found? What does this suggest?

Submit

Homo sapiens likely emerged in Africa about 200,000 years ago and later migrated throughout the world.

Based on the locations where early hominin fossils are found, most scientists agree that hominins first evolved in Africa and then spread to other parts of the world through a series of **migrations**. Evidence suggests that *H. erectus* was the first hominin to migrate out of Africa, sometime between 1 and 2

million years ago. *Homo erectus* appears to have migrated through the Middle East into Asia and then Europe. Modern humans did not evolve and migrate until much later. They did not reach the Americas until about 15,000 years ago, although some evidence suggests an earlier date.

How do scientists determine patterns and dates of human migration? Fossils are one type of evidence. Another is the rate of DNA mutations. Siblings have highly similar DNA, whereas distantly related people have slightly less similar DNA. Scientists have found that some regions in DNA mutate at uniform rates. By comparing those regions in different people living in different locations, scientists can measure how long ago those people shared a common ancestor. This technique is often called the molecular clock.

BIOSKILL

Describe the Use of Mitochondrial DNA Analysis to Trace Human Evolution.

One type of DNA often used in molecular clock analysis, especially in humans, is mitochondrial DNA (mtDNA). Recall that mitochondria are organelles that produce cellular energy. All the mtDNA is maternally inherited and is not affected by genetic recombination, as male mitochondria do not pass into the egg during fertilization. Human mitochondria contain 37 genes, and certain regions of those genes mutate much more rapidly than nuclear DNA does. Scientists speculate that mtDNA mutates more rapidly because it lacks many of the repair mechanisms found in nuclear DNA.

What have scientists learned from mtDNA analysis? In 1987, Rebecca Cann and colleagues published a seminal paper showing results of mtDNA analysis of people in five different parts of the world. They concluded that the variations were few enough to indicate that all modern humans had a common ancestor who lived about 200,000 years ago in Africa. MtDNA is inherited almost entirely from the mother, so the press quickly termed this ancestor "Mitochondrial Eve."

Cann's group hypothesized that all modern humans descended from a single, small group of humans that migrated out of Africa about 100,000 years ago. These humans spread widely, replacing (not breeding with) populations of other hominins that had become established elsewhere. In this hypothesis, called the "Out-of-Africa" hypothesis, modern humans evolved just once, in Africa. Many studies since Cann's support the Out-of-Africa hypothesis, as does much fossil evidence. The earliest known fossils of modern humans were discovered in Ethiopia and are 195,000 years old.

However, there are other hypotheses for the origin of modern humans. For example, the multiregional hypothesis posits that modern humans did not evolve just once, 200,000 years ago, but resulted from many small adaptive changes over millions of years of evolution throughout their range. A twist on this idea that is supported by both fossil and genetic evidence is the trellis hypothesis, first described in 2002 by Alan Templeton. Templeton analyzed data from mtDNA, X and Y chromosomes, and certain regions of autosomal chromosomes and compared the results with the fossil record. He found DNA signatures with ancient origins, which implied that hominins bred with each other throughout their history. His evidence also suggests that hominin populations migrated out of Africa in two waves after the initial migration of *Homo erectus*. According to Templeton's analysis, genes derived from interbreeding during the times of these migrations are specific to people living in certain geographic regions today (Figure 7).

