Human Evolution: Overview

Introductory article

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The fossil evidence for human evolution can be traced from close to 4.5 Ma to the present. The new term for modern humans and the human clade is 'hominin', which replaces the older name 'hominid'.

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Evolutionary Context

There is abundant evidence that the living animals most closely related to modern humans (*Homo sapiens*) are the chimpanzee (*Pan*) and the gorilla (*Gorilla*). Both are nonhuman in their appearance and behaviour and it was assumed that they were more closely related to each other than either was to modern humans. However, when their genetic identities are compared there is evidence that the DNA in both the nucleus and the mitochondria of the cells of modern humans and the chimpanzee are very similar. An increasing number of researchers are convinced that the similarities between them suggest a shared common ancestry to the exclusion of the gorilla, but others maintain that the relationships between *Homo sapiens*, *Pan* and *Gorilla* are so close that it is not possible to link two of them to the exclusion of the third.

Differences in the DNA can be used to provide an estimate of how long lineages have been independent. The molecular differences between living people and the living African apes suggest that the lineage which includes modern humans has been separate from the rest of the apes (or hominoids) for between 5 and 8 Ma. Animals in the fossil record that are judged to be more closely related to modern humans than to the apes have traditionally been called 'hominids', and those that are closer to the apes than to modern humans have been called 'pongids'. Now that there is good evidence that *Homo* and *Pan* are so closely related, scientists are using 'hominid' to refer to the family Hominidae, which includes *Homo* and *Pan*, and they use 'hominin' to refer to the Tribe Hominini, which includes only modern humans and the human clade. Modern humans and their ancestors are thus known as 'hominins'.

For many years human evolution was likened to a ladder, with earlier, more primitive, species being 'replaced' by later, more advanced ones, with modern humans at the top of the ladder of ascent. Recent evidence suggests that the metaphor of a ladder is no longer an appropriate one. Instead, the hominin evolutionary tree is much better likened to a bush that has multiple stems leading off from close to the base, as well as closer to the crown (**Figure 1**). All but one of the stems stop well short of the highest point of the bush; these are hominin lineages that have no living descendants.

The Earliest Hominins

The first creature to show rudimentary human specializations is known as *Ardipithecus ramidus*, the 4.5 Ma-old remains of which were recovered at a site called Aramis, in Ethiopia, in late 1992. The fossils share some features with living chimpanzees, others with the African apes in general but, crucially, several significant features of the teeth and forearm bones are shared with later hominins. Thus, the discoverers suggested that these fossils belong to a hominin species, and not an ape one, and although they initially allocated it to another group of extinct hominins, *Australopithecus*, they have subsequently assigned it to a new genus, *Ardipithecus*. This genus, together with all the other non-*Homo* genera, are informally referred to as 'australopithecins'.

Judging from the size of one of the bones that make up the shoulder joint, at least one individual of this early hominin weighed about 40 kg. The chewing teeth were relatively small. The opening through which the spinal cord passes was close to the centre of the skull, suggesting that the posture and gait of *Ardipithecus* was respectively more upright and bipedal than is the case in the living apes. The remains of the animals and the plants found with *A. ramidus* suggest that the bones had been buried in a location that was close to, if not actually within, woodland. The thin enamel covering on the teeth suggests that the diet of *A. ramidus* may have been similar to that of the chimpanzee, including fruit, vegetation and some small animals. Although evidence of only one species of *Ardipithecus* has been recovered, it is likely that it will prove to be just one variant of this group.

A little later in time there is fossil evidence of another australopithecin known as *Australopithecus afarensis*. This name was given in 1978 to fossils recovered from Laetoli, in Tanzania, and from the site of Hadar in Ethiopia. Material allocated to *A. afarensis* has been dated to between 3 and 4 Ma.

