Chapter 5: Hominin Evolution

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Learning Objectives

- Explore how we first began to study our own ancestors and how we continue to do so today
- Examine the fossil evidence of some of our earliest ancestor species: *S. tchadensis, O. tugenensis,* and *A. ramidus*
- Examine the unique features of the Australopithecines
- Consider the members of our own genus that we are still learning about: *Homo naledi*, *Homo floresiensis*, and *Homo luzonensis*
- Discover why *Homo erectus* was so successful and widespread
- Examine the similarities and differences between us and our closest extinct relatives, the Neanderthals

Learning about Human Evolution

When discussing human evolution, it is important to remember a few key points: The first is that evolution is not about progress. It is about adaptation and survival. Some species were very well adapted to survive in their environment and lasted for hundreds of thousands of years while others were quickly outcompeted and went extinct relatively quickly. Evolution doesn't follow a straight line – one species doesn't simply replace the next species – there are overlaps and starts and stops. While modern chimpanzees are our closest relatives, the modern chimpanzees of today did not evolve into the modern humans of today. Rather, both of those species evolved from a species that exist in the past (that does not exist today) but followed different evolutionary paths as they adapted to different environments and different modes of survival. And we haven't recovered one hundred percent of the fossil record – we haven't recovered a fossil example of every species that ever existed in the past. The following chapter is based on the fossil evidence that we have recovered so far and the information we know about those species.

Discovering Human Ancestors

Paleoanthropology is an active subfield of anthropology and we are constantly adding to our knowledge about the past through the discovery of fossil evidence. The fossil record currently offers only a small glimpse into the diversity of beings that existed in the past. Some estimates suggest that the fossil evidence shows less than 5 percent of all primate species that ever existed in the past. We have found most of this fossil evidence in a few select locations, primarily in Africa and Asia; however, there could have been primates in other places that we haven't discovered yet. Therefore, any discussion of primate and human evolution has to be tentative because we are constantly adding new information to our understanding of what happened in the past.

Usually, when a new fossil is discovered, the credit for the discovery is given to the lead Paleoanthropologist on the project. Although the finds are usually attributed to a single individual, the discovery of new fossils is actually done by teams of scientists, led by a paleoanthropologist but including students and local workers from the surrounding region.

Figure 1: Replica of the Taung Child with endocast, American Natural History Museum, NY. Source: Wikimedia Commons

We have been studying human evolution and trying to understand the relationship between the humans who exist today and the species that came before us for hundreds of years. The first fossil human ancestors were found in a cave in the Neander Valley in Germany in 1856, three years before Darwin published *On the Origin of Species*. We now know that the fossils were Neanderthal skulls. At the time people knew that these skulls were not human, but they also knew that the skulls were more similar to humans than to anything else alive in the world. The idea that humans evolved, let alone that they could have evolved from an Ape, was very unpopular in the late 1850s and there wasn't enough fossil evidence to support the idea at that point. But slowly, we found more evidence of human ancestor species. In 1891, Eugene Dubois found the first *Homo erectus* fossils in East Java, Indonesia and these fossils were very clearly not human but not an ape either. People began to accept the idea that humans evolved from apes, so they started looking for the "missing link" in human evolution – a species that connects humans to apes (the problem is that no such species ever existed because that is not how evolution works). At the time, everyone assumed that the thing that made humans different from apes was our big brain and use of tools. But by the early 20th century, we started finding fossils of human ancestors that were clearly human ancestors but had small brains. This included specimens such as the Taung Child, discovered in 1924 by Raymond Dart's student in a limestone quarry in South Africa (Figure 1). The student thought that he had found a baby baboon skull, but instead, it was a baby small-brained human ancestor, *Australopithecus* *africanus*. This disproved the idea that big brains are what makes humans "human". Instead, we discovered that it was **bipedalism**, the ability to walk upright on two legs, that separated humans from the rest of the primates.

Walking Upright: The First Human Ancestors

During the Miocene, environments began to change, and the rich forests that had dominated since the beginning of the Cenozoic began to be replaced with pockets of grasslands and savannas. When the forests began to contract, the ape species that evolved in the Miocene had to find ways to survive and find food in an environment with fewer trees and fruits and more open spaces and grasses and leaves. The ape species that survived the end of the Miocene must have possessed some characteristic or characteristics that helped them survive in this new environment, likely the ability to walk on two legs which all living primates today possess.

Scholars agree that bipedalism is the evolutionary adaptation that separates humans from non-human primates. The ability to walk upright appears to have given these species an adaptive advantage in the changing climate of the late Miocene. It allows individuals to see over long grasses and scrub to detect any approaching threats and see potential resources. It frees up the front two arms to carry resources from one location to another more easily, instead of having to rely solely on carrying things in their mouths as other mammals do. And it reduces the body's exposure to solar radiation by having only the top of the head facing the sun, rather than the whole back. All of these features would be beneficial in an environment that is transitioning from tropical rainforest to open grasslands and savanna. The anatomical changes that make species better suited for walking upright are what paleoanthropologists examine when trying to determine if a species is a human ancestor or not. These anatomical changes didn't happen all at the same time or in a single species. There were likely many different species that were able to walk upright on two legs that existed over the last 7 million years, but not all those species left descendants behind who would eventually become us.

Based on comparing the genetic evidence from living humans and living chimpanzees, we estimate that the last common ancestor of chimpanzees and humans lived approximately 6 to 9 million years ago. After this point, the species that would become chimpanzees and the species that would become humans were genetically separated. Unfortunately, this period is particularly difficult to study because there aren't many archaeological sites with preserved and datable hominoid fossils from this time period. Therefore, we aren't exactly sure which species represents the last common ancestor of chimpanzees and humans, but we have a few good possibilities.

One possibility is a species known as ***Sahelanthropus tchadensis*****.** *Sahelanthropus tchadensis* was first discovered in Chad in 2001 and dates to between 7.2 and 6.8 million years ago (Figure 2). There is not a lot of fossil evidence for this species and most of the evidence consists of skull fragments. This species had a relatively small brain (even slightly smaller than a modern-day chimpanzee), and very prominent brow ridges. However, *Sahelanthropus* also had a slightly **shifted foramen magnum**. The foramen magnum is the opening at the bottom of our skull where the spinal cord connects to the brain. For humans, this opening is underneath our skull, which helps us balance the weight of our upper bodies over our lower bodies. For modern chimpanzees, that opening is at the back of their skulls because their bodies are not designed for habitual upright walking. *Sahelanthropus tchadensis* had a foramen magnum that was slightly more underneath his skull than other hominids from this period, suggesting that he might have been better at walking upright on two legs than other species of the time. However, the forward curving ulna shaft in *Sahelanthropus tchadensis* suggests that this species knuckle-walked, like chimpanzees and apes (Meyer et al. 2023). It is, therefore, unclear if *Sahelanthropus* was truly bipedal, or if the shifted foramen magnum simply means that he would have been better able to walk upright than other Miocene apes.

Figure 2: Replica of *Sahelanthropus tchadensis* cranium in the Musée de l'Homme (Museum of Man), Paris. In the background is the cranium of the *Ardipithecus ramidus*. Source: Wikimedia Commons.

Another possible first human ancestor is ***Orrorin tugenensis*.** This species was discovered in 2001 in central Kenya and dates to between 6 and 5.8 million years ago. We have slightly more fossil evidence for this species, although it is still a small number of fossils. We believe that *Orrorin tugenensis* was approximately the size of a modern chimpanzee, but it had a wear pattern on the upper left femur that is consistent with bipedalism (a wear pattern is the marks left on bones from repeated motion, and the upper left femur is the part of the leg bone that connects to the hip socket). The wear pattern on *Orrorin tugenensis*' femur is typical for species that walk upright on two legs and indicates that *Orrorin tugenensis* must have walked upright with some regularity. Additionally, *Orrorin*'s femoral neck was angled, which would help bring his knees together and assist with walking on two legs. However, the rest of his post-cranial evidence indicates that he also climbed trees, suggesting that, like *Sahelanthropus tchadensis*, this was not a species that was fully bipedal but rather one that was becoming bipedal.

