

## Australopithecine

**A**ny of the seven species that belong to the family Hominidae (comprising humans and their closest relatives). These species are not attributable to the genus *Homo*, but belong to at least three genera that existed between about 4.4 million years ago (Ma) and 1.2 Ma during the Pliocene and early Pleistocene epochs. All seven species are known only from Africa. Although some workers regard all of them as belonging to one genus, *Australopithecus*, it is clear that a second genus, *Ardipithecus*, should be recognized for the earliest known hominid fossils, and that the three "robust" species belong to a third genus, *Paranthropus*.

### Historical context

The name australopithecine comes from the taxon *Australopithecus* ("southern ape") *africanus*, which was coined by Raymond Dart for a fossil skull discovered in 1924 in Taung, South Africa (Fig. 1). The Taung skull had several distinctly hominid, or humanlike, features, but the claim that *A. africanus* was a human forebear was disputed by many of the leading paleoanthropologists of that time. The hominid status of *A. africanus* became widely accepted more than a decade later, largely because of work on *Australopithecus* fossils from Sterkfontein. Specimens of *A. africanus* are known also from the sites of Makapansgat and Gladysvale in southern Africa (Fig. 2). Faunal comparison with radiometrically dated sites in eastern Africa indicates that this species existed between about 3.0 and 2.3 Ma.

**Fig. 1** Lateral view of the Taung skull of *Australopithecus africanus*, the type specimen of *Australopithecus* and the first early hominid specimen to be discovered in Africa. (Courtesy of F. E. Grine)



**Fig. 2** Principal sites at which fossils of *Australopithecus* have been discovered in Chad, Ethiopia, Kenya, Tanzania, and South Africa.



The name *Paranthropus* ("beside human") was coined in 1938 when fossils from Kromdraai, South Africa, were attributed to the taxon *P. robustus*. Fossils of this species are also known from the nearby sites of Swartkrans and Drimolen. These bones are dated, also by faunal comparisons with radiometrically dated sites in eastern Africa, to between about 1.8 and 1.5 Ma.

In 1959, a cranium with very large cheek teeth was discovered at Olduvai Gorge, Tanzania (Fig. 2). It represents a separate species of *Paranthropus*, *P. boisei*. Numerous *P. boisei* fossils have been discovered in Tanzania at Olduvai Gorge and Lake Natron, in southern Ethiopia along the Omo River (Shungura Formation), and especially in Kenya on the eastern side of Lake Turkana (Koobi Fora Formation). Fossils of *P. boisei* are dated to between 2.3 and 1.2 Ma.

In 1935, the fossil site of Laetoli was discovered south of Olduvai Gorge, but it was only during the 1970s that most of the hominid jaws and teeth were found there among volcanic ash layers that preserve spectacular hominid footprint trails. Between 1973 and 1977, numerous specimens, including the partial skeleton known as Lucy, were recovered from the Hadar Formation sediments in Ethiopia. It was proposed that the Laetoli and Hadar fossils belonged to a primitive species of *Australopithecus* named *A. afarensis*. *Australopithecus afarensis* fossils are known also from Maka in the Middle Awash of Ethiopia, and from Koobi Fora, Kenya. Fossils that possibly belong to *A. afarensis* (although their specific attribution is open to question) are known from the Ethiopian sites of Belohdelie and Fejej. *Australopithecus afarensis* is dated radiometrically to between 3.7 and 2.9 Ma; it may extend back to 4.0 Ma if the specimens from Belohdelie and Fejej belong to it.

In 1993, the anterior part of a mandible and an upper premolar fragment were discovered in the Bahr el Ghazal region of Chad (Fig. 2). The associated fauna includes several taxa found also in the Hadar Formation of Ethiopia, indicating an age of some 3.0 to 3.4 Ma. It has been suggested that the Chadian fossils represent a separate species, *A. bahrelghazali*. However, the Chad specimens do not afford a definitive diagnostic differentiation from *A. afarensis*; thus, as a conservative approach, the Bahr el Ghazal fossils are considered here as being tentatively attributable to *A. afarensis*.