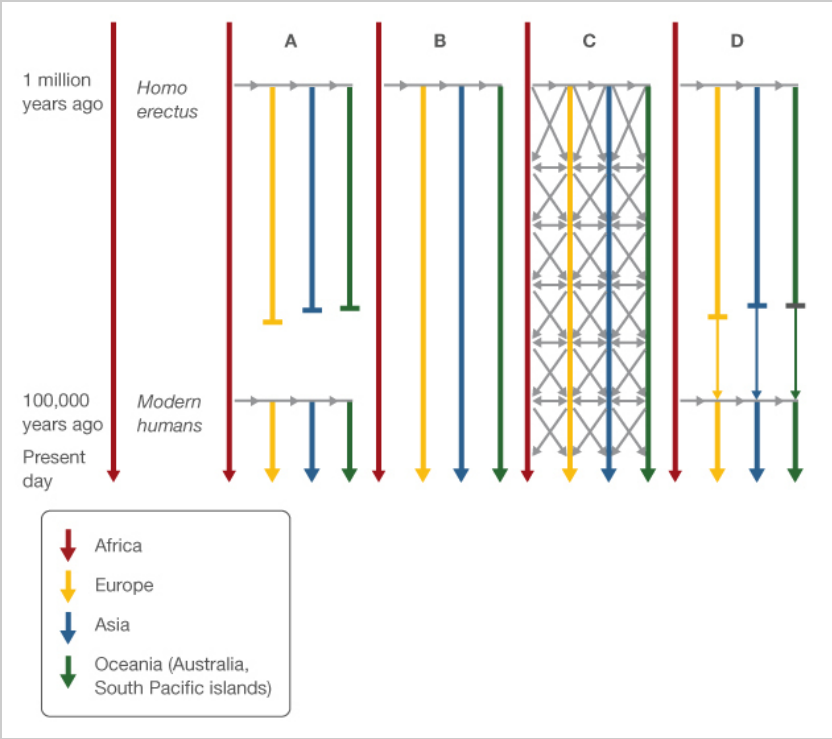


Figure 7: Hypotheses about human migration.
A) The "Out-of-Africa" hypothesis proposes that modern humans, *H. sapiens*, evolved once from African *H. erectus*. In this hypothesis, the European, Oceanic, and Asian *H. erectus* lineages went extinct. B) The multiregional hypothesis suggests that modern humans evolved independently from African, European, Oceanic, and Asian *H. erectus*. C) The trellis, or shared multiregional, hypothesis suggests a multiregional origin, as in (B), but that gene flow existed among the populations of *H. erectus*, such that any adaptive mutations could rapidly spread among the populations. D) This model represents a compromise between the "Out-of-Africa" and multiregional hypotheses by suggesting that humans evolved from African *H. erectus*; but these African *H. erectus* did have low levels of gene flow with European, Oceanic, and Asian *H. erectus*, causing modern *H. sapiens* to carry genes from these other populations. (Figure adapted from Templeton, A. Out of Africa again and again. *Nature* 416, 45-51 (2002)).
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Test Yourself

According to the trellis hypothesis, how are modern humans related to *H. erectus*? How are they related in the "Out-of-Africa" hypothesis?

Submit

BIOSKILL

Humans and Neanderthals.
In 2010, an international consortium of scientists led by Richard Green published a draft sequence of the genome of Neanderthals (*Homo neanderthalensis*). They sequenced the DNA from well-preserved bones of three female Neanderthals from a site in Croatia. They also compared the sequences to that from modern humans and concluded that a small proportion of the DNA of European and Asian populations is derived from Neanderthals, suggesting that *Homo sapiens* and Neanderthals had limited

interbreeding; much less interbreeding was evident in Africa, where both species originated.

How long did Neanderthals coexist with modern humans? Neanderthals went extinct about 30,000 years ago, more than 10,000 years after modern humans joined them in Eurasia. Scientists do not know why Neanderthals went extinct, but many hypotheses have been developed to explain their extinction. Neanderthals were physically larger and more robust than modern humans (Figure 8), and they were well adapted to cold climates, but some scientists speculate that they were not well equipped to deal with the fluctuations in the climate that characterized Europe and Asia 30,000 years ago. Other scientists implicate competition with modern humans as contributing to their demise.



Figure 8: Neanderthal and modern human skeletons.
Neanderthals (*Homo neanderthalensis*) (left) were bigger and had thicker bones than modern humans (*Homo sapiens*) (right).
(left) Martin Shields/Science Source. (right) BSIP/Science Source.

What about behavioral and cognitive differences between Neanderthals and modern humans? One significant difference likely involved the capacity for symbolic thought. Though Neanderthals were capable of symbolic thought, as evidenced by their practice of burying their dead, modern humans probably had a greater ability to plan, predict consequences, and communicate. Early modern humans also made elaborate art. Modern humans in southern Africa were engraving ochre with geometric designs 77,000 years ago, and by 36,000 years ago they were creating large, elegant cave paintings in France (Figure 9). Could these paintings signify cognitive abilities that helped the species succeed?



Figure 9: Cave paintings at Lascaux and Chauvet.
In 1940, four teenagers in Lascaux, France, stumbled onto an amazing discovery. The cave paintings they found date from around 17,000 years ago. Paintings from nearby caves date to about 36,000 years ago.
Francois Ducasse/Photo Researchers, Inc./Science Source.