Whether *Sahelanthropus tchadensis, Orrorin tugenensis,* or some other yet-to-be-discovered species is the first member of the human family tree is unclear. However, by 4.5 million years ago, a new species emerged that is clearly more closely related to modern humans than to any of the other living primates:

Ardipithecus ramidus. First discovered in 1992 by Tim White and his team and dating to between 4.5 and 4 million years ago, evidence of *Ardipithecus ramidus* comes primarily from Ethiopia. *Ardipithecus ramidus* is still relatively small in size, with body proportions more similar to a chimpanzee, particularly short legs, long arms, and a small brain size (Figure 3). However, *Ardipithecus ramidus* has a number of anatomical changes that indicate that this was a species that was evolving to be better able to walk upright on two legs. *Ardipithecus ramidus* had a fully shifted foramen magnum like a modern human. Their pelvic bones were also better adapted for walking upright, although they are still considered transitional: partially well adapted for walking upright and partially well adapted for climbing in trees. While *Ardipithecus ramidus'* legs, spine, and pelvis were better for walking upright, this species still had a **divergent, opposable big toe** that would have been capable of grasping branches. The rest of Ardipithecus ramidus's toes were more rigid, a feature that helps with walking upright. It is unclear what these feet adaptation would mean in terms of how Ardipithecus ramidus would have walked upright, but we do believe that this species could and did walk on two legs and that it was probably not the first Miocene ape to be able to do so. It is likely that *Ardipithecus ramidus* spent as much time in trees as they did on the ground, but the way they moved around in both locations is unlike any species that is alive today. *Ardipithecus ramidus* is clearly a species that is more closely related to modern humans than to any of the other living primates, including chimpanzees and bonobos. The most famous, and most complete, specimen of *Ardipithecus ramidus* recovered so far is known as **Ardi**. Ardi dates to 4.4 million years ago and is a partially complete, female skeleton. She is one of only a few partially complete skeletons older than a million years old that have been found to date.

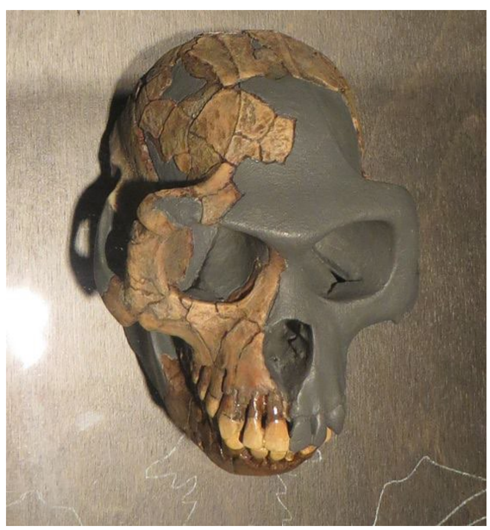

Figure 3: Replica of *Aridpithecus ramidus* skull from Royal Belgian Institute of Natural Sciences, Brussels. Source: Wikimedia Commons

The Australopithecines

After 4 million years ago, we have an abundant fossil record of the genus of hominins that dominated the landscape of the new African savanna and woodlands – the Australopithecines. The Australopithecines are among the most well-known of our ancestor species and there are many species within the genus[1] (Figure 4). In general, the Australopithecines were species that were fully bipedal with many adaptations for walking on the ground on two legs, in some cases in very similar ways to those used by modern humans. However, they were also a species that still had many adaptations for life in the trees, including long arms, short legs, a primarily plant-based diet, few (if any) tools, and small brains.

Figure 4: Map of Australopithecine sites in Africa. Source: Wikimedia Commons

One of the best-known and longest-lived early human species is ***Australopithecus afarensis***. *Australopithecus afarensis* dates to between 3.85 million years ago to 2.95 million years ago and is found throughout Eastern Africa. This species had many adaptations for walking upright on two legs that are also found in modern humans. This includes a curve in the lower spine which helps transfer the weight of the upper body to the pelvis and legs and moves the center of gravity from the front of the body (where it is found in chimpanzees) to the center of the pelvis (where it is found in humans). It also includes a foot that lacked a divergent big toe, with their toes mostly in a single line at the top of the foot. Finally, Australopithecus afarensis had a pelvis shaped more like a basket, which is also designed to help support the weight of the upper body over the lower body. *Australopithecus afarensis* had a slightly larger brain than the earlier hominin species, about 20 percent larger than a modern chimpanzee but only a third of the size of a modern human brain (Figure 5). Their overall brain structure appears more similar to that of a chimpanzee and appears to have grown at about the same rate as a modern chimpanzee brain, but the

[1] There are many species of Australopithecines so this chapter only covers some of them. For more information about the other Australopithecus species, please see: https://humanorigins.si.edu/evidence/human-fossils/species

slightly larger size indicates a longer period of infant dependency, a trait seen in modern humans. In addition to their small brains, *Australopithecus afarensis* had several other **retained ancestral traits** that made them appear more ape-like. This includes finger bones that were long and curved, arms that were long relative to their legs and slightly curved, and shoulder blades with more rotation than those found in *Homo sapiens*. These retained ancestral traits indicate that *Australopithecus afarensis* retained some arboreal abilities and spent time in trees (Figure 6). *Australopithecus afarensis* also had an ape-like jaw that juts out from the face, giving the impression of a snout (known as prognathism) and large molars, more like apes. However, analyses of their teeth indicate that they ate mostly soft foods, such as fruits and plants, which is consistent with their funnel-shaped rib cages which could hold a big stomach for digesting plant materials. Finally, *Australopithecus afarensis* had pronounced **sexual dimorphism**, with males that were almost twice as large as females in the species. These features make Australopithecus afarensis look more like a chimpanzee from the waist up. But from the waist down, *Australopithecus afarensis* moved around and looked more like a modern human. Having adaptations for living both on the ground and in trees may have been why this species was able to survive for almost a million years in a variety of different environments.

Figure 5: Reconstruction of an *Australopithecus afarensis* skull. Source: Wikimedia Commons

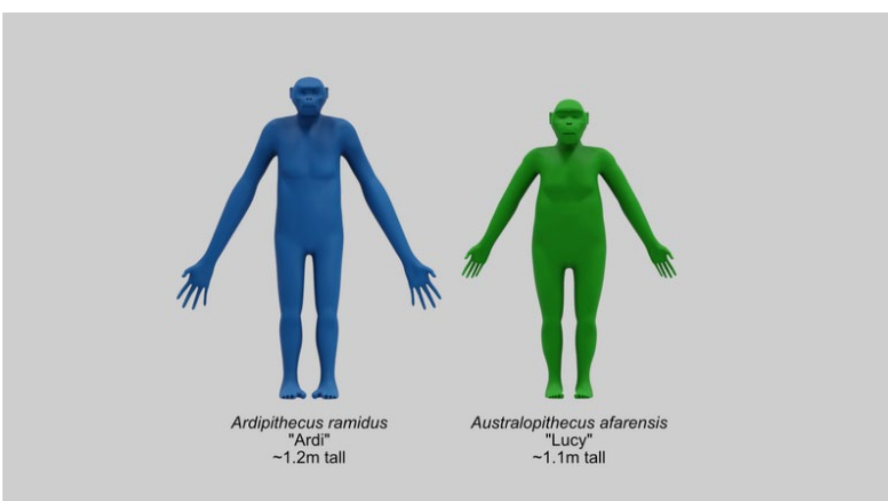

Figure 6: Reconstruction of *Ardipithecus ramidus* (left) and *Australopithecus afarensis* (right). Source: Keith Chan, Wikimedia Commons