In 1985, the discovery of a nearly complete skull in the Nachukui Formation on the western side of Lake Turkana, Kenya, led to the recognition of a third "robust" australopithecine species, *P. aethiopicus*. A handful of fossils attributable to this species are known also from southern Ethiopia (Shungura Formation). This species is known from about 2.7 to about 2.3 Ma.

Fossils found in the Aramis region of Ethiopia in 1992 and 1993 were recognized as belonging to a separate taxon, *Ardipithecus* ("ground ape") *ramidus*. It is the most primitive hominid species known. In some morphological features, it is more similar to apes than to other, later hominids. Most of the Aramis bones date to 4.4 Ma. Three fragmentary fossils from Kenya may be attributable to *Ar. ramidus*. One is from the site of Lothagam; it is likely between 5.0 and 5.5 million years old. The other two are from Tabarin and Baringo. Volcanic rocks beneath the Tabarin jaw are 5.1 million years old, and the fauna provides an upper age of 4.2 million years for the hominid. The fauna from Baringo also predates 4.2 Ma.

In 1995, the species *A. anamensis* was named to accommodate fossils that were found at the Kenyan sites of Kanapoi and Allia Bay. These specimens date to between about 3.9 and 4.2 Ma.

## Species

Thus, at least seven australopithecine species, belonging to at least three genera, can be recognized in the Pliocene and early Pleistocene of Africa:

*Ardipithecus ramidus* (?5.0–4.4 Ma)

*Australopithecus anamensis* (3.9–4.2 Ma)

*Australopithecus afarensis* (?4.0–2.9 Ma)

*Australopithecus africanus* (3.0–2.3 Ma)

*Paranthropus aethiopicus* (2.8–2.3 Ma)

*Paranthropus boisei* (2.3–1.2 Ma)

*Paranthropus robustus* (1.8–1.5 Ma)

All are defined on the basis of craniodental morphology.

## **Ardipithecus ramidus**

This is the most primitive hominid species known. It has large canine teeth coupled with comparatively small molars. The anterior lower deciduous premolar is chimpanzeelike, and the anterior permanent premolar is asymmetrical, dominated by a single large cusp. It is unique among all hominids in having thin tooth enamel. The temporal bone has a very shallow glenoid fossa (jaw joint) without a distinct articular eminence; the external auditory meatus is small, the tympanic bone is tubular, and its lateral edge is positioned far laterally. The temporal bone is extensively pneumatized (filled with air cells). The upper limb bones display some features in common with modern humans, as well as characteristics found in living apes. The latter include a large styloid process at the end of the radius, a strong elbow–stabilizing mechanism of the radius and humerus, and strong muscle ridges. These features almost certainly indicate that *Ar. ramidus* was an accomplished climber.

The Aramis fauna is dominated by primates, and arboreal colobine monkeys are the most common of these. The mammalian remains and the presence of fossil seeds suggest that *Ar. ramidus* occupied a wooded habitat.

## **Australopithecus anamensis**

This species has several primitive features in common with *Ardipithecus*, but it also exhibits some derived traits in common with taxa such as *A. afarensis*. It has a few unique characteristics. Thus, the anterior lower permanent premolar is virtually single–cusped and asymmetrical, and the canine crowns and especially the roots are very large (at least in presumptive males). The temporal bone is also extensively pneumatized, the glenoid fossa is shallow without a distinct articular eminence, the tympanic bone is tubular, and the external auditory meatus is small. The palate is shallow anteriorly. The postcanine tooth rows are nearly parallel to one another and close together. The mandibular symphysis, which has a marked postero–inferior slope, extends as far back as the first molar tooth. Its molar crowns have sloping sides, but its tooth enamel appears to be similar in thickness to that of other *Australopithecus* species.

The tibia has features that clearly indicate that this species was a biped. It is a large bone; its owner is estimated to have weighed 47–55 kg (103–120 lb). A wrist bone (the hamate) has a long hook, suggestive of large, powerful hand flexors running through the carpal tunnel. The radius and distal humerus have several apelike characters that are associated with vertical climbing. These bones suggest that *A. anamensis* was a terrestrial biped that was also heavily engaged in tree climbing. Current reconstructions of the paleoecology at Kanapoi and Allia Bay are consistent with this hypothesis. The fauna suggests a woodland–bushland habitat along a large river (at Kanapoi), and a gallery forest associated with a large river that formed a local delta into a large lake (Lake Lonyumun).

