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*It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; as these two species are now man's closest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.*

Charles Darwin *The Descent of Man*

Perusing a zoo housing all living animals on Earth, most of us would conclude that out of all of them we most closely resemble the great apes. And among the great apes, we are closest to the chimpanzee in body and behaviour. It was this resemblance that led Darwin to reason that humans most likely evolved in Africa, home to the chimpanzees. He was proved correct many years later, starting with the discovery in 1924 of the 'Taung Child' skull in South Africa. The implication that humans and apes are related caused the greatest public resistance to Darwin's theory of evolution, and many objected strongly to Raymond Dart's interpretation of the Taung Child as a fossil intermediate between apes and humans. Despite all the subsequent fossil finds and artistic renditions of what our extinct ancestors looked like, many people today remain unwilling to acknowledge our evolutionary link to these distant relatives. This reluctance perhaps reflects the unsettling mix of the familiar and unfamiliar that we see in them. Culturally accustomed to thinking of ourselves as unique and separate from all other living as well as extinct life forms, and to believing we were created independently by a god, many find it difficult to accept that we evolved from an ape-like ancestor.

Raymond Dart holding the Taung Child skull

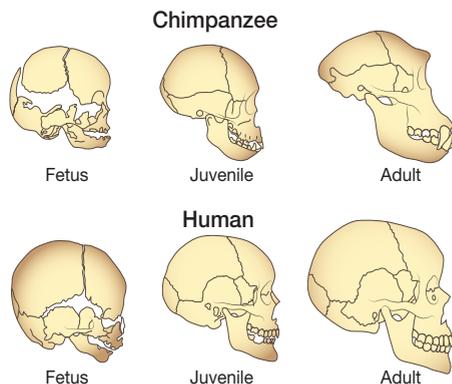


## HUMAN ORIGINS

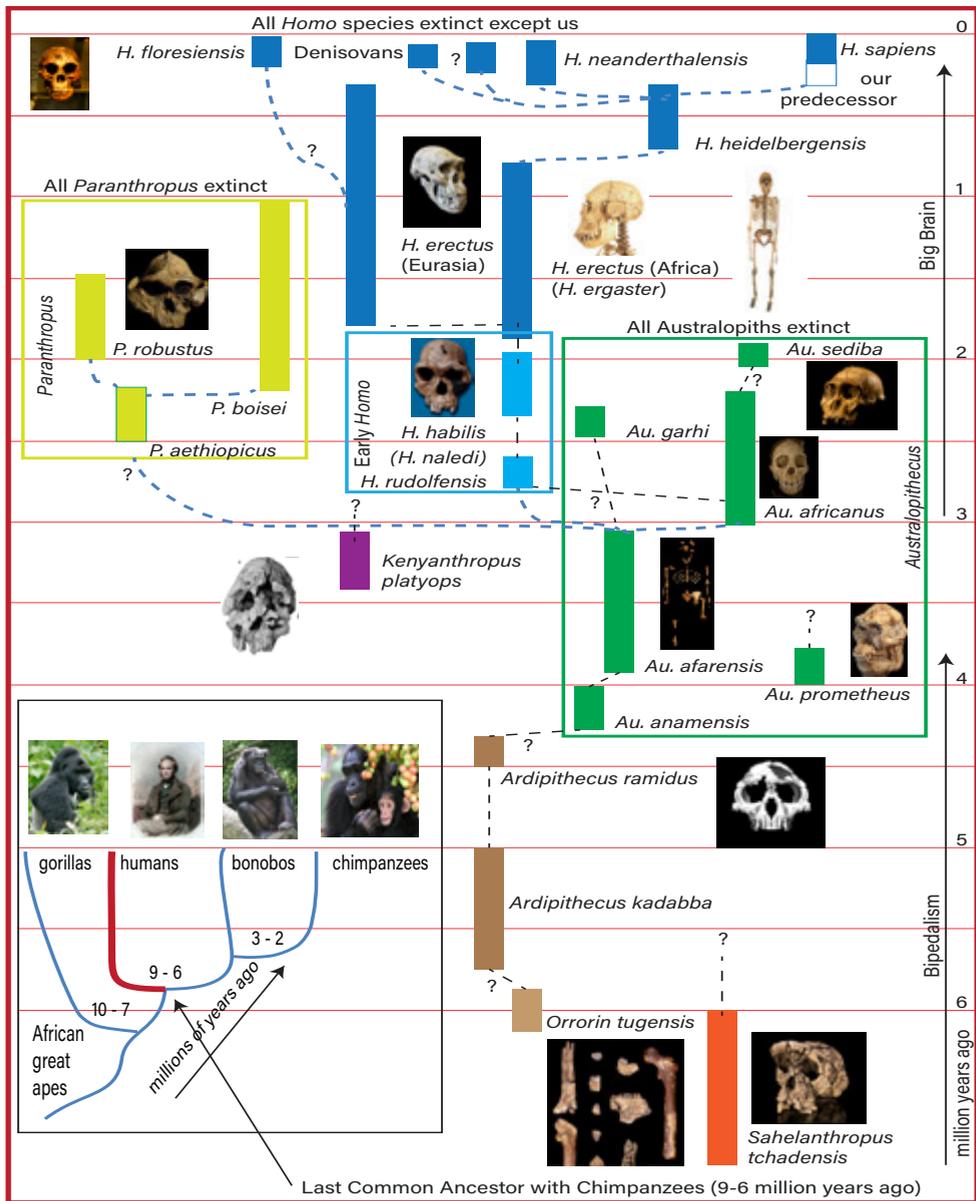
Although we may be closer to chimps than to any other animal alive today, most would also agree that we are, if not in kind then in degree, vastly different from chimps. These differences reflect just how far we have diverged from the apes since our lineage broke away. Chimps may be our closest living relative, but we did not descend from chimps. Rather, humans and chimps share a common ancestor from which both we and chimps diverged over the last 7 million years. Our shared ancestor was probably more gorilla- or chimp-like than human-like because our ancestors progressively left the forest to occupy the increasingly open habitats of woodland, savannah and grassland. It was in adapting to living on the ground as opposed to in the trees that our lineage first diverged from the other great apes.

