

# Australopithecines, australopiths

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“Australopithecine” is the informal adjective designating members of the taxonomic subfamily Australopithecinae, which with the Homininae constitute the family Hominidae. The Hominidae are humans, human ancestors and collateral species after the lineage branched from that leading to chimpanzees. Recently, paleontologists, influenced by evidence from genetics that apes and humans are more closely related than traditional taxonomy reflected, have pulled African apes into the Hominidae, with repercussions right down the taxonomic scale. Under the new scheme, gorillas are in the subfamily Gorillinae and chimpanzees and humans are in the Homininae. The Homininae is divided into two tribes, the Panini for chimpanzees and Hominini for our own lineage. Our tribe, the Hominini, is divided into two subtribes, the Australopithecina (less formally “australopiths”) and the Hominina, which contains only the genus Homo.

Except for specialists, the new taxonomy hardly affects the australopithecines. There is but a single difference: “australopithecines” are now referred to as “australopiths.” The old and new schemes are given in Table 1 (adapted from Wood and Richmond, 2000). Taxa in bold are discussed in this entry.

Table 1. Traditional and Revised Ape and Human Taxonomy

## Traditional taxonomy

Superfamily Hominoidea (apes and humans; informally “hominoids”)

Family Hylobatidae

Genus Hylobates

Family Pongidae (great apes; informally “pongids”)

Genus Pongo

Genus Gorilla

Genus Pan

Family Hominidae (humans and relatives; informally “hominids”)

Subfamily Australopithecinae (informally “australopithecines”)

Sahelanthropus, Orrorin, Ardipithecus and Australopithecus (see below)

Subfamily Homininae (informally “hominines,” but rarely used)

Members of the genus Homo (more detail below)

## Revised taxonomy

Superfamily Hominoidea (apes and humans; informally “hominoids”)

Family Hylobatidae

Genus Hylobates

Family Hominidae (great apes and humans; informally “hominids”)

Subfamily Ponginae

Pongo pygmaeus (orangutan)

Subfamily Gorillinae

Gorilla gorilla (gorilla)

Subfamily Homininae (chimpanzees and humans, “hominines”)

Tribe Panini (chimpanzees and bonobos; informally “panins”)

Pan paniscus

Pan troglodytes

Tribe Hominini (hominids in the old scheme; informally “hominins”)

Subtribe Australopithecina (informally “australopiths”)

**Genus and species**

**Dates**

Sahelanthropus tchadensis (6.5 Ma [6-7 Ma])

Orrorin tugenensis (~6 Ma)

Ardipithecus kadabba (5.8-5.2 Ma)

Ardipithecus ramidus (4.4-4.2 Ma)

Australopithecus anamensis (4.2-3.9 Ma)

Australopithecus afarensis (3.6-2.9 Ma)

synonym: Kenyanthropus platyops

synonym: Australopithecus bahrelghazali

Australopithecus aethiopicus (2.3-2.7 Ma)

Australopithecus boisei (1.4-2.3 Ma)

Australopithecus africanus (2.5 Ma [2-3 Ma])

Australopithecus garhi (~2.5 Ma)

Australopithecus robustus (~1.9-1.5 Ma)

Australopithecus “habilis” (1.9-1.4 Ma)

Subtribe Hominina (informally “homins”)

Homo habilis (OH 7 and ER 1470 e.g.)

Homo erectus (including “ergaster” and “antecessor”)

Homo sapiens (including “heidelbergensis” and “neanderthalensis”)

Australopiths as a group differ from chimpanzees and other apes in possessing more robust, less protruding (i.e. more orthognathic) faces. Australopith mandibles lack a “simian shelf” (a ridge of bone behind the chin that joins the two sides of the jaw), and are more robust. Australopiths have a shallower supratotal sulcus (groove behind the browridge), and a more caudally oriented nuchal plane (i.e., the attachment of the neck muscles faces downward, reflecting a vertical spine). Australopith incisors are slightly smaller to much smaller than chimpanzees, molars and premolars are larger, dental enamel thicker to much thicker, and canine less projecting though still roughly triangular. Whereas ape lower first premolars have a sloping face that sharpens the back of the upper canine when the individual closes its mouth, australopith first premolars start out a little more molar-like in early species, and have lost all evidence of this honing shape by 2.5 million years ago (Ma). Australopith canines typically wear from the tip, rather than along a knife-like rear edge, as in apes. The robusticity of the skull is thought by many to reflect an adaptation to chewing more fibrous foods. Fruits in open habitats are less succulent and

more fibrous than the fruits chimpanzees eat, and australopiths likely also included fibrous underground storage organs in their diet.

Australopith skulls differ from those of Homo in having cranial capacities of less than 700 c.c. and usually < 600 c.c. Australopiths have more prognathic (protruding) faces. All australopiths lack a true external nose, but rather they quite resemble chimpanzees in this feature. Aside from cranial capacity, the skulls of earliest Homo, Homo habilis, as exemplified by ER 1470 and OH 7, are quite like those of South African australopiths.

Postcranially, australopiths differ from chimpanzees and vary in the direction of modern humans in having a large calcaneus (heel bone), a robust tibial platform, a valgus femur, a quite human like pelvis, a long lower back, short fingers and longer, more powerful thumbs.

Postcranially, australopiths differ from Homo and vary in the direction of chimpanzees in possessing body weights of 25-60 kg, with males at the high end, females at the low. That is, australopiths were sexually dimorphic with females somewhere between half and 3/4 of male body weight, versus 85% in humans. The long bones of australopiths were more robust, that is, they have thicker walls than those of chimpanzees, which are in turn more robust than humans. Australopiths had long curved toes, some gripping capacity of the big toe (perhaps with the exception of A. robustus), the absence of the ball of the foot (i.e. swelling at the base of the big toe), a robust peroneal groove of the fibula (suggesting a gripping great toe), short legs, small femoral heads, small knee joints surface that are particularly small from front to back, long arms with particularly long forearms, a robust lateral epicondylar crest on the humerus (suggesting powerful elbow flexing), topographically distinct elbows suggesting greater stability, curved robust fingers with concavities on the inner surface to accommodate large tendons to flex the fingers, scapula or shoulder blade with tilted-up joint surfaces, large joint surfaces above the waist and small joint surfaces below the waist, cone-shaped ribcages, ribs that are round in profile, and small vertebrae. These features suggests australopiths were bipedal when walking on the ground, but bore weight with their arms more often during their daily routine than do modern humans, presumably in trees. Australopith knee joints are less stable and have greater flexibility than modern human knees. Human knee joints are designed more for stability than mobility; to accomplish this they are shaped so that the joint surfaces of the femur and tibia conform closely. The round surface of the femoral joint surface has a concave or cup-shaped complement on the tibia. The knee of A. afarensis is more ape-like, with the tibial joint flat or even convex, so that it conforms less closely to the round femoral joint surface, allowing more mobility.

A number of australopith features are neither chimpanzee-like nor human-like. All the specimens we possess show evidence of having six lumbar vertebrae, versus five in humans and four in great apes. The base of the great toe, far back in the foot, is unique. In humans, this joint is flat, making the big toe a relatively rigid strut. In chimpanzees, the joint is a modified ball and socket joint that allows mobility in all planes—the great toe joint has the mobility of the human thumb. In A. afarensis the joint has a hinge-

like function, allowing the