While paleoanthropologists have discovered many *Australopithecus afarensis* fossils, the two most famous discoveries are the Laetoli footprints and Lucy. **The Laetoli footprints** aren't an *Australopithecus afarensis* fossil, but rather they are evidence of *Australopithecus afarensis* bipedalism. The footprints were found in 1978 by Mary Leakey and her team and consist of a trail of 70 footprints made by two individuals walking side by side over a distance of 88 feet 3.59 million years ago in Laetoli, Tanzania (Figure 7). The footprints were made in a volcanic ash-mud, which is why they preserved so well and why we can date them so accurately. What this trail of footprints shows is that the species who made them, which we believe to be *Australopithecus afarensis*, was not only anatomically capable of walking upright on two legs but that they actually did. The footprints show a slow swinging gait, well-defined arches, heel-toe prints, and toes that were mostly in-line with one another. The footprints also show a short stride, which indicates the short legs of this species. Finally, the two sets of footprints are very different sizes, one large set and one small set, which likely indicates that these footprints were made by individuals of different sizes and likely a male and a female due the sexual dimorphism of this species.

Figure 7: A replica of the Laetoli footprints at the National Museum of Nature and Science, Tokyo, Japan. Source: Wikimedia Commons

Figure 8: Skeleton of Lucy in the National Museum of Ethiopia. Source: Wikimedia Commons

Lucy is a partially complete *Australopithecus afarensis* skeleton (Figure 8). She was discovered in 1974 by Don Johanson and his team in Hadar, Ethiopia. She is approximately 40 percent complete, making her one of the most complete *Australopithecus afarensis* specimens recovered, dates to 3.2 million years ago, and her nickname comes from a Beatles song, “Lucy in the Sky with Diamonds”. She confirms that *Australopithecus afarensis* was a species that had adaptations from tree-climbing and walking bipedally. Recent analyses of her skeleton also show that she may have died from injuries sustained from falling out of a tree, indicating that she must have spent part of her time in trees in addition to walking on the ground on two legs.

After *Australopithecus afarensis*, the Australopithecus genus seems to split into two main groups, which we refer to as the Robust and the Gracile species. Initially, paleoanthropologists thought that the Gracile species evolved into the Robust species, but now we know that these species were contemporaries and both likely evolved from an earlier Australopithecine, possibly *Australopithecus afarensis or Australopithecus anamensis*. Most paleoanthropologists now think that the Robust Australopithecines are different enough from the rest of the Australopiths that they belong in their own genus and are usually referred to as the genus *Paranthropus*.

The Robust Australopithecines are distinctive because of the presence of a **sagittal crest** – a thin line of bone on the top of the skull that acts as a platform for muscle attachment found in animals with small brains (Figure 9). It develops in animals that do heavy chewing and forms as the bone grows. It allows these animals to have larger, stronger jaw muscles which can be used to eat course, fibrous plant materials.

Figure 9: Replica of *Paranthropus aethiopicus* at the Natural History Museum, London showing the sagittal crest. Source: Wikimedia Commons

There were several species of Robust Australopithecines in Eastern Africa between 3 and 1 million years ago. The last of the Robust Australopithecines was ***Paranthropus boisei***. *P. boisei* was found throughout East Africa between 2.3 and 1.2 million years ago and had the most pronounced features of the Robust Australopithecines, with a very large teeth, very large sagittal crest, and large zygomatic arches (cheekbones) that give them a characteristic dish-shaped face. *P. boisei* was slightly larger than the other Australopithecines, in terms of overall size, tooth size, and brain size (although their brains are still considered small) (Figure 10). These distinctive features all suggest that *P. boisei* was capable of eating a diet based on coarse, fibrous plant material if necessary. Analyses of their teeth indicate that this wasn't the only thing this species was eating and instead they probably primarily ate mostly grasses and sedges. However, if those grasses and sedges weren't available, *P. boisei* could eat tougher, harder-to-eat plant material and this may have been the reason that this species was the last of the Australopithecines. The recent dates of *P. boisei* and the fact that this species was contemporary with members of the genus *Homo* raises questions about the capabilities of this species. Recent analyses of the hand and shoulder bones of *P. boisei* indicate that this species could have been capable of making stone tools, although no stone tools have been found in association with this species so far (Richmond 2020).

Figure 10: Replica of *Paranthropus boisei* skull. Photo take at the University of Zurich. Source: Wikimedia Commons.

The Australopithecines were a successful genus of human ancestors. From the waist down, these species had human-like characteristics, with numerous adaptations for walking upright. But from the waist up, these species still had many retained ancestral traits, such as small brains and arboreal arms. The last of the Australopithecines were contemporary with the genus *Homo*. They were likely able to co-exist with them members of our own genus because of their adaptations for an ecological niche that the members of the genus *Homo* could not occupy.

The Genus *Homo*

About 2.5 million years ago, at the same time that the robust Australopithecines diverged from the rest Australopithecines, another group of hominins seems to have broken off from the main Australopithecine line[2]. It is unclear why this split happened, but it seems to be related to an increase in brain size. One

[2] This is about the same time that chimpanzees and bonobos split into two separate species.

possible explanation for this increase is the introduction of a genetic mutation that prevents jaw muscle growth. This is a mutation that all humans today have but that is absent in apes and **the molecular clock** calculates that this mutation first appeared between 2.1 and 2.7 million years ago. This coincides with the emergence of the first members of the genus *Homo.* Developing a big brain may have just been an accidental byproduct of not having heavy jaw muscles pressing down on the skull, restricting brain growth.

Around the same time that *Paranthropus* and the first members of the Genus *Homo* were emerging, cycles of wet and dry climatic periods characterized the environment in Africa, ultimately moving toward a cooler and drier climate than that of the Pliocene. In the Pleistocene, which began approximately 2.6 million years ago, pockets of woodlands, especially in northern Africa, were gradually replaced by savannas and grasslands during a period of fairly unstable climate. Many researchers believe that these periods of climate instability were one of the major reasons why the species in our genus had to have increased intelligence, tool use, and are better generalists than their ancestors.

Homo habilis and Homo erectus

The first evidence of the genus *Homo* was discovered in 1960 by Louis and Mary Leakey at Olduvai Gorge in Tanzania. The species they discovered, ***Homo habilis***, dates to between 2.4 and 1.4 million years ago and is found throughout Eastern and Southern Africa. This makes *Homo habilis* contemporary with both *Paranthropus boisei* and *Homo erectus. Homo habilis* is much more like modern humans than any of the Australopithecines. Their brains are a more modern shape, with a higher forehead and a more rounded overall shape, and were larger than any living ape species. However, their brains were still only about half the size of a modern human's brain. But *because Homo habilis* was fairly small in terms of overall size, their brains were big relative to their body size. *Homo habilis* also had smaller teeth and reduced sexual dimorphism compared to the species that came before them. Although *Homo habilis* was more like modern humans, this species did still have some retained ancestral traits including longer arms relative to their body size which suggests some retained ability to climb trees.

Because *Homo habilis* was the first human ancestor found with stone tools, Louis and Mary Leakey thought that *Homo habilis* must have been a hunter. However, the stone tools that *Homo habilis* made, **Oldowan tools**, were not tools that were useful for hunting (Figure 11). These tools consisted of simple stone cobbles with one or two flakes removed from the original stone. They are sharp on one end, but they are large and not suitable for butchery. Oldowan tools are good for smashing. Microscopic analyses of the cut marks on the fossil bones found with *Homo habilis* show tool marks that were made after marks made by the teeth of carnivores. This indicates that *Homo habilis* wasn't a hunter but instead was a tertiary scavenger using tools to access protein and fat-rich bone marrow.