Our close relationship to chimps is substantiated by the fact that we share an estimated 95 to 98.8% of our DNA with chimps. And yet we appear to be a lot more than 5 to 1.2% different from chimps. This discrepancy reflects how far a little tweaking of the genome can go in producing two closely-related but very different species. Although we share many identical genes with chimps, how strongly and when these genes are expressed can produce very different outcomes. For example, by either slowing development up to when our ancestors reached sexual maturity (neoteny) or speeding up when we reached sexual maturity (progenesis) could explain why we more closely resemble infant as opposed to adult chimps. Relatively few changes in our DNA can produce significant differences because the expression of our traits and features involves the complex interaction of many genes as well as factors outside our genome, such as environmental and cultural influences.

Seven million years is a long time over which natural selection and other processes of evolution could shape our lineage. Since our breakaway, a total of perhaps as many as 25 different species or subspecies have so far been discovered. These different species of our lineage define our hominin (Hominini) tribe, which sits as a nested side branch



We more closely resemble infant than adult chimps

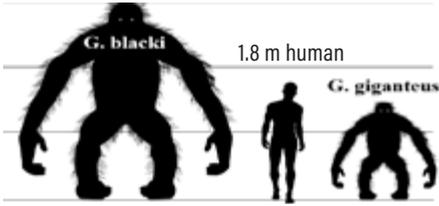


within the great ape family tree. Similar to our descent through the much larger vertebrate tree of life presented in Chapter 2, our hominin tree or lineage includes species both within and outside of our direct line of descent. Many gaps in the fossil record remain and the details are debated as to how all of the known fossils in our lineage relate to one other. However, the many discoveries since the Taung Child provide a reasonable outline of our evolution away from our ape ancestor.