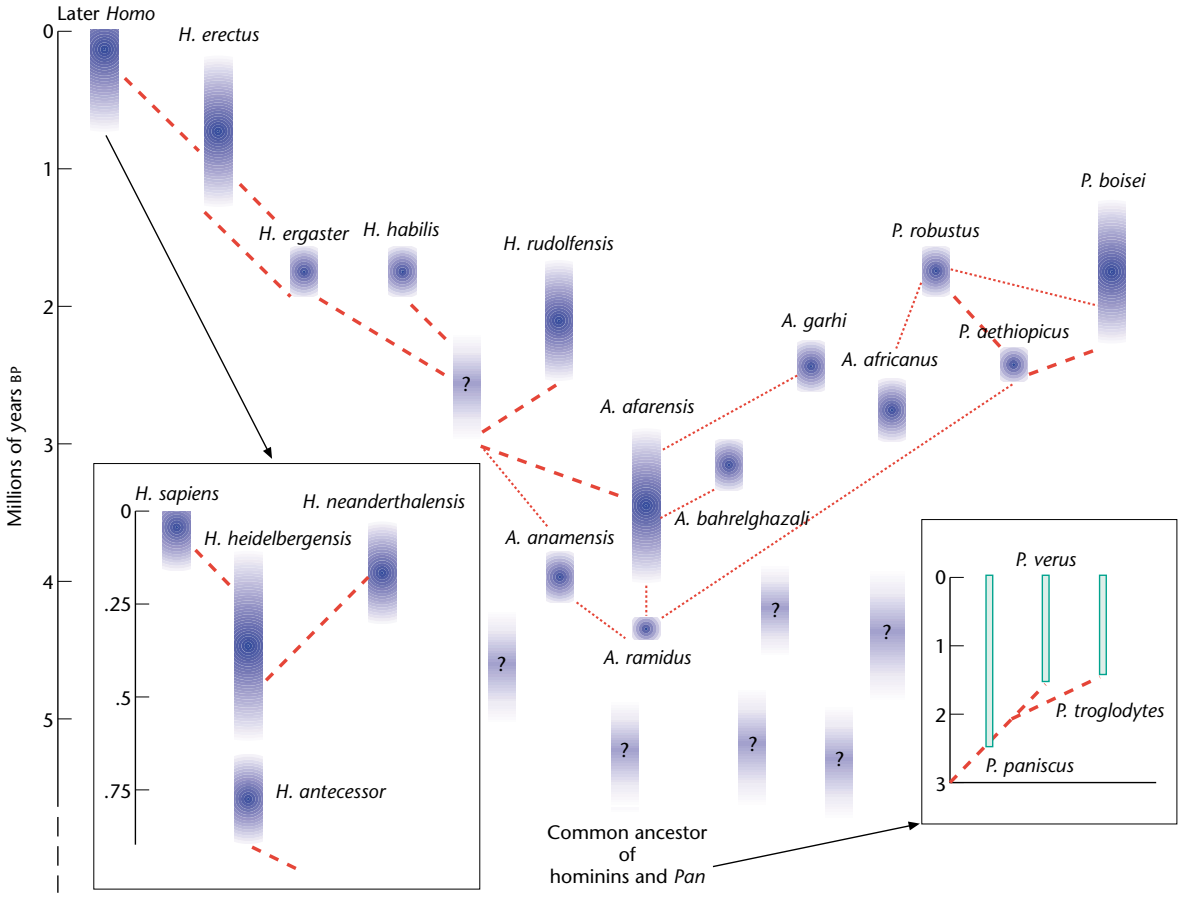


Figure 1 This diagram shows the approximate temporal ranges of the main hominid taxa. It assumes that modern humans and the chimpanzees shared a common ancestor; one interpretation of the taxonomy of *Pan* is given in the right-hand box. The unnamed taxa, marked with a question mark, are based on the informed speculation that there is likely to be as much variety in the early phase of hominid evolution as there is between 3 and 1.5 Ma. Bold dashed lines represent likely evolutionary relationships; dotted lines are even more speculative statements about ancestor–descendant relationships. The left-hand box shows one interpretation of the taxonomy of later *Homo*.