Once modern humans were established, their populations grew quickly. Why? Many scientists think that a major reason was the development of agriculture, the purposeful growing of crops and rearing of animals for food. Ancient human tribes obtained their food by hunting animals and gathering fruits, vegetables, and grains. Some populations still live as hunter-gatherers today. Hunter-gatherer societies are usually limited in size and often must migrate to find food year round. Agriculture is a more efficient method of calorie production; a wheat field (Figure 10) typically generates more calories available to humans than an equivalent area of forest. With agriculture, people can stay in one place, near their fields, and because they stay in one place they can store more food, which helps them survive through times when food production is scarce. Once humans developed agriculture and were able to remain in one place, human populations could focus on tasks other than finding food, such as making weapons and keeping written records; their pursuit of these other activities eventually lead to the development of culture and technology.



Figure 10: Invention of agriculture.
Agriculture, like growing the wheat pictured here, enabled the human

population to remain in one place, increase in size, and eventually develop culture.
James Steinberg/Science Source.

When did agriculture develop? The earliest evidence of the domestication of several major crops is from about 11,500 years ago in the region of the Middle East called the Fertile Crescent. Soon afterward, agriculture independently appeared in China. Over time, agricultural practices spread to the rest of the world.

Controversy.

Molecular studies and fossil discoveries continue to expand and refine the hominin evolutionary tree. However, few discoveries are without controversy. In 2004, Brown and colleagues reported on the finding of a nearly complete hominin skeleton, along with bones and teeth from other individuals, in a rock shelter on the Indonesian island of Flores. The bones were not fossilized and were quite fragile. Two dating methods agreed they were about 18,000 years old.

The full skeleton was only 1 meter (3.3 feet) tall, with the skull (Figure 11) large enough to accommodate a brain one-third the size of a human brain — about the size of an australopith brain. At first, the researchers thought the skull belonged to a child, but its teeth were worn and later forensic analysis suggested that it belonged to a 30-year-old adult female. Because of its small stature, the researchers nicknamed the individual the "hobbit."



Figure 11: New species?
The skull of *Homo floresiensis*. This mold was made from fragments of a skull found in a cave on the island of Flores, Indonesia. Other evidence shows that an adult *Homo floresiensis* was not much taller than 1 m (3 ft) in height.
Javier Trueba/MSF/Science Source.

Controversy soon erupted. The research team thought the Flores "hobbit" represented a new species, possibly descended from *H. erectus* or even from an australopith. They named it *Homo floresiensis*. The researchers argued that the species' short stature might have evolved in response to the island's scarce resources, citing evidence from many other species that evolve smaller bodies when on islands. Other scientists believed the skeleton was not a new species at all but was simply a *H. sapiens* pygmy (accounting for its short stature) with a disease (accounting for its small brain).

In 2009, Jungers and colleagues reported an analysis of the large feet of *H. floresiensis* (Figure 12), which would have been good for walking but not running, and concluded that *H. floresiensis* likely descended from hominins predating *H. erectus*. In the same year, Westin and Lister analyzed

relationships between body size and brain size on extinct dwarf *Hippopotamus* spp. from the island of Madagascar and suggested that a similar mechanism could account for the unusually small brain size of the island-living *H. floresiensis* relative to other species in its lineage . In 2010, Brumm and colleagues dated materials associated with primitive stone tools of *H. floresiensis*, finding a minimum age of at least 1.2 million years, suggesting that the species was present on the island much longer than previously thought. What does all of this mean? Scientists do not yet know.



Figure 12: "Hobbit" foot and leg bones.
This image shows *H. floresiensis* leg and foot bone proportions. Compared to its legs, *H. floresiensis* had exceptionally long feet relative to modern humans.
© 2009 Nature Publishing Group Jungers, W. L. *et al.* The foot of *Homo floresiensis*. *Nature* 459, 81–84 (2009) doi:10.1038/nature07989. Used with permission.