## **Australopithecus afarensis**

This species is characterized primarily by a suite of primitive craniodental features, including a strongly protruding jaw (prognathism), a flat (unflexed) cranial base, and a relatively flat glenoid fossa without a distinct articular eminence. It has a tubular tympanic bone, although the external auditory meatus is large. The parietal mastoid angle is strongly flared, and there is close approximation of the cranial points lambda and inion at the back of the skull. The palate is anteriorly shallow, the mediolaterally and supero–inferiorly convex nasoalveolar clivus is demarcated from the floor of the nose by a horizontal sill, and the upper lateral incisor roots are situated to the side of the lateral walls of the nasal aperture. The canines are relatively large, and the anterior lower premolar tends to be asymmetrical and dominated by a single large cusp. The teeth are relatively large in comparison to body size. Endocranial capacity ranges about 310–500 cm<sup>3</sup> (19–30 in.<sup>3</sup>). In addition, *A. afarensis* has a high incidence of an occipital–marginal sinus by which blood is drained from the brain.

There is a high degree of (presumed sexual) dimorphism in body size. Estimates range 30.5–80.5 kg (67–177 lb), which is similar to body size ranges for gorillas and orangutans.

In 1978–1979, volcanic–ash layers bearing hominid footprint trails were discovered at Laetoli. These trails and the bones of the postcranial skeleton indicate that *A. afarensis* was a terrestrial biped, but its gait was not exactly the same as that of modern humans. It was not able to employ a full striding gait. Furthermore, a host of postcranial features, such as strongly curved finger bones, a superiorly oriented shoulder joint, a relatively long upper limb, and a relatively long forearm, indicate that *A. afarensis* was well adapted to arboreal climbing. This species almost certainly spent a considerable amount of time in an arboreal milieu, perhaps feeding and sleeping. The knee joints from Hadar suggest that the smaller (presumptive female) and larger (presumptive male) individuals varied in their reliance on arboreality, such as shown by orangutans.

Paleoenvironmental reconstructions indicate diverse habitats, from well–watered and wooded, to forested environments with edaphic grasslands (at Hadar), to more woodland–bushland conditions (at Laetoli). *Australopithecus afarensis* probably had a fairly broad range of locomotor abilities and dietary proclivities.

## **Australopithecus africanus**

This is the type species of the genus *Australopithecus*. Its cranium is more globular and less pneumatized than that of *A. afarensis*. In comparison to *A. afarensis*, this species has a more steeply inclined forehead, a greater separation of the cranial points lambda and inion at the back of the skull, and a high glabella that is separated from the nasion. The nasoalveolar clivus is prognathic but flattened, the palate is anteriorly deep (shelved), and the maxillary lateral incisor roots are situated medial to the lateral margins of the nasal aperture. The glenoid fossa is deep, and there is a distinct articular eminence. The tympanic plate is vertically disposed, and the external auditory meatus is large. The lower anterior premolar is bicuspid. Endocranial capacity estimates for eight specimens range 428–515 cm<sup>3</sup> (26–31 in.<sup>3</sup>), although the latter value is likely underestimated. In contrast to *A. afarensis*, *A. africanus* has a high incidence of the transverse sinus route for blood drainage from the brain.

Dental and skeletal dimensions indicate that sexual dimorphism in *A. africanus* was also of considerable magnitude. Body weight estimates range 33.5– 67.5 kg (67–149 lb) for presumptive females and males. Postcranial elements are generally similar to those of *A. afarensis*, suggesting that *A. africanus* retained adaptations for tree climbing along with the adaptations for bipedal terrestrial locomotion. Some features, such as foot bone structure indicating a greater range of motion of the big toe, limb proportions indicating a relatively long upper limb, and the structure of the proximal end of the tibia, suggest that the skeleton of *A. africanus* may be somewhat more primitive (chimpanzee-like) than that of *A. afarensis*.