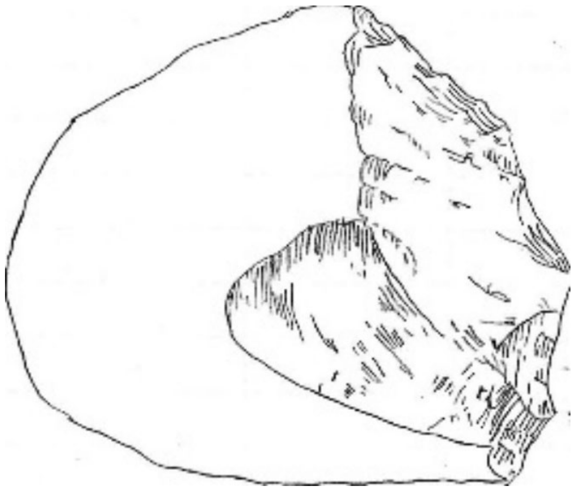

Figure 11: A rough sketch of stone tools found in Olduvai Gorge, Oldowan tools.
Source: Wikimedia Commons

The existence of *Homo habilis* was relatively short, in evolutionary terms. But for about a half million years, several hominin species were able to co-exist in East Africa because they were able to occupy different ecological niches. But after 1.9 million years ago, a new species of hominin appeared on the landscape that had a bigger brain, made sophisticated tools, and had a greater capacity for culture. Using these new advantages, this species, *Homo erectus*, was able to displace most of the species that came before it.

Scientists used to think that *Homo habilis* was the ancestor of *Homo erectus*; however, a recent discovery in northern Kenya proves that *Homo habilis* and *Homo erectus* co-existed in eastern Africa for almost half a million years. ***Homo erectus*** first appeared in Africa approximately 1.9 million years ago and was one of the longest-lasting human ancestor species, finally disappearing around 110,000 years ago. Although *Homo erectus* still had some retained ancestral traits, including a prominent brow ridge, and a flatter, less sloping forehead, this species was much more like us than any of the previous species. *Homo erectus* had a much bigger brain than the species that came before him (Figure 12). They were also the first species to have a projecting nose instead of inset nostrils, the first to have a barrel-shaped ribcage (which would have housed a smaller stomach), and the first to have modern human-like body proportions with long legs and short arms, although they were more heavily muscled than modern humans. *Homo erectus* also had smaller teeth than the species that came before them, although they were slightly larger than the teeth of modern humans. *Homo erectus* had a sharply angled femur, even more sharply angled than modern humans, which would make them very efficient at walking upright on two legs. They likely also had significantly reduced sexual dimorphism. *Homo erectus* also probably had lost their thick covering of fur, giving them the ability to sweat across their whole body. All these changes indicate that Homo erectus lost the features that would help them climb trees but gained the ability to walk, and probably run, long distances efficiently.

Figure 12: Replica of *Homo erectus* crania, Museum of Natural History, Ann Arbor, Michigan. Source: Wikimedia Commons

Thanks to their large brain, *Homo erectus* was the first species to really survive using culture, things that were invented, learned, and passed down from one generation to the next. *Homo erectus* developed a new stone tools known as **Acheulean tools** (Figure 13). These tools are first found in Africa about 1.4 million years ago and represent the first major innovation in lithic technology. These biface tools are known for their distinctive oval or pear shape, and would have been hard to make and required time, practice, and knowledge to be done well. While still not a tool that could be used at the end of a hunting spear, these tools would have been excellent for butchery. In addition to Acheulean tools, *Homo erectus* was still making and using Oldowan-style tools. While *Homo erectus* likely continued to act as a scavenger, they almost certainly would have needed to hunt as well, due to the energy needs of their bigger brain and digestive limitations of a smaller stomach. *Homo erectus* would have had to be hunting in groups, likely using persistence hunting, which requires language in order to work. Evidence of *Homo erectus'* brain structure from **endocasts** indicates that *Homo erectus*' Broca's region was nearly identical to modern humans, and therefore they likely would have been able to produce some kind of speech. Though it was likely not identical to human language, being able to transmit information through a symbolic, learned system would have been a tremendous adaptive advantage for *Homo erectus*. Finally, the best available evidence indicates that *Homo erectus* was the first of our ancestors to have controlled use of fire. The ability to make and use fire was another major advantage for *Homo erectus* because it provides protection from animals, produces light allowing for continued activities after dark, and enables cooking. Cooking makes more calories available for large brains and may have played a role in the reduction of tooth size and food sharing. Fires also provide warmth, which would be important for a species living during the Pleistocene, also known as the last Ice Age. With their bigger brain and better technology, *Homo erectus* was very successful. When a species is successful, its population sizes increase. When population sizes increase, that species usually spread out to find new habitats and environments to live in.

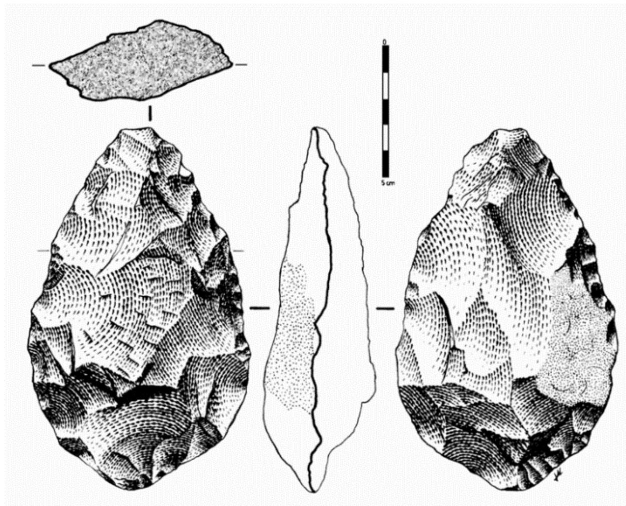

Figure 13: Drawing of an Acheulean handaxe stone tool from Spain, showing front, back, and side profile. Source: Wikimedia Commons

Like all other species discussed so far, the oldest evidence of *Homo erectus* comes from Africa. Unlike all of the other species, we also find *Homo erectus* in Asia, Europe, and the Middle East. *Homo erectus* spread out of Africa relatively quickly. We first find evidence of *Homo erectus* in southern Africa dating to 1.9 million years ago, and they arrived in the Middle East by 1.8 million years ago. We find them in east Asia, in Indonesia, by 1.75 million years ago. *Homo erectus* was in China by 1.66 million years ago and Western Europe by 1.2 million years ago. Some people argue that everything that came after *Homo habilis* and before *Homo neanderthalensis* is *Homo erectus*. Others argue that these species in Africa should be called *Homo ergaster*, in central and east Asia: *Homo erectus*, and in Europe: *Homo antecessor*.

Homo erectus was a successful species and were around almost nine times longer than *Homo sapiens.* They were the first species to have body portions more similar to a modern human, the first species to have a big brain, and the first species to survive by relying on culture and technology. We assume that *Homo erectus* was likely the ancestor of the species that came next, including the Neanderthals and us.

The Mysterious Members of the Genus Homo

Although *Homo erectus* was very successful and seems to have driven many species extinct, there are still some species that were able to co-exist with *Homo erectus* during the last Ice Age including *Homo floresiensis, Homo naledi*, and *Homo luzonensis*. These species are a bit of a mystery to the paleoanthropological community and represent an unexpected mix of modern and archaic traits.

Homo floresiensis was first discovered on the island of Flores in Indonesia in 2003 and was surprising because of two key features: their small stature and their recent date, dating to between 95,000 and 54,000 years ago. *Homo floresiensis* has short legs and would have stood only about three feet six inches tall. Because of their short legs, *Homo floresiensis*' arms and feet look big by comparison, earning them the nickname “the Hobbit”. *Homo floresiensis* also has a small brain, but it is fairly modern in its shape.