The fossil record of *A. afarensis* includes substantial fragments of several skulls, many lower jaws and sufficient limb bones to be able to estimate the likely body size of *A. afarensis*. The collection also includes just less than half of the skeleton of an adult female. Its field number is AL-288, but it is better known as 'Lucy'. The picture of *A. afarensis* that emerges is of a species which ranged in body mass from about 25 kg, for a small female, to more than 50 kg for a large male. The brain volume of *A. afarensis* was between 400 and 500 cm^3. This is larger than the average brain size of a chimpanzee, but, if the estimates of the body mass of *A. afarensis* are anything like correct, then relative to its estimated body mass the brain of *A. afarensis* is no larger than that of the chimpanzee. However, there is little doubt that the chewing teeth – the premolars and molars – of *A. afarensis* are relatively larger than those of the living apes. *A. afarensis* apparently lived in a more 'open' woodland environment than *A. ramidus*. The shape of the pelvis and the lower limb suggests that although *A. afarensis* was capable of upright, bipedal, walking, it was not adapted for long-range bipedalism. This indirect evidence for the locomotion of *A. afarensis* is complemented by the discovery, at Laetoli, of several trails of fossil footprints. These were made more than three million years ago when several individuals walked across a wet layer of volcanic ash and they provide very graphic and direct evidence that *A. afarensis* was capable of bipedal locomotion. The size of the footprints and the length of the stride provide corroboration for stature estimates between 1 m and 1.5 m, which were based on the lengths of the limb bones of *A. afarensis*.

Fossil hominin remains dating to between 4 and 4.5 Ma have been found at Kanapoi in northern Kenya. In some ways these resemble *A. afarensis*, but in others they are more primitive and in yet other ways they show some incipient *Paranthropus* features (see below). They have thus been placed in a separate species, *Australopithecus anamensis*. Hominin fossils dating to *c.* 3.5 Ma have been

recovered from the desert, in Chad, West Africa. These differ from *A. afarensis*, yet they also differ from *A. anamensis*. The West African fossils have thus been placed in a new species, *Australopithecus bahrelghazali*. The discovery of *Australopithecus garhi* suggests that cranially-primitive hominins were still extant 2.5 Ma ago.

Discoveries in Southern Africa

Nearly 50 years before the discovery of the Ethiopian fossils belonging to *A. afarensis*, an early hominin child's skull had been found in 1924 in a cave at the Buxton Limeworks at Taung, in the northernmost part of Cape Province, South Africa. The new hominin was described by Raymond Dart and placed in a new genus and species, *Australopithecus africanus*, which literally means the 'southern ape' of Africa.

Since the discovery at Taung, fossils belonging to *A. africanus* have been found at other cave sites in southern Africa. The vast majority of the additional evidence has come from Sterkfontein, with contributions from Makapansgat and, more recently, from Gladysvale. The age of the *A. africanus*-bearing breccias in the southern African caves has been estimated to be between 2.4 and 3 Ma.

Males and females of *A. africanus* differed in body size, but probably not to the degree they did in *A. afarensis*. The picture that has developed of *A. africanus* suggests that its physique was much like that of *A. afarensis* except that its chewing teeth were larger and the skull was not as ape-like. Its brain was larger than that of *A. afarensis*, but not substantially so, and the postcranial skeleton suggests that although *A. africanus* was capable of walking bipedally, such a gait was probably energetically relatively inefficient. The remains of other animals found with *A. africanus* suggest that the habitat was a combination of grassland and trees.

Paranthropus – A Genus of Large-toothed Hominins

Just as there were East African and southern African regional variants of *Australopithecus*, there are two regional variants of another hominin genus called *Paranthropus*. They are often referred to as 'robust' australopithecines because of their relatively massive faces and lower jaws.

Remains of the southern African variety, *Paranthropus robustus*, come from caves at Swartkrans, Kromdraai, Drimolen and Gondolin, and are dated to between 2 and 1.5 Ma. The brain, face and chewing teeth are larger than those of *A. africanus*, yet the incisor teeth are smaller. Little is known about the postcranial skeleton except that the shape of the hip joint is much like that of *Australopithecus*.