Paleoenvironmental reconstructions suggest that *A. africanus* inhabited well–watered environments with notable bush and tree cover. The microscopic details of tooth wear indicate that the diet of *A. africanus* consisted principally of fruits and leaves.

## **Paranthropus robustus**

The three species in the genus *Paranthropus* are characterized by cranial and dental features indicative of powerful chewing. Thus, the *Paranthropus* face is flattened and somewhat "dished," with the cheeks located anterior to the margins of the nasal aperture. The facial skeleton is hafted high onto the neurocranium, which results in a low forehead with a concave frontal trigone. The prominent glabella is situated below the level of the supraorbital margin and is nearly coincident with the nasion. The nasoalveolar clivus is flattened and grades imperceptibly into the floor of the nose. The palate is extremely thick. The cheek bones are very robust, and males possess a sagittal crest from which the large

temporalis muscles originate. In addition, the petrous portion of the temporal bone is coronally inclined, and the bulbous mastoid region of the temporal bone is laterally inflated. The premolars are fully bicuspid, and they and the molars are greatly enlarged. Tooth enamel is exceptionally thick.

*Paranthropus robustus* is the type species of the genus *Paranthropus*. It is further characterized by the presence of a triangular depression on the front of the cheek bone (maxillary trigone), a palate that is anteriorly shallow, and a deep glenoid cavity with a distinct articular eminence. The tympanic bone is a vertically deep plate, and the external auditory meatus is very large. An endocranial capacity estimate of some 530 cm<sup>3</sup> (32 in.<sup>3</sup>) has been recorded for the single reliable specimen. The upper canines are in the same coronal plane as the incisors, and the anterior teeth not only are absolutely smaller than those of *Ardipithecus* and *Australopithecus* but are especially diminutive in relation to the sizes of the premolars and molars.

Analysis of the postcranial skeleton of *P. robustus* is complicated by the presence of specimens of the genus *Homo* in the same deposits at Swartkrans. Nevertheless, it appears that *Paranthropus robustus* bones share some features with those of *A. afarensis* and *Australopithecus africanus*. These features include a relatively small femoral head with a long and anteroposteriorly flattened femoral neck. The morphology of the proximal radius is like that seen in earlier australopithecine species and living great apes, suggestive of arboreal capabilities. Foot bones indicate bipedal terrestrial locomotion, with evidence of a more humanlike foot than is present in either *A. afarensis* or *A. africanus*. It has also been suggested that the hand of *P. robustus* may have been more similar to that of modern humans, indicating that *P. robustus* had the manual capability to manufacture stone tools. Body size estimates for *P. robustus* range 42.5–65.5 kg (93.5–144 lb); these values suggest that *P. robustus* may not have been larger, on average, than either *A. afarensis* or *A. africanus*. Size (presumed sexual) dimorphism in cranial, dental, and postcranial elements of *P. robustus* appears to be somewhat less prominent than in the other two species of *Paranthropus* (*P. boisei* and *P. aethiopicus*) or in species of *Australopithecus* (such as *A. afarensis* and *A. africanus*). However, it is unclear whether this apparent pattern reflects a specific reduction of body size dimorphism in *P. robustus*, or whether it is a taphonomic artefact that reflects the preferred prey size of the predators (such as leopards) that were primarily responsible for the accumulation of *P. robustus* remains.

Paleoenvironmental reconstructions suggest an open habitat with a nearby river that probably supported a woodland or gallery forest, and also more open, wooded grassland or savanna conditions during the accumulation of *P. robustus* remains. Tooth wear suggests that the diet of *P. robustus* was composed of harder items than were chewed by *A. africanus*. Studies of the carbon isotope signatures of *P. robustus* teeth indicate that this species had an overall reliance on C3–based foods (that is, trees, shrubs, forbs, and tubers). Overall, the cranial and dental anatomy of *P. robustus* indicates a primary adaptation to the mastication of foods that required the application of powerful chewing forces.