Initially, scientists thought that *Homo floresiensis* was an example of a population of *Homo erectuses* that experienced insular dwarfism, a phenomenon that happens on islands where natural selection favors smaller body sizes because of limited resources. We know that this phenomenon happened on Flores in the past because we have found fossil evidence of a pygmy elephant species on the island. In fact, we have evidence that *Homo floresiensis* was making stone tools and hunting these pygmy elephants. However, some scientists now think that *Homo floresiensis* may have already been small when they reached the island and may be more closely related to *Homo habilis* than to *Homo erectus.*

Homo naledi was discovered by Lee Berger's team in 2013 in Rising Star Cave, South Africa. We have a large number of fossils for this species and it is an interesting mix of very modern traits and very ancestral traits, which is surprising given its recent date of between 236,000 and 335,000 years ago. This means this relatively primitive species was not driven extinct by *Homo erectus* and was actually contemporary with the first *Homo sapiens*. Like the Australopithecines, *Homo naledi* had shoulder blades that were well adapted for tree climbing and a wide rib cage. But unlike the Australopithecines, *Homo naledi* appears to have eaten both meat and plants, and rather than being curved, their fingers are very modern in their overall shape. *Homo naledi* had very modern-looking legs and feet and long legs relative to their body size. Their brain was small, less than half the size of modern humans, but it was very modern in its shape – even more modern than *Homo habilis* or *Homo erectus* (Figure 14). This indicates that brain growth was not simply a pattern of gradual increase over time. Berger and his team argue that *Homo naledi* also demonstrated many behaviors that were very modern, despite their small brain size, including intentional burial and possibly producing art. We have not yet been able to extract any ancient DNA (aDNA) from this species, so we do not know how it is related to the other members of the genus *Homo* and for now, represents one of the more intriguing mysteries of Paleoanthropology.

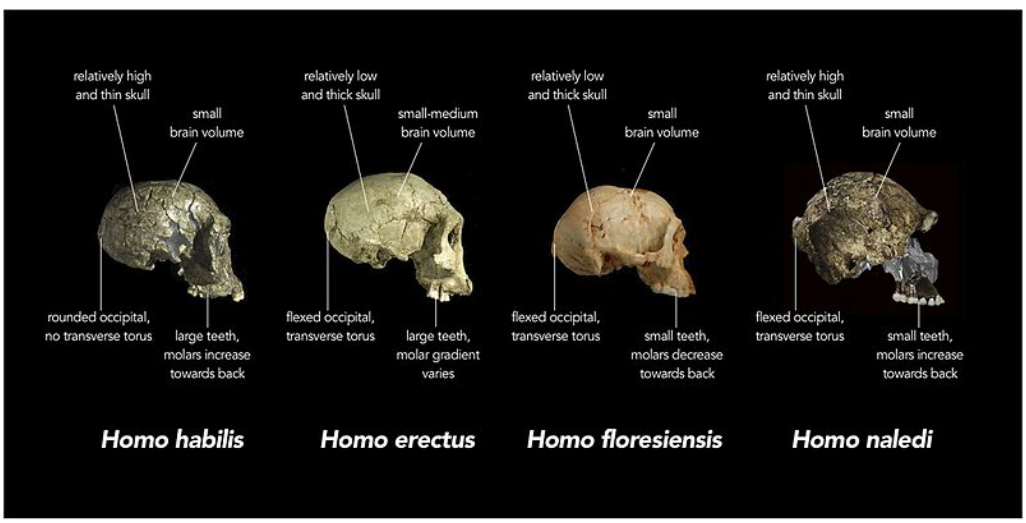

Figure 14: Comparison of skull features of Homo naledi and other early human species. Source: Stringer, Chris. eLife. https://doi.org/10.7554/eLife.10627

The newest addition to the human family tree is *Homo luzonensis*, which was discovered in 2007 in Callao Cave in Northern Luzon, the Philippines. Like *Homo naledi, Homo luzonensis* was a mix of Australopithecine-like and modern-like traits. Their fingers and toes were more curved, suggesting that they spent some amount of time in the trees. But their teeth, especially their premolars, are a very modern shape. In addition to being an interesting mix of ancestral and modern traits, *Homo luzonensis* is also interesting because of its recent date, dating to approximately 67,000 years ago.

The Neanderthals

Of our ancestor species, probably the best known and most misunderstood are the Neanderthals. Neanderthals are usually presented in pop culture as brutish thugs who were anatomically, intellectually, technologically, and culturally inferior to modern humans. However, the more we learn about Neanderthals, the more we realize that this presentation of Neanderthals is far from the truth. We know a lot about ***Homo neanderthalensis*** for several reasons. First, Neanderthals were the first ancestor species we discovered and we have known about them since the middle of the 19^{th} century. Additionally, they lived relatively recently, dating between 400,000 and approximately 40,000 years ago, and they extensively used caves, where archaeological material preserves better. They lived in Europe and southwestern and central Asia (so far, we have no evidence of Neanderthals in Africa).

Figure 15: Replica of a Neanderthal skull at the Natural History Museum in Augsburg, Germany. Source: Wikimedia Commons

When we first discovered Neanderthals, we knew that they were clearly human and very similar to modern humans in many ways, but were still anatomically different enough to be considered strange and abnormal (Figure 15). Like modern humans, Neanderthals had very large brains. Their brains were actually slightly larger on average than modern humans. In addition to their brains being like modern humans, Neanderthals also had a growth pattern like modern humans, with a long, slow childhood that gave Neanderthal children enough time to learn what they needed to know to survive using culture and technology. Neanderthal skulls show a species with huge brow ridges, a flat, sloping forehead, a slightly prognathic jaw, and no chin – all of which make Neanderthals' heads look slightly different from modern humans.

Neanderthals first appeared in the world during a period of extreme cold in the late Pleistocene. As a result, Neanderthals had a number of adaptations that help them survive in this cold climate. Their noses were very large which increased the distance between outside air and the arteries that carry blood to the brain and gives that air more time to warm up before it entered their brains. Neanderthals had broad, squat torsos with short extremities and thick ribs which helped minimize their surface area and conserve heat in the center of their bodies. This made Neanderthals shorter and stockier than modern humans, but Neanderthals were also stronger than modern humans, particularly in terms of upper-body strength. They had extremely well-developed shoulders, especially in their right arms, which indicates that they were using their right arms a lot to do activities that required a lot of strength. The injury patterns seen on Neanderthal skeletons also confirm that Neanderthals performed activities that required a lot of strength and were also dangerous. The closest modern analog for the injuries seen on Neanderthal skeletons is in the injuries seen on professional bull-riders. Neanderthals also had lighter skin, hair color, and eye color, which are all genetic factors that are connected to each other, resulting from reduced production of melanin and are likely an adaptation to living in a colder climate with less sunlight. Although Neanderthals were not identical to modern humans, there is nothing anatomically that would make Neanderthals inferior (or superior) to modern humans, and were likely anatomically similar enough to humans that if you saw a Neanderthal walking down the street you wouldn't look twice at them (Figure 16).

Figure 16: Reconstruction of a Neanderthal wearing modern clothing from the Neanderthal Museum, Mettmann, Germany Source: Clemens Vasters

Behaviorally, Neanderthals were very sophisticated and engaged in the same behaviors as early modern humans. Their stone tools, known as **Mousterian tools**, were technologically sophisticated and advanced (Figure 17). Mousterian tools were a flake technology, which means that for the first time, human ancestors were making more than one tool from a single core stone. These tools were lighter than previous technologies, were a more efficient use of raw material, and allowed Neanderthals to make a variety of different kinds of tools. Mousterian tools are very standardized across a large geographic region, indicating that these tools required a lot of learning and skill to make. These tools were also the first stone tools that could be attached, or hafted, to wooden handles to make stone-tipped hunting spears.