The other living great apes have their own separate evolutionary lineages, but we know little about these. Once the land bridge connecting Africa to Eurasia was too

Fossils define as many as 25 different extinct species that make up our hominin tribe,  
 nested within the African great ape family tree

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Estimated size of extinct giant apes

dry to support forests, the great apes evolved separately in Asia and Africa. Asia has two species of orang-utans, but the fossil record reveals extinct giant apes (*Gigantopithecus*) up to 3 m (9.8 ft) tall and over 500 kg (1100 lbs) that lived up until around 300 thousand years ago. Among the African great apes there are two species of the genus

*Gorilla*, the western gorilla and the eastern gorilla, and two species of the genus *Pan*, the chimpanzee and the bonobo. DNA evidence suggests chimpanzees and bonobos shared a common ancestor as recently as one to two million years ago. And, of course, there is us. Although perhaps as many as 4 to 5 species in our lineage – closely related to us and belonging to our genus *Homo* – managed to live until fairly recently, we *Homo sapiens* are the only member of our lineage still standing today. How did we initially break away from our great ape family and what were the major events that led to the evolution of our human genus *Homo*?

### Walking on two legs

Besides birds, who carry it forward from their distant Cretaceous ancestors the dinosaurs, we are one of just a few animals to move about fully upright on two legs. It was the evolution of our unique striding gait that first set us apart from all other apes; our big brain only evolved much later. Walking upright on two rather than four limbs to become fully bipedal has for a long time been explained by the savannah hypothesis, which views walking upright as a straightforward adaptation to an increasingly open, less treed habitat. How might the transition to walking have come about?

Tropical forests with their nearly continuous tree cover are the principal habitat of many modern apes. The orang-utans are mostly tree dwelling, and when they do



Some bipedal dinosaurs evolved into birds; gorillas and chimps knuckle walk, while we stride fully upright



walk on all fours on the ground they use their fists for support, whereas African ground-dwelling gorillas, as well as chimpanzees and bonobos, walk on all fours using the knuckles of their hands. Chimps do occasionally walk on two legs, such as when carrying valuable food items, but they are not habitual walkers. Chimps will travel a fair distance in search of food, especially in habitats where food is patchily distributed, while gorillas eat more monotonous and locally abundant vegetation. Our common ancestor 7 million years ago was probably more chimp-like, needing to traverse large areas in its quest for a variety of foods, including those that required them spending time on the ground to pick up.

At the close of the Miocene epoch 7 to 5 million years ago, the heyday of the apes was long over, but African and Asian forests were still extensive and likely supported more species of apes in greater numbers than today. However, their forest habitat continued to contract in connection with a drop in CO<sub>2</sub> and global cooling between 7 and 5 million years ago. In the African Rift Valley, tectonic forces as well as climate change promoted the fragmentation of forests into diverse habitats. Apes living in undisturbed forest carried on as before, but apes whose territories extended increasingly to the edges of shrinking forests were under pressure. More open woodland habitats were pressing on them from the one side, while on the other side highly territorial and uncooperative apes prevented them from trespassing further into the forest interior.

Those apes living on the forest fringe had few options and had to increasingly venture out beyond the forest to forage for food in the adjacent woodlands. But navigating the woodland's widely spaced clusters of trees separated by large bushes and patches of grass required a very different mode of movement than did climbing through forest tree canopies. An ape walking on two legs cannot move as fast as one using all four limbs, but can cover the same ground using about a third less energy. In addition to its greater efficiency, walking upright on two legs may have been selected for because it freed up the hands for carrying things, made it easier to see over tall grass and

Tropical forests gave way increasingly to seasonal woodland habitats

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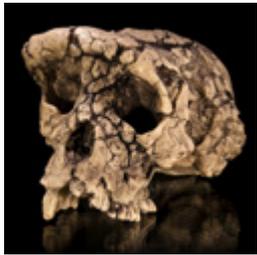
bushes, and reduced exposure to the hot sun while out from under the shade trees. Whatever combination of factors were involved, the woodland dwelling apes evolved distinct traits like walking as they became increasingly isolated from and no longer mated with apes dwelling exclusively in the forest.