In East Africa *Paranthropus* is represented by two species (**Figure 1**), both of which have large jaws and chewing teeth. The earlier and more primitive of the two species is referred to as *Paranthropus aethiopicus*. It has a smaller brain, around 400–450 cm^3, a more ape-like face and larger anterior (i.e. incisor and canine) teeth than does the later species, which is called *Paranthropus boisei*.

The earlier of these two East African species of *Paranthropus* spans the interval between 2.5 and 2.3 Ma, and the later one between 2.3 and 1.4 Ma. The relatively large chewing teeth in the two species has prompted the suggestion that the East African forms were specialist feeders on a diet that required heavy mastication. What little information exists about their postcranial skeleton suggests that it was much like that of *Australopithecus*.

The Beginnings of *Homo*, or Are They?

Long before Louis and Mary Leakey's patient fieldwork at Olduvai Gorge had been rewarded with the discovery of the OH (Olduvai Hominid) 5 cranium (initially attributed to *Zinjanthropus boisei*, then to *Australopithecus boisei*, but later to *Paranthropus boisei* (see above)), their efforts had resulted in the discovery of stone chopping and flake tools belonging to what was to become known as the Oldowan industry. This stone tool industry was more primitive than any of the handaxes that had been recovered in the previous century from European sites and from younger strata at Olduvai Gorge. It was perhaps natural to assume that OH 5 represented the hominin species that made the stone tools, but discoveries made in the 1960s were to challenge this assumption.

The new material included the remains of the vault, or roof, of a skull and a piece of a lower jaw, which was given the designation OH 7. Subsequently the remains of a hand, foot and lower leg were found. Although these specimens were frustratingly incomplete, the Leakeys and their colleagues were convinced that the larger cranial capacity and smaller tooth size of the new material, together with what were then regarded as the advanced features of the limb bones, made it a stronger contender for the role of toolmaker than *Zinjanthropus*. The new material was included as a new species, within the genus *Homo*. The name given to it, *Homo habilis*, literally means 'handy man', or 'maker of the tools'.

Fossils that resemble the Olduvai *H. habilis* remains were subsequently unearthed from the site of Koobi Fora in northern Kenya. As this evidence accumulated it became apparent that variation within *H. habilis* was beginning to exceed that which could reasonably be expected in a single hominin species. In particular, the differences between two crania from Koobi Fora, such as KNM-ER 1470 and

KNM-ER 1813, and between mandibles such as OH 13 and KNM-ER 1802, were cited as being too extreme to be subsumed within *H. habilis*. This led to the suggestion that specimens like KNM-ER 1470 and 1802 represented a second species of 'early *Homo*', and this was given the name *Homo rudolfensis*.

Present evidence suggests the *H. habilis sensu stricto* (i.e. a subset of 'early *Homo*') dates from just less than 2 Ma to around 1.6 Ma, and *H. rudolfensis* from perhaps as old as 2.5 Ma to 1.8 Ma. Compared to *H. rudolfensis* the face of *H. habilis sensu stricto* is reduced in width and the opening of the nose is more sharply defined than it is in *H. rudolfensis*. The brain volume of *H. habilis sensu stricto* is around 500–700 cm^3, whereas the estimated brain volume for *H. rudolfensis* is in the order of 700–800 cm^3, with an average of 750 cm^3. Contrary to initial interpretations, the body shape of *H. habilis sensu stricto* more closely resembled that of its australopithecine forerunners than later species of *Homo*. This suggests that the posture and locomotion of *H. habilis sensu stricto* were much like that of *Australopithecus* and *Paranthropus*. Unfortunately, there are no postcranial bones definitely associated with any of the cranial remains of *H. rudolfensis*.

Overall, the case for including *H. habilis sensu stricto* and *H. rudolfensis* within our own genus, *Homo*, is weaker than it was in the 1960s and 70s and some scientists have suggested that they should either be included in *Australopithecus*, or referred to a new genus. However, as we shall see in the next section, by around 1.9 Ma ago there is good evidence from East Africa of an early hominin that has stronger claims for inclusion in our own genus.