Figure 17: Mousterian spear points (Image rotated 90° and cropped) Source: Gary Todd, Israel Museum, Jerusalem, Israel

Based on the fossils recovered at sites associated with Neanderthals, it is clear that Neanderthals were very successful big game hunters. They were using their stone-tipped spears to hunt the Megafauna that dominated the late Pleistocene landscape. The left-to-right asymmetry seen in Neanderthal arms indicates that Neanderthals were thrusting (rather than throwing) their spears, which also explains the injury patterns we see on Neanderthal skeletons. Isotopic chemical analyses of Neanderthal bones show that while Neanderthals' diets did consist of a lot of meat, they were also eating plants. Toward the end of Neanderthals' existence, it appears that Neanderthals began to also incorporate seafood into their diet. Neanderthals were also the first hominins to wear some kind of clothing. The tools that Neanderthals made could be used to make loose-fitting clothing from animal hides, which would be another adaptative advantage for a species living in the colder climates of the Northern Hemisphere during the last Ice Age. Neanderthals were also engaging in symbolic behaviors, such as making jewelry and possibly adorning their clothing with feathers and shells. New dating techniques used on painted caves in Europe indicate that some of these paintings, first thought to be made exclusively by modern humans, were made by Neanderthals. While Neanderthals probably didn't speak the same way that modern humans do, they likely did have complex communication systems and likely language. Neanderthals have the same mutation to the FOXP2 gene that modern humans have and their anatomy indicates that they would be capable of making the same range of sounds that modern humans can make. There is also evidence that Neanderthals intentionally buried their dead in burial pits and practiced altruism, the practice of selflessly caring for others.

Despite being anatomically, culturally, and behaviorally very similar to modern humans, Neanderthals were largely extinct by approximately 40,000 years ago and completely gone by 28,000 years ago. Although there we are confident that *Homo sapiens* and *Homo neanderthalensis* were similar enough to be able to mate and produce viable offspring (see the chapter case study), the fact that there is only a small portion of Neanderthal DNA present in each modern human indicates that the mating events between the two species were intermittent and not widespread. Instead, we think that the world today is largely the result of the large-scale replacement of Neanderthals by *Homo sapiens*. We aren't completely sure why Neanderthals ultimately went extinct. The last traces of Neanderthals are found in western Europe, suggesting that the influx of *Homo sapiens* into Europe and Asia, and the resulting competition for resources, likely contributed to their extinction. Other factors that may have contributed to the demise of the Neanderthals include changes to the environment at the end of the last Ice Age and the small population sizes of individual Neanderthal groups (see Resource Links for more information) .

The Denisovans

While modern humans of European and Asian ancestry can trace two percent of their DNA back to the Neanderthal genome (see chapter Case Study), some people from East Asia and the Pacific Islands can trace up to six percent of their DNA back to another ancient genome, the Denisovan genome.

The Denisovans were first discovered in Denisova Cave in Siberia from DNA testing on a fragment of a pinky bone. The DNA from this sample shows a species that is genetically distinct from both *Homo sapiens* and Neanderthals but the nuclear DNA shows that the Denisovans interbred with both species. We are still finding fossil evidence of these hominins, and as a result, we don't know much about their anatomy. Based on their DNA, we think that they were similar to Neanderthals in terms of their anatomy, with skulls that were wider and flat and more prognathic, and may be more genetically closely related to Neanderthals as well. Scientists believe that Neanderthals and Denisovans shared a common ancestor – Neandersovans – that spread out from Africa about 750,000 years ago and then split into distinct populations – Eastern and Western – after they left Africa. Denisovans are therefore sometimes referred to as the "eastern cousins" of Neanderthals.

At the end of the Pleistocene, the Old World was full of different hominin species. Some of these species were able to co-exist with minimal interaction. Others appear to have interacted with each other, occasionally interbred, but remained largely independent. But after 40,000 years ago something changed. And by 28,000 years ago there was only one species of bipedal ape left in the world: *Homo sapiens*.

The Last Man Standing: Homo sapiens

The oldest evidence of our own species, *Homo sapiens*, comes from finds at Jebel Irhoud in Morocco and dates to 300,000 years ago. But the controversy surrounding the origins of our own species is one of the most vigorous in Paleoanthropology. There are two main hypotheses about the origins of *Homo sapiens*: the **Out of Africa hypothesis** (also known as the Replacement or Recent African Origin Hypothesis) and the **Multiregional hypothesis**. The Multiregional hypothesis argues that Anatomically Modern Humans originated in multiple places at multiple times from multiple different populations of *Homo erectus*. This hypothesis argues that *Homo erectus* left Africa during the early to middle Pleistocene and that there were no later migrations out of Africa. Instead, those different populations of *Homo erectus* evolved independently into populations of *Homo sapiens,* and then those populations of *Homo sapiens* encountered each other resulting in the modern humans of today. The Out of Africa or Replacement hypothesis argues that *Homo sapiens* evolved in one place, Africa, and then, relatively recently, left Africa to replace any other hominin species left in the Middle East, Europe, and Asia.

According to the Multiregional Hypothesis, *Homo erectus* populations throughout the Old World evolved independently, first to archaic *Homo sapiens* (species that were almost anatomically modern but not exactly like us) then to fully anatomically modern humans. If this hypothesis is true, then we would expect to find a lot of genetic distance within the modern human population because the last time all humans were part of a single population was approximately two million years ago when they were still *Homo erectus* living in Africa. There should also be little chronological overlap between archaic *Homo sapiens* and anatomically modern *Homo sapiens* in a particular region and archaic *Homo sapiens* should be found in multiple regions. If you consider Neanderthals and Denisovans to be part of the *Homo sapiens* species, rather than separate species, then there is both fossil and genetic evidence to support the Multiregional Theory. The Neanderthals and Denisovans fossils could be considered the archaic *Homo sapiens* fossils in different regions and the genetic variation we see in these groups could be intra-species variation, rather than interspecies variation. Finally, there should be a continuity of features found within local populations, or "regional features of high antiquity", meaning that a trait that *Homo erectus* had in a particular region should also be seen in *Homo sapiens* in that region. This is seen in the presence of shovel-shaped incisors in both Asian *Homo erectus* and Asian *Homo sapiens*.

The Out of Africa hypothesis argues that *Homo sapiens* evolved in one place, relatively recently and from a relatively small founding population, and then spread out to all other parts of the world, out competing and replacing any other species that they encountered. If this hypothesis is true, then all archaic *Homo sapiens* fossils, the ones that are not fully anatomically modern, should be restricted to Africa and there should be anatomical and behavioral discontinuity between *Homo sapiens* and the other species found outside of Africa. And when *Homo sapiens* are found outside of Africa, their arrival should be relatively sudden. *Homo sapiens* should also be genetically distinct from non-*Homo sapiens* species. So far, the fossil evidence of *Homo sapiens* does seem to support the Out of Africa hypothesis, with all of the oldest and all of the transitional *Homo sapiens* fossils found in Africa. The mitochondrial DNA (mtDNA) evidence also supports the Out of Africa hypothesis. *Homo sapiens* have very little mitochondrial variation as a species, which is consistent with a relatively small founding population, numbering perhaps only 10,000 to 50,000 people. The most mitochondrial variation among *Homo sapiens* is found in populations that trace their ancestry back to Africa, which also supports the Out of Africa hypothesis. The oldest evidence of *Homo sapiens* outside of Africa comes from the Middle East, with *Homo sapiens* fossils dating to 180,000 years ago found in a cave site in Israel. Evidence for *Homo sapiens* in Asia dates to approximately 120,000 years ago, and in Western Europe, by 54,000 years ago (almost ten thousand years earlier than previously thought).