Our ancestors were perhaps primed initially in their transition to walking by cautious upright climbing of trees, wading through water and possibly by doing a form of tightrope walking in which they, like modern gibbons and orang-utans, move on two legs along branches while using their arms to grasp other branches to steady themselves as they go. All of these activities may have modified the body in ways that facilitated walking on the ground while still residing mostly in the trees. And we were not the only forest primates to come down from the trees. Baboons are also adapted to living outside the forest, but they move over ground using all four limbs. Some have



Baboons move on all four limbs

argued that bipedalism evolved among the highly diverse European apes as well, but all European apes went extinct along with whatever mode of walking they may have had. Hence, it was only in Africa that walking apes persisted and among them were our earliest ancestors. What does the African fossil record reveal about our initial bipedal divergence in the great ape family?



Fossil skull from Chad

The currently available fossil record suggests that the transition to the way we walk on two legs was a long, drawn-out affair spanning several millions of years. Among the oldest fossils indicating upright walking 7 to 6 million years ago are a skull with heavy brow ridges and a flat lower face from Chad (*Sahelanthropus tchadensis*) and leg bones from Kenya (*Orrorin tugenensis*). The age of these fossils is consistent with the DNA molecular clock estimate of when we last shared a common ancestor with chimps. However, uncertainties in the DNA molecular clock and the limited number of fossils make it unclear just how these fossils fit in, if at all, to our lineage.

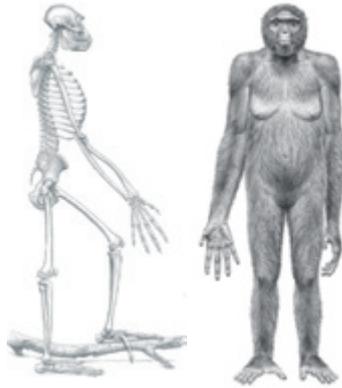


The next oldest fossils of a bipedal ape yet recovered are those of *Ardipithecus*. The oldest known species (*Ardipithecus kadabba*) was identified from a few teeth and bits of bone dated to 5.8 million years ago. But an exceptionally near-complete skeleton belonging to *Ardipithecus ramidus*, or 'Ardi' for short was recovered

Fossil leg bones from Kenya

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from 4.4-million-year-old sediment in Ethiopia. Ardi displays an array of features intermediate between apes and humans, although whether or not Ardi is an ancestral member of our lineage is debated. Ardi had small canine teeth to eat a broad diet gathered from woodland settings and a



Ardi reconstructed and map of early hominid fossil sites in Africa

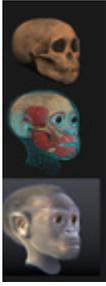
brain similar in size to modern chimps. But the most striking feature about Ardi is its feet. The big toe sticks out sideways for grasping branches similar to the way we use our opposable thumb to grasp objects with our hands. Although Ardi was capable of walking, the opposable big toe made for an odd gait not ideally suited for walking, at least not as we do it. The long fingers and flexible wrists were well suited for moving on all four limbs in trees and walking upright over ground. Ardi's lower pelvis is more ape-like and good for climbing, while the upper pelvis is more like ours, short and broad, to assist with walking upright. Therefore, Ardi appears to be intermediate between a tree- and ground-dweller, and a species having a balance of compromised features making it well adapted to living across the forest to woodland habitat spectrum.

## The australopiths

Look around at those walking ahead of you or at a group of runners as they take off in a road race and you will see a large variety of gaits and running styles. The fossil record suggests there were a far greater range in styles reflecting the many evolutionary variations in hips, legs, feet and toes in the transition to walking. Many different variants of bipedalism were likely to have emerged among isolated groups making the transition to walking besides those preserved by Ardi. However, the one that would end up enduring in our lineage was that developed by the australopiths. The fossil skeleton of 'Lucy' (*Australopithecus afarensis*) is one of the most complete and best known from eastern Africa, but the australopiths (or australopithecines) include the Taung



Skeleton of *Au. afarensis* (Lucy)



Skeleton of *Au. sediba*, (far left) and reconstruction of the skull of the Taung child (*Au. africanus*)

Child of South Africa (*Australopithecus africanus*) and a growing number of newly discovered australopith species (*Australopithecus sediba* from South Africa, for example), and a species from Kenya (*Kenyanthropus platyops*). At least several of these species appear to have coexisted in the same area, suggesting they occupied particular niches defined perhaps by dietary or behavioural differences.