Future perspectives.
Reich and colleagues (2010) reported on another fossil mystery following their analysis of a 40,000-year-old bone fragment discovered in a cave in the Siberian mountains (the Denisova cave). DNA sequencing revealed that the bone belonged neither to *Homo sapiens* nor *Homo neanderthalensis* — although both species were living in those mountains at that time — but to a previously unknown species. The researchers also found a tooth in the same cave with mtDNA that was highly dissimilar to the mtDNA of both modern humans and Neanderthals (Figure 13). The size and shape of the tooth distinguish it as more closely resembling teeth of the australopiths or *H. habilis*. Was this a new hominin species?



Figure 13: Molar found in Denisova cave.
This Denisovan tooth looks more like an *Australopithecus* third molar than a Neanderthal or modern human third molar.
© 2010 Nature Publishing Group Reich, D. *et al.* Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468, 1053–1060 (2010) doi:10.1038/nature09710. Used with permission.

The researchers suggested that these individuals belonged to a novel hominin group called "Denisovan," which had left Africa before modern humans but after *H. erectus*. Based on the differences among the DNA sequences of modern humans, several Neanderthal fossils, and the Denisovan fossils, the researchers estimated that the three groups shared a common ancestor about 1 million years ago (Figure 14). Unlike Neanderthals, Denisovans apparently did not contribute to the genome of modern Europeans. But they did appear to contribute genes to Melanesians, which include the Papuan people of New Guinea. If they bred with these peoples' ancestors, Denisovans could not have lived only in Siberia. It is possible they bred with modern humans in East Asia.

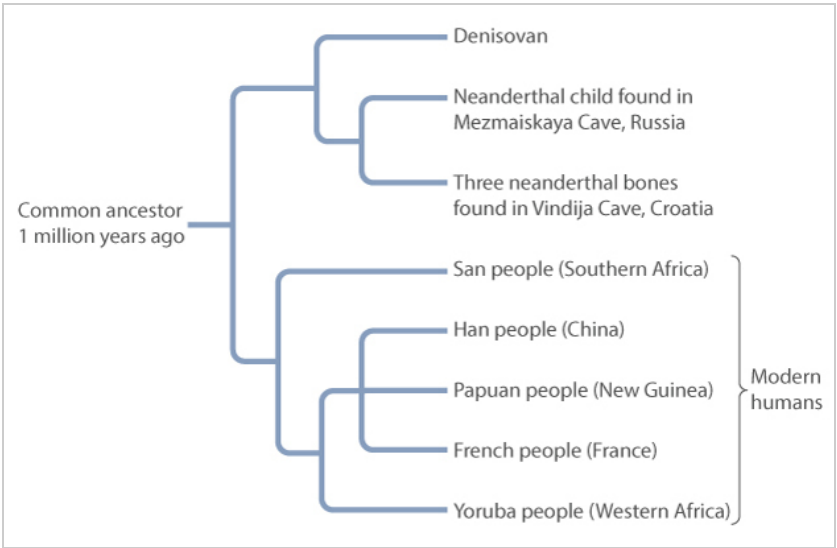


Figure 14: Possible Denisovan relationships.
Researchers used molecular-clock analyses to determine how the Denisovan cave-dwellers were related to Neanderthals and modern humans.
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Test Yourself

The Denisovan bone and tooth and many Neanderthal bones were all found in caves. Why might this be? And what does this imply about the fossil record?

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Explain Radioisotope Dating Methods

How do scientists determine the age of a fossil, tool, or sediment? One common method is radioisotope dating. Many substances contain radioactive isotopes, which decay over time at predictable rates. The amount of the radioactive isotope that is left in a sample — the amount that has not decayed into another form — can be used to infer how old the sample is. The time needed for half the "parent" isotope to decay into the "daughter" isotope is called the half-life. Different isotopes have different half-lives.

The age of relatively young objects that contain carbon, such as the *Homo floresiensis* bones, can be determined using a type of radioisotope dating called carbon dating. How does carbon dating work? All living organisms contain multiple carbon isotopes. When the organism dies, its carbon-12 isotope is stable, but its carbon-14 radioisotope is unstable and decays with a half-life of 5,730 years. A 6,000-year-old bone would have about half the ratio of carbon-14 to carbon-12 that a living organism would have. A bone 18,000 years old, such as the *Homo floresiensis* skull, has been through three half-lives. It would have a ratio of carbon-14 to carbon-12 of $1/(2^3)$, or one-eighth.