## Paranthropus boisei

Most of the morphological features that characterize this species are also possessed by *P. robustus*, although the dental and bony characteristics that are associated with mastication appear to be even more exaggerated in *P. boisei*. Thus, *P. boisei* differs from *P. robustus* in having a deeper maxilla, an anteriorly deep (shelved) palate, the absence of a maxillary trigone, zygomatics that tend to be laterally bowed with a visorlike configuration of the cheek, and a heart-shaped foramen magnum with a straight or posteriorly convex anterior margin. The cheek teeth of *P. boisei* tend to be larger than those of *P. robustus*; indeed, *P. boisei* premolars and molars are the largest of any hominid taxon. The canines and incisors, however, are diminutive. Endocranial capacity estimates range about 500–530 cm<sup>3</sup> (30–32 in.<sup>3</sup>) with an average of approximately 515 cm<sup>3</sup> (31 in.<sup>3</sup>). Thus, as in *P. robustus*, the brains of *P. boisei* specimens tend to be somewhat larger than those of most *Australopithecus* specimens. *Paranthropus boisei* has a high incidence of an occipital–marginal sinus by which blood is drained from the brain.

Although cranial and dental remains of *P. boisei* are quite abundant, there are comparatively few postcranial bones that can be attributed to this species with certainty. The bones that are reasonably attributed to *P. boisei* reveal a picture of a biped that retained adaptations to arboreal locomotion (for example, it had relatively long arms, such as displayed by *Australopithecus anamensis*, *A. afarensis*, and *A. africanus*, and an apelike proximal radius morphology that suggests a long lever arm of the biceps muscle as is found in *Australopithecus*). The ankle bones (talus and calcaneus) are generally humanlike, and the femur has a relatively small head coupled with a long and anteroposteriorly flattened neck.

Cranial and postcranial elements indicate considerable sexual dimorphism. Body weight estimates from more complete bones range 52–60 kg (114–132 lb), although other, less complete postcranial elements indicate a greater range, from less than 30 kg (66 lb) to greater than 100 kg (220 lb).

Paleoenvironmental reconstructions reveal a variety of potential habitats, including scrub woodlands with extensive wetlands, open woodlands with edaphic grasslands (in which the soil has been periodically inundated with water, for

example, a bank overflow), riparian woodlands, and grassland or shrublands, with a possible preference for well-watered sites such as riverine gallery forests. Overall, it appears that *P. boisei* preferred fairly open habitats (woodland to scrub woodland) associated with water and edaphic grasslands. Wear on *P. boisei* cheek teeth suggests the mastication of some hard items, although they may have played less of a role than in the dietary regimen of *P. robustus*. The diet of *P. boisei* may have required the prolonged chewing of tough or fibrous vegetable foods, perhaps with relatively little nutritional value.

### Paranthropus aethiopicus

This species is known from comparatively few fossils (one fairly complete cranium, two incomplete mandibles, and a handful of isolated teeth). Like *P. robustus* but unlike *P. boisei*, this species possesses a maxillary trigone and an anteriorly shallow palate. Like *P. boisei* specimens, *P. aethiopicus* has a heart-shaped foramen magnum with a straight anterior margin. The premolars and molars of *P. aethiopicus* are similar in size to those of *P. boisei*; thus, they tend to be larger than most *P. robustus* cheek teeth.

The cranium of *P. aethiopicus* differs from, and is more primitive than, those of *P. boisei* and *P. robustus*, in that it possesses a long, unflexed base, marked alveolar prognathism, a shallow glenoid fossa without a distinct articular eminence, and a strongly flared parietal mastoid angle. In addition, the anterior teeth of *P. aethiopicus* may have been larger than those of the other two *Paranthropus* species. The endocranial capacity of the single known (male) cranium is 410 cm<sup>3</sup> (25 in.<sup>3</sup>), which is noticeably smaller than estimates for *P. boisei* and *P. robustus* crania. In addition, *P. aethiopicus* appears to have employed the transverse sinus rather than the occipital–marginal sinus to drain blood from the brain.