Laetoli footprints



Whether the australopiths evolved from Ardi or not, they show a number of major changes in anatomy centred on the way they walked. Two sets of what are believed to be footprints of australopiths preserved as fossils in an ash fall at Laetoli in Tanzania indicate that an upright, near-modern gait was established as early as 3.6 million years ago. These footprints suggest that the divergent big toe had become more – although not fully – aligned with the other toes. Unfortunately Lucy's recovered skeleton is missing any foot bones, but her uniformly broad and short pelvis would have made walking upright much more straightforward than Ardi's. The available fossil foot bones suggest there were many different styles of walking among the australopiths, but none was probably as radical as those leading up to them.

The age of the footprints at Laetoli and of fossils from South Africa (*Au. prometheus*) indicate that the australopiths were widespread in Africa by 3.7 million years ago and they lived up until at least 2.5 million years ago in eastern Africa and 2 million years ago in South Africa (*Au. sediba*). They specialised in walking efficiently while still being able to climb trees. Although many places where australopith fossils are found today are not forested, they probably included woodland and nearby forests at the time the australopiths lived there. A resurgence of forests during the relatively warm climates of the Pliocene between 5 and 3 million years ago perhaps promoted retention of strong links to the forest. Like modern chimps, they likely built individual tree nests to sleep in at night for safety, while during the day they were increasingly active on the ground – making forays into the open areas and expanding their diet to include fallen tree nuts and fruits as well as the seeds and roots of woodland plants. Larger, flatter molar teeth along with a more rotary mode of chewing in some australopiths suggest a shift in diet from mostly fruit to fruit plus a mix of seeds, nuts, roots and



Skull of *Au. prometheus* ('Little Foot') from South Africa

other woodland hard foods requiring more forceful crushing and grinding.

In addition to the many changes in anatomy associated with fully upright walking, the australopiths had evolved hands capable of the power (squeeze) grip and the precision-pinch grip. The power grip is used when grasping a stick and swinging it like a club. A precision-pinch grip allows us to grasp objects between the pads of our fingers and our opposable thumb. These two grips were possible by shortening the lengths of our fingers relative to our thumb – already evident in *Orrorin tugenensis* 6 million years ago and well developed in australopiths whose hands were more similar to humans than to apes. Rather than by natural selection, the shortening of our fingers may have been mostly an outcome of a correlated response to selection for shorter toes to permit walking on two legs. And the earliest evidence of stone tool use in our lineage indicates that the australopiths used their hands in the human-like manipulation of objects.

### Stone tools

For a long time it was our use of tools that was thought to set us apart from all other animals, but tool use has now been shown to occur widely among many different animals, from primates to crows. In fact, observations of tool use by chimps is now fairly extensive: they modify twigs to insert in termite mounds to extract termites, they use stones to crack open nuts or to hurl at nearby baboons, they chew up leaves into a wad to sponge up water in tree boughs, and they use sticks to hunt bushbabies or access non-stinging honeybee nests. Such a wide range of tool use among chimps makes it reasonable to assume our common ancestor to chimps also made use of tools. However, evidence of tool use in the early stages of our lineage is hard to come by.

Sticks and stones lying about naturally make for obvious first tools and it seems reasonable to assume that australopiths, like chimps, picked them up to use as tools. However, wood is soft and only rarely ever preserved in comparison to bone and especially stones. After all, it was for their hardness that stones were selected as tools in the first place. But as hard as they are, stone tools are not indestructible. Many stone tools were reduced through use, worn down bit by bit, while some made from rocks



Cracking nuts with stone anvil and hammer