Carbon dating is only useful for relatively young fossils (i.e., those 50,000 years old or less) and is subject to several important assumptions and expected variation. Once they complete their analysis, researchers give the age of the fossil as a range rather than as a specific date. For fossils older than the limits of radiocarbon dating, many other techniques based on similar principles are available. For example, rather than collecting material from the fossil itself, scientists can collect geological materials from the sediments in which the fossils are embedded. Scientists then measure within those geological materials the ratios of other radioisotopes, such as Uranium-238, which has a half-life of 4.5 billion years and can be used to date very old rocks.

What other methods can scientists use to determine a fossil's age? The *H. floresiensis* team used a technique called luminescence dating to develop estimates of dates that they could compare to their carbon dating estimates from cave sediments. Certain crystalline minerals, including quartz, store energy from sunlight. Heating quartz crystals releases the stored energy. The amount of luminescence released indicates the amount of time since the crystals last encountered sunlight or intense heat. Luminescence dating of quartz crystals is useful especially for fossils that are buried in the absence of nearby volcanic ash layers.

Another recently developed method of dating that uses quartz crystals is called cosmogenic-nuclide burial dating. This method dates crystals based on the decay rates of the radioactive isotopes aluminum-26 (^{26}Al) and beryllium-10 (^{10}Be). Quartz crystals on Earth's surface that are exposed to cosmic radiation produce these isotopes in a known ratio. When the crystals are buried in sediment, they no longer produce the isotopes. The longer they are buried, the more the isotopes decay, changing the ratio of ^{26}Al to ^{10}Be.

Scientists can use the cosmogenic-nuclide method to date crystals as old as

3 million years. In 2009, Shen and colleagues used this method it to recalculate the age of "Peking Man," a famous *Homo erectus* fossil found in 1918 in the Zhoukoudian caves near Beijing, China (Figure 15). They estimated that the fossil was ~770,000 years old — 250,000 years older than previous estimates. The new date suggests that *H. erectus* could survive a much colder climate than scientists had previously thought, as geological evidence indicates that this area of China was quite cool 770,000 years ago.



Figure 15: Replica of a *Homo erectus* skull reconstructed from fossils. Cosmogenic $^{26}Al/^{10}Be$ burial dating in China's Zhoukoudian caves indicated that the *Homo erectus* fossil known as "Peking Man" is much older than scientists thought.
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Dalton, R. Peking Man older than thought. *Nature* (2009) doi:10.1038/news.2009.149. Used with permission.

As dating methods become more precise, scientists can more easily fill in gaps in human migration patterns and better understand relationships among extinct hominins. As well, they can better understand how extinct hominins are related to modern humans. New hominin fossils continue to be discovered and analyzed all the time. Without a doubt, human evolution and migration promise to remain vital areas of active research for centuries to come.

BIOSKILL

IN THIS MODULE

- **Human Evolution**
- Summary
- Test Your Knowledge

PRIMARY LITERATURE

Classic paper: The discovery of *Australopithecus africanus* (1925)
Australopithecus africanus: The Man-Ape of South Africa.
View | Download

Unearthing the secrets of ancient human DNA
Ancient human genome sequence of an extinct Palaeo-Eskimo.
View | Download

SCIENCE ON THE WEB

Early Humans
Explore this Smithsonian resource about the evolution of humans

Summary

OBJECTIVE **Describe adaptations of major hominid lineages.**

The family Hominidae includes the living great apes (chimpanzees, bonobos, gorillas, and orangutans) along with modern humans. Hominins are the subset of hominids that evolved after the split between modern humans and chimpanzees and bonobos; these include several species of *Australopithecus* and *Homo* species. Many hominin species have been identified. Hominin evolution is characterized by an increasing reliance on bipedal walking and increase in brain size (along with tool use and other complex behaviors). Much evidence indicates that although most hominins evolved in Africa, several species migrated out of Africa into the Middle East, Europe, and Asia. Some species co-occurred and even interbred in these areas. *Homo erectus* was the first hominin to migrate out of Africa. This species was likely quite similar to the modern human ancestor, if not the ancestor itself.