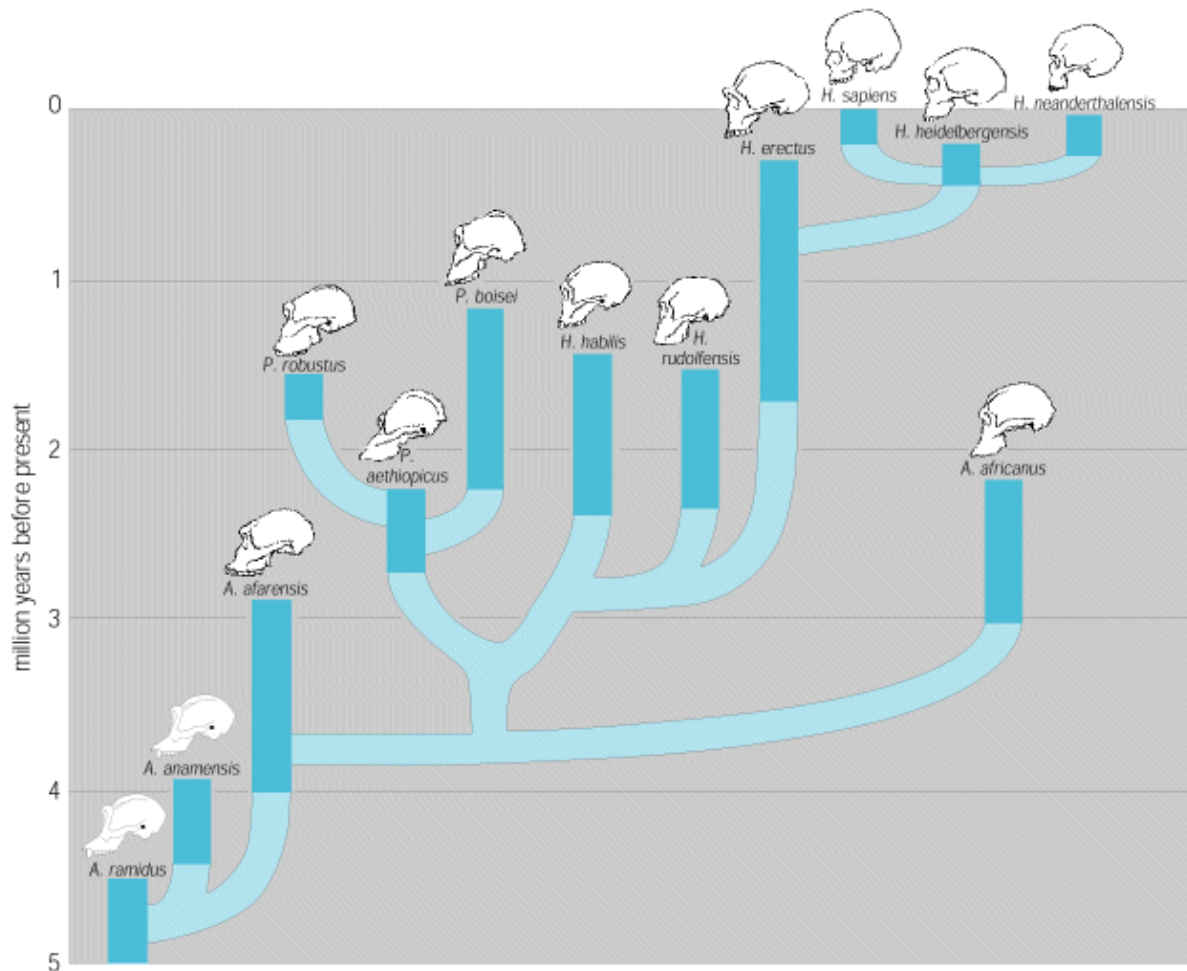
Cranial remains reveal considerable size (possibly sexual) dimorphism in *P. aethiopicus*. Postcranial bones that may belong to *P. aethiopicus* include a large ulna that is notable for its considerable length and substantial dorsoventral curvature, features also found in apes and associated with arboreal climbing. It seems safe to assume that the postcranium of *P. aethiopicus* will exhibit those characters that are possessed in common by other early hominid species, including considerable differentiation in size, features related to bipedal terrestrial locomotion, and other characteristics associated with arboreal climbing.

### Evolutionary relationships

Paleoanthropologists disagree over the assignment of early hominid fossils to different genera and species. Such arguments over what is known as Alpha Taxonomy are to be expected, as different workers view the fossil record from different philosophical perspectives. Such differences also account for disagreements over the phylogenetic relationships of these species, including the issue of which (if any) is most closely related to the human genus, *Homo*. Every phylogenetic hypothesis that has been put forward since the 1950s has been either falsified outright or at least substantially altered by ongoing research and new discoveries.