Case Study: The Genetic Relationship of Neanderthals and Us

Since we first discovered Neanderthals in the 1850s, the biggest question that we had about Neanderthals has always been "how are they related to us?". Initially, we thought that Neanderthals were our direct ancestors, and that Neanderthals evolved directly into modern humans. However, we now know that this is not possible because Neanderthals and *Homo sapiens* were alive at the same time and lived in the same regions. We now think that Neanderthals and *Homo sapiens* share a common ancestor who lived approximately 550,000 to 690,000 years ago in Africa, probably either *Homo erectus* or *Homo heidelbergensis*.

If Neanderthals didn't evolve into modern humans, then how closely related to modern humans are Neanderthals? Are they a separate species from humans? Or are they a subspecies within *Homo sapiens*? Looking at the mtDNA evidence, Neanderthals and *Homo sapiens* are separate species. *Homo sapiens* have very little mtDNA variation, as a species. Most humans differ from each other by an average of eight mtDNA mutations. Neanderthals have even less mtDNA variation within them, about a third of the amount found in modern humans, which likely indicates a very small founding population size and/or a small geographic range for this species. Modern humans and Neanderthals differ by an average of 27.2 mutations, which is too many for Neanderthals and Homo sapiens to be considered part of a single species (For comparison: chimpanzees and modern humans, which are widely accepted as distinct species, differ by an average of 55 mutations).

If Neanderthals and *Homo sapiens* are separate species, how similar are these two species? Anatomically, we see that these two species are very similar but not identical. Behaviorally, we see that Neanderthals and modern humans engaged in the same activities but had stylistic differences. Thanks to new advances in ancient DNA, we can now see that while Neanderthals and *Homo sapiens* are genetically distinct, they were similar enough to be able to interbreed and produce viable offspring. The Max-Planck Institute in Germany has sequenced the nuclear DNA of several Neanderthals and comparing that DNA to the nuclear DNA of *Homo sapiens* we see that for most people today of European or Asian descent, the average modern human genome contains between 1.8 and 2.6% Neanderthal genes. Scientists estimate that combined, approximately 70 % of the Neanderthal genome is theoretically present in modern humans. People who trace their ancestry back to Africa only have approximately 0.3 % of their genes that can be traced back to the Neanderthal genome, which is likely due to the fact that Neanderthals never lived in Africa and therefore couldn't directly interbreed with *Homo sapiens* in Africa. The Neanderthal genes in the African genome are therefore likely the result of back-breeding, where Neanderthal-*Homo sapiens* hybrids, individuals who had both Neanderthal and *Homo sapiens* genes, went back to Africa and interbred with the *Homo sapiens* there. Why *Homo sapiens* interbred with Neanderthals is still a bit of a mystery, but some scientists think that this interbreeding may have provided *Homo sapiens* with an evolutionary "short-cut" – providing them with adaptations for surviving in a colder climate quickly (within the span of a single generation) rather than having to evolve those adaptations independently. This could help explain why *Homo sapiens* are the only two-legged primate left in the world today. However, the same traits that may have helped our *Homo sapiens* ancestors survive the last Ice Age may be harming us today. For example, a trait that helped Neanderthals store fat in their bodies was probably very useful for a species that was trying to survive during the last Ice Age, but is leading to obesity and diabetes in modern humans. Scientists are currently working to identify what traits we have inherited and how they are affecting us today. So far, scientists have connected Neanderthal genes to many aspects of modern human health, including our skin, immune systems, risk for cancer, risk of addiction, and risk for osteoporosis. Researchers at the Max Planck Institute have announced that modern humans inherited major genetic risks for Dupuytren's disease (a disease that leaves fingers permanently bent in a flexed position) from Neanderthals (Argen et al. 2023). Studying the ancient DNA of Neanderthals is a very active line of research in Paleoanthropology, and we are learning a lot about both modern humans and Neanderthals as a result of these ongoing studies.

Chapter Summary

Paleoanthropologists have been studying humans and human ancestors for hundreds of years. Human evolution is not a simple story of progress, but rather a complicated process of adaptation and survival that we are still learning about through ongoing research and discovery. Studying what separates humans from other primates – bipedalism – opened up new questions about other species' relations to humans and what that evolution looked like. Species like *Sahelanthropus tchadensis* and the *Orrorin tugenensis* are both speculated to be some of the first ancestors of humans. Both species had anatomy more like humans than other apes, yet they still retained primitive features like a smaller brain and had not yet fully developed bipedalism. The Australopithecines—one of the most well-known human ancestor genera – share a remarkably similar anatomy to humans from the waist down, but from the waist up, looked more like a chimpanzee. The genus *Homo* consists of species that featured the emergence of larger brains and anatomical characteristics that are more closely aligned with human beings than that of the Australopithecines. What set *Homo erectus* apart and gave them greater commonality with modern humans wasn't just similarities in anatomy, but similarities in behavior and survival using culture. Modern humans' closest extinct relatives, the Neanderthals, are similar to us while also having their own unique characteristics. Neanderthals survived through the creation and use of culture and technology, reflecting our behaviors in using stone tools to hunt and making clothes from animal hides. They were shorter, denser, and stronger than humans, as these attributes gave them an advantage in their environment. They had a similar diet to modern humans and engaged in numerous symbolic behaviors, such as making jewelry and burying their dead. The Neanderthals were similar enough to our own species that we interbreed with them on a small scale. For millions of years, there were several species of bipedal apes surviving in our world. But by 28,000 years ago, only one species remained: *Homo sapiens*. Our own species was so well adapted at surviving that they were able to out compete all of the other species of hominins to be the only remaining bipedal ape today.

Key Terms

Paleoanthropology
Bipedalism
Sahelanthropus tchadensis
Shifted foramen magnum
Orrorin tugenensis
Ardipithecus ramidus
Divergent big toe
Ardi
Australopithecus afarensis
Retained ancestral traits
Prognathism
Sexual dimorphism
Laetoli footprints
Lucy
Sagittal crest
Paranthropus boisei
The molecular clock
Homo habilis
Oldowan tools
Homo erectus
Acheulean tools
Endocasts
Homo floresiensis
Homo naledi
Homo luzonensis
Homo neanderthalensis
Mousterian tools
The Denisovans
Out of Africa hypothesis
Multiregional hypothesis

Comprehension Questions

1. Based on the fossil evidence, what is the one feature that all members of the human family tree possess?
2. Does human evolution follow a straight line where one fossil species turns into the next? Why or why not? How do we know?
3. Which three species are considered our oldest ancestors? Why are these species considered more like us than like any other primate?
4. Why is *Australopithecus afarensis* one of the best-known human ancestor species?
5. Why is *Homo erectus* such an important species in human evolution?
6. Who are the Neanderthals and what is their relationship to us and to the Denisovans?
7. Where did the first *Homo sapiens* come from? Why is this controversial?

Critical Thinking and Engagement Questions

1. Most of the fossil evidence of human ancestors recovered so far has come from Africa. As research in other parts of the world, especially Asia, increases, how might this impact our understanding of human evolution?
2. The importance of ancient DNA in understanding human evolution has only recently come to light in paleoanthropology. How do you think new DNA evidence is going to impact our understanding of human evolution? Going forward, how should scholars address potential disconnects between the DNA and fossil records?
3. What is the relationship between environmental change and human evolution? Given how much humans rely on culture, rather than biology, to survive today, do you think humans will continue to evolve biologically in the future?