OBJECTIVE **Explain how hominin evolution is characterized by diversification and the concurrent existence of multiple hominin species.**

The earliest known hominin lived 6.5 million years ago. Hominins are characterized by bipedalism, complex tool use, and increasingly large brains. Early hominins likely moved both on the ground and in trees. Full bipedalism likely evolved around 1.9 million years ago. Evidence suggests that hominins used stone tools as long ago as 3.4 million years. Brain size increased stepwise over time as new hominin species evolved, expanding from 300 cm^3 in the earliest hominin species to about 1,350 cm3 in modern humans.

OBJECTIVE **Describe the major features of human evolution, including bipedalism, migration, technology, and culture.**

Modern humans, *Homo sapiens*, appear in the fossil record about 200,000 years ago. They evolved first in Africa and migrated to populate other continents. One theory, based on mitochondrial DNA evidence, suggests that all living humans descended from a single group that left Africa about 100,000 years ago, replacing other hominin populations around the world. Another hypothesis suggests that human evolution is a continuum. The trellis hypothesis, supported by analyses of multiple DNA regions, suggests that there has been significant gene flow between hominin groups over 1.5 million years. Elaborate cave paintings in France are as old as 36,000 years. The presence of art indicates a capacity for symbolic thought that may have helped *Homo sapiens* persist while other groups (e.g., Neanderthals) died out. Agriculture developed around 11,500 years ago in the Middle East and likely played a large role in population expansion and the development of the complex civilization that characterizes modern humans.

Key Terms

bipedalism
Walking upright on two legs; a characteristic of hominins.

hominid
Member of the great apes in the family Hominidae, including humans, chimpanzees, gorillas, and orangutans.

hominin
Hominid species that evolved after the split from chimpanzees and bonobos.

Homo sapiens
The anatomically modern human, which appeared in the fossil record about 200,000 years ago and is the only extant hominin species.

migration
Movement of people or other animals from one region to another.

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- Human Evolution
- **Summary**
- Test Your Knowledge

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Test Your Knowledge

1. How old are the oldest fossils thought to have at least some human characteristics (*Sahelanthropus tchadensis*)?

- 36,000 years
- 200,000 years
- 350,000 years
- 3 million years
- 6.5 million years

2. What is the significance of early cave paintings?

- Specific bone structures would have been required to create such paintings.
- They indicate a capacity for symbolic thought.
- They indicate that Neanderthals and modern humans both made art.
- They show the specialization of professions that postdate agriculture.
- They trace the path of human migration.

3. When did *Homo sapiens* appear in the hominin evolutionary tree?

- 36,000 years ago
- 3 million years ago
- 11,500 years ago
- 6.5 million years ago
- 200,000 years ago

4. What does the position of the foramen magnum indicate about a hominid?

- It indicates the size of the brain.
- It indicates the size of the hominid.
- It indicates what type of food the hominid ate.
- It indicates whether the hominid is a modern human.
- It indicates whether the hominid walked upright.

5. Which description of increases in brain size over evolutionary time is most accurate?

- Australopiths had ape-sized brains, but by the time of *Homo erectus* hominin brains had reached modern proportions.
- The evolution of brain size was gradual and consistent, with each successive species having a marginally larger brain.
- Humans survived when Neanderthals died out because humans had bigger brains.
- The largest leap in brain size was between *Homo habilis* and *Homo erectus*.
- Stepwise increases in brain size are seen throughout hominin evolution.

6. How was *Australopithecus afarensis* different from *Homo ergaster*?

- It had a smaller brain.
- It had large teeth adapted for tough foods.
- It lived in Asia.
- It evolved later.
- It was fully bipedal.

7. In what way does the trellis hypothesis of human migration differ from the out-of-Africa hypothesis?

- It hypothesizes that humans evolved in Africa.
- It is based on evidence from mtDNA.
- It hypothesizes that hominins interbred frequently for over 1 million years.
- It hypothesizes that modern humans evolved in Europe.
- All answers are correct.

8. How are the genomes of living Europeans different from the genomes of living Africans?

- DNA suggests the two groups evolved from different hominin species.
- European DNA has regions suggesting interbreeding with *H. erectus*.
- European DNA has regions suggesting interbreeding with both *H. erectus* and *H. neanderthalensis*.
- European DNA has regions suggesting more interbreeding with *H. neanderthalensis*.
- European DNA suggests that they evolved from *H. neanderthalensis*.

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