At present, no scientifically rigorous phylogenetic analysis has been undertaken that incorporates all seven of the species discussed above. The most comprehensive study of "australopithecine" evolutionary relationships to date is that by David Strait and colleagues (1997). That study does not include *Ar. ramidus* or *A. anamensis*. Nevertheless, it is evident from the descriptive account of *Ar. ramidus* that it very likely resembles the stem hominid taxon in its morphology (Fig. 3). *Australopithecus anamensis* shares some evolved (derived) traits with later species such as *A. afarensis*, but retains some primitive features that are displayed also by *Ar. ramidus*. Thus, *A. anamensis* most likely evolved from a species that was at least morphologically similar to *Ar. ramidus* in some respects. For the moment, *Ar. ramidus* represents the best candidate for the ancestor of *A. anamensis*. *Australopithecus anamensis*, in turn, possesses some unique features that make it unlikely to be the immediate ancestor of *A. afarensis*, but it is probable that *A. afarensis* evolved from a species that had a strong morphological resemblance to *A. anamensis*.

**Fig. 3** Phylogenetic tree showing hypothesized evolutionary relationships among species of *Australopithecus*, *Paranthropus*, and *Homo*.



*Australopithecus afarensis* likely gave rise to a lineage that provided the ancestry of both *A. africanus* and another lineage that included the common ancestor of the genera *Paranthropus* and *Homo*.

Although *A. africanus* shares a number of derived morphological characters with species that are part of the *Paranthropus* and *Homo* lineage, it is not considered to be directly ancestral to that line because it exhibits derived morphology in several characters (for example, glenoid fossa depth and anterior palatal depth) that are more primitive in both *A. afarensis* and *P. aethiopicus*. It is perhaps more likely that the derived traits which *A. africanus* shares with some species of *Paranthropus* and *Homo* were evolved in parallel. Other workers, however, have argued cogently that *A. africanus* constitutes a reasonable morphotype for the last common ancestor of the lineage that leads to *Homo* and *Paranthropus*. In this case, the primitive features displayed by *P. aethiopicus* would represent evolutionary reversals. At present, then, it is safest to conclude that the phyletic position of *A. africanus* remains ambiguous.

*Paranthropus aethiopicus* is considered to be a likely candidate for the ancestry of both *P. boisei* and *P. robustus*. The reason is that *P. aethiopicus* shares a number of primitive features with *A. afarensis*, but at the same time it shares a host of derived features with the later species of *Paranthropus*, namely *P. robustus* and *P. boisei*.

The lineage leading to *Paranthropus* shares a number of morphological features with that leading to *Homo*. For example, all species of *Homo* and *Paranthropus* share a coronally oriented petrous temporal bone, a foramen magnum that is roughly horizontal in disposition, and a vertically oriented mandibular symphysis. Thus, it is most parsimonious to assume that these two lineages shared a common ancestor at some time prior to 2.8 Ma.

The apparent increase in cranial capacity that is shown by some species of *Paranthropus* (*P. robustus* and *P. boisei*) would appear to parallel the increase in brain size that characterized the evolutionary history of the lineage that led to *Homo sapiens*. Tools made of stone or bone are not known to be associated with *Ardipithecus* or the three species of *Australopithecus*. Stone tools are known from sites that contain *P. boisei* fossils, and both bone and stone tools are known from sites that preserve *P. robustus* remains. However, early members of the genus *Homo* are known also from these same localities. Thus, it is difficult to determine whether *Paranthropus* species may have been responsible for some of the

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late Pliocene and early Pleistocene archeological record. Indeed, it has been argued that the later species of *Paranthropus* may have been driven to extinction through competition with early *Homo*, because the latter possessed a distinct ecological advantage through the utilization of lithic technology in the procurement of food. While the evidence for this is not compelling, it is possible that ecological interactions between *Paranthropus* and early members of *Homo* may have influenced the evolutionary course of the human genus. See also: Apes; Fossil humans

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