Homo Emerges in Africa

The discovery in 1984 of the remains of a virtually complete juvenile male skeleton, known as KNM-WT 15000 at West Turkana confirmed the presence of *Homo* in East Africa. Over the previous decade similar-looking skulls, jaws and limb bones had been recovered from Koobi Fora. Although many of these had been recognized as resembling *Homo erectus* remains from Asia and elsewhere in Africa, it was not until the discovery of KNM-WT 15000 that their affinities could be confirmed. Although the West Turkana skeleton was dated at around 1.5 Ma, other remains attributed to the same species are as old as 1.9 Ma. Some workers have given the species a new name *H. ergaster*, while others refer to it as 'early African *H. erectus*'.

What makes the inclusion of these remains in the genus *Homo* more soundly based than is the case for *H. habilis sensu stricto* or *H. rudolfensis*? The lengths of the long bones of skeleton from West Turkana confirm that this hominin species has limb proportions much like those of modern humans; its trunk, however, is relatively short. However, there are signs of a pathology called skeletal dysplasia in the WT 15000 skeleton and it would be unwise to assume that all the individuals in this species have the same proportions. Turning to the teeth and jaws of *H. ergaster*, when they are related to body size they are no larger than those of African and Australian samples of modern humans. Likewise, the timing and pattern of tooth development in *H. ergaster* is closer to that in modern humans than is the case for any of the other early hominin species for which we have evidence. When we turn to evidence about the brain, the affinities with modern humans are not so strong. While *H. ergaster* has a cranial capacity of between 800 and 900 cm^3 – greater than that of *H. rudolfensis* – when this capacity is related to the larger estimated adult body mass of *H. ergaster*, then the relative brain size of *H. ergaster* is similar to that of *H. rudolfensis* and *H. habilis sensu stricto*.

Homo Moves Out of Africa

More than a century ago, in 1891, Eugene Dubois reported the discovery of a skull and femur that were collected on the bank of the Solo River at Trinil in what was then called Java, now Indonesia. Since then many more similar-looking remains have been located in Indonesia, mainly from the Sangiran region where the Solo River cuts through Pliocene and Pleistocene rocks that have been thrown up into a dome.

Much of modern Indonesia is intensively farmed and little soil remains undisturbed. This makes the exact location of many of the finds difficult to pinpoint, and the paucity of volcanic ash and the weakness of the magnetic signals in the sediments means that the rocks are difficult to date with any accuracy. There is, however, reasonably sound evidence that some of the finds at Sangiran may be around 1 Ma, and there have been recent claims that other sites may be in the order of 1.8 Ma old. This would mean that the first hominins must have left Africa some time before this, and the first species to do so was likely to have been a *H. ergaster*-like hominin, or a more primitive precursor of it.

Archaeological evidence suggests that hominins had occupied Europe and the Near East by around less than 1 Ma and perhaps even earlier, and at the southern African site of Swartkrans there is evidence of an 'early *Homo*'-like hominin around 1.5 Ma. Remains of *H. erectus* persist in the Far East, at the Chinese site of Zhoukoudian, formerly Choukoutien, near to Beijing, as late as 200 ka before the present. This means that *H. erectus* was present in at least one region while hominin species that are closer in appearance to modern humans – *Homo heidelbergensis* – were making their appearance.

Archaic *Homo*

Before we turn to the origin of modern humans we must first consider a substantial collection of fossils that are more modern human-like than *H. erectus*, yet which are not fully modern in appearance. The best known material in this 'archaic *Homo*' category are the remains that have been attributed to *Homo neanderthalensis*. The characteristics of this species include a large, globular-shaped cranium, jaws and teeth that are set well forward in the face, and particularly robust limb bones with large joint surfaces. The earliest Neanderthals come from Spain and France and they are dated to 300–400 ka, with some evidence being as old as 700–800 ka. The youngest Neanderthal fossils are dated to around 30 ka. The precursors of *H. neanderthalensis* belong to *Homo heidelbergensis*, and fossils referred to this taxon are known from Europe, Africa and Asia.