Resource Links

Because paleoanthropology is such an active field in Anthropology, there is always new information being produced about human evolution and new discoveries being made. Some of the best resources for that information are below:

- https://humanorigins.si.edu/ This website, produced by the Smithsonian Natural History Museum, has great interactive resources. It has information about the different hominin species and highlights the newest discoveries in paleoanthropology through their various social media pages.
- https://www.nhm.ac.uk/discover/human-evolution.html The Natural History Museum in London has particularly good resources for understanding Neanderthals
- https://www.sciencedirect.com/journal/journal-of-human-evolution The Journal of Human Evolution is the academic journal that publishes much of the cutting-edge research on Paleoanthropology
- https://www.pbs.org/wgbh/nova/series/becoming-human/ PBS has produced some good, although slightly dated, videos about human evolution
- https://www.sapiens.org/archaeology/hominin-extinctions/ This is Sapiens.org article about the connections between climate change and hominin extinctions
- https://www.sapiens.org/archaeology/neanderthals-outlived-homo-sapiens/ This is an interesting article about what the world would be like if Neanderthals hadn't gone extinct

References

Ågren, Richard, Snehal Patil, Xiang Zhou, FinnGen., Kristoffer Sahlholm, Svante Pääbo, and Hugo Zeberg
2023 Major genetic risk factors for Dupuytren's disease are inherited from Neandertals. *Molecular Biology and Evolution* Volume 40, Issue 6, June 2023, msad130, https://doi.org/10.1093/molbev/msad130

Argue, Debbie, Colin P. Groves, Michael S.Y. Lee, and William L. Jungers
2017 The affinities of Homo floresiensis based on phylogenetic analyses of cranial, dental, and postcranial characters. *Journal of Human Evolution* 107(2017):107-133. https://doi.org/10.1016/j.jhevol.2017.02.006

Conroy, Glenn C.
2005 *Reconstructing Human Origins, Second Edition*. New York, NY: W.W. Norton & Company

DeSilva, Jeremy
2021 *First Steps: How Walking Made Us Human*. HarperCollins Publishers: New York, NY.

Détroit, Florent, Armand Salvador Mijares, Julien Corny, Guillaume Daver, Clément Zanolli, Eusebio Dizon, Emil Robles, Rainer Grün and Philip J. Piper
2019 A new species of *Homo* from the Late Pleistocene of the Philippines. *Nature* 568, 181–186 (2019). https://doi.org/10.1038/s41586-019-1067-9

Eswaran, Vinayak, Henry Harpending, and Alan R. Rogers
2005 Genomics refutes an exclusively African origin of humans. *Journal of Human Evolution* 49(1):1-18. https://doi.org/10.1016/j.jhevol.2005.02.006

Granger, Darryl E., Dominic Stratford, Laurent Bruxelles, and Kathleen Kuman
2022 Cosmogenic nuclide dating of Australopithecus at Sterkfontein, South Africa. *PNAS* 119 (27) e2123516119. https://doi.org/10.1073/pnas.2123516119

Hardy, Karen, Hervé Bocherens, Jennie Brand Miller, and Les Copeland
2022 Reconstructing Neanderthal diet: The case for carbohydrates. *Journal of Human Evolution* 162(2022): https://doi.org/10.1016/j.jhevol.2021.103105

Harvati, Katerina, and Hugo Reyes-Centeno
2022 Evolution of Homo in the Middle and Late Pleistocene. *Journal of Human Evolution*. 173(2022). https://doi.org/10.1016/j.jhevol.2022.103279

Lague, Michael R., Habiba Chirchir, David J. Green, Emma Mbua, John W.K. Harris, David R. Braun, Nicole L. Griffin, and Brian G. Richmond,
2019 Humeral anatomy of the KNM-ER 47000 upper limb skeleton from Ileret, Kenya: Implications for taxonomic identification. *Journal of Human Evolution* 126(2019):24-38. https://doi.org/10.1016/j.jhevol.2018.06.011

Lahr, Marta Mirazon Lahr
1994 The Multiregional Model of modern human origins: a reassessment of its morphological basis. *Journal of Human Evolution*. 26(1):23-56. https://doi.org/10.1006/jhev.1994.1003

Macchiarelli, Roberto, Aude Bergeret-Medina, Damiano Marchi, and Bernard Wood
2020 Nature and relationships of Sahelanthropus tchadensis. *Journal of Human Evolution* 149(2020). https://doi.org/10.1016/j.jhevol.2020.102898

Meyer, Marc R., Jason P. Jung, Jeffrey K. Spear, Isabella Fx. Araiza, Julia Galway-Witham, and Scott A. Williams
2023 Knuckle-walking in Sahelanthropus? Locomotor inferences from the ulnae of fossil hominins and other hominoids. *Journal of Human Evolution* 179 (June 2023): https://doi.org/10.1016/j.jhevol.2023.103355

Pomeroy, Emma, Marta Mirazón Lahr, Federica Crivellaro, Lucy Farr, Tim Reynolds, Chris O. Hunt, and Graeme Barker
2017 Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. Journal of Human Evolution 111(2017):102-118. https://doi.org/10.1016/j.jhevol.2017.07.001

Reyes-Centeno, Hugo, Mark Hubbe, Tsunehiko Hanihara, Chris Stringer, and Katerina Harvati, 2015 Testing modern human out-of-Africa dispersal models and implications for modern human origins. *Journal of Human Evolution*. 87(2015):95-106 https://doi.org/10.1016/j.jhevol.2015.06.008

Richmond, B.G., D.J. Green, M.R. Lague, H. Chirchir, A.K. Behrensmeyer, R. Bobe, M.K. Bamford, N.L. Griffin, P. Gunz, E. Mbua, S.R. Merritt, B. Pobiner, P. Kiura, M. Kibunjia, J.W.K. Harris, D.R. Braun,
2020 The upper limb of Paranthropus boisei from Ileret, Kenya. *Journal of Human Evolution*, Volume 141 (2020): https://doi.org/10.1016/j.jhevol.2019.102727.

Stamos, Peter A. and Zeresenay Alemseged
2023 Hominin locomotion and evolution in the Late Miocene to Late Pliocene. *Journal of Human Evolution* 178(2023): https://doi.org/10.1016/j.jhevol.2023.103332

Sykes, Rebecca Wragg
2020 *Kindred*: Neanderthal Life, Love, Death, and Art. London, UK: Bloomsbury Sigma

Tattersal, Ian
2022 *Understanding Human Evolution*. New York, NY: Cambridge University Press.

Timmermann, Axel, Kyung-Sook Yun, Pasquale Raia, Jiaoyang Ruan, Alessandro Mondanaro, Elke Zeller, Christoph Zollikofer, Marcia Ponce de León, Danielle Lemmon, Matteo Willeit & Andrey Ganopolski
2022 Climate effects on archaic human habitats and species successions. *Nature* 604, 495–501 (2022). https://doi.org/10.1038/s41586-022-04600-9

Villaseñor, Amelia, Kevin T. Uno, Rahab N. Kinyanjui, Anna K. Behrensmeyer, René Bobe, Eldert L. Advokaat, Marion Bamford, Susana C. Carvalho, Ashley S. Hammond, Dan V. Palcu, Mark J. Sier, Carol V. Ward and David R. Braun
2023 Pliocene hominins from East Turkana were associated with mesic environments in a semiarid basin. *Journal of Human Evolution* 180:(2023). https://doi.org/10.1016/j.jhevol.2023.103385

Weaver, Timothy D.
2012 Did a discrete event 200,000–100,000 years ago produce modern humans?. *Journal of Human Evolution* 63 (1):121-126. https://doi.org/10.1016/j.jhevol.2012.04.003

Zanolli, Clément, Yousuke Kaifu, Lei Pan, Song Xing, Armand S. Mijares, Ottmar Kullmer, Friedemann Schrenk, Julien Corny, Eusebio Dizon, Emil Robles, and Florent Détroit
2022 Further analyses of the structural organization of *Homo luzonensis* teeth: Evolutionary implications. *Journal of Human Evolution* 163(2022): https://doi.org/10.1016/j.jhevol.2021.103124