Hominins that show the characteristic Neanderthal morphology are confined to Western Europe, the Near East and adjacent parts of Asia. For much of the period when Neanderthals are present the climate was oscillating between cold, glacial, phases and shorter, warmer, interglacial, periods. The short stature and robust limb bones of the Neanderthals are thus just the body-build that would be expected under the influence of Allen's rule. Neanderthals are often portrayed as primitive hominins who lacked the sophisticated technology and artistic sophistication of the populations that replaced them in Europe. This interpretation belies the fact that the tools that are associated with many, but not all, Neanderthal sites are a good deal more varied in design than the handaxes that characterize the Lower Palaeolithic. There is also evidence that they buried their dead and used grave goods.

Populations of 'archaic *Homo sapiens*' peoples from other regions are not so characteristic in their appearance, but all have some distinguishing features. It is the extent to which those characteristics are continued within the regional populations that succeeded them that lies at the root of ongoing debates about the origin of anatomically modern humans.

Modern Human Origins

Two hypotheses for the origins of modern humans have been put forward. One, called the 'out of Africa' or 'Noah's Ark' hypothesis, suggests that the genetic modifications that were responsible for the shift to an anatomically modern human morphology only occurred once, and in Africa. The rival 'multiregional' hypothesis proposes that the shift to an anatomically modern human morphology occurred several times, but only once in each of the major population centres.

The earliest fossil evidence of hominins with skulls, jaws, teeth and limb bones equivalent to those of contemporary humans comes from Koobi Fora, in northern Kenya; Klasies River Mouth, southern Africa; from the Omo, in Ethiopia; and from the Skhul and Qafzeh caves in the Near East. All of these remains date from as early as 250 ka to around 100 ka. Evidence about modern human origins also comes from the pattern of variation of the modern human genotype. The prediction of the 'out of Africa' hypothesis is that any adaptively neutral variation in the genotype would be greatest in the regional modern human population that had existed for the longest time, namely that from Africa. Analysis of the variation in mitochondrial and nuclear DNA suggest that this was the case, but antiquity of the gene pool is not the only explanation for there being less admixture in Africa than in other regions. A similar pattern would result if the African population had been larger than that in other parts of the world. The case for an African origin for early modern humans is a strong one, but for the moment it must be judged to be probable, but 'not proven'.

Peopling the Planet

Modern humans were dispersed across the Old World by 25 to 35 ka. By that time, and perhaps as early as 150 ka and certainly by 59–60 ka, they had also managed to cross the water barriers between the Asian mainland and Australasia. Reductions in sea level associated with the major glaciations would have shortened any sea crossings; nonetheless the colonization of Australia must have involved the ability to make a raft, or an equivalent seagoing craft.

Present archaeological evidence suggests that the occupation of the New World did not take place until 10–12 ka. Modern humans could have entered the New World across the landbridge that was established between Siberia and Alaska between around 7 and 20 ka, but the earliest archaeological evidence of modern human occupation of Siberia dates from 20–30 ka.

Artefacts and the remains of animals found in association with anatomically modern human remains in the Old World provide compelling evidence that by 40 ka, if not before, organized hunting was part of the survival strategy of these early populations. Some archaeologists place the origin of hunting much earlier, but in many cases it is possible to point to other explanations for the association of animal bones with evidence of human occupation. The first evidence of sea shell middens occurs in coastal archaeological sites by around 15–20 ka.

Farming and permanent settlement do not become evident in the archaeological record until about 12 ka before the present. While the best known evidence comes from the 'fertile crescent' in the Near East, the discovery of

drainage ditches in New Guinea, and of herding in East Africa, around the same time as the evidence for grass domestication along the Nile, demonstrates that changes from a hunter–gatherer lifestyle were occurring across the globe. Thereafter, the balance between physical and cultural evolution has shifted so far towards the latter that evidence of morphological change all but disappears. There are changes in the nature of the inhabitants in some parts of the world, but these are predominantly the result of migrations and not of evolution within a local region.

Further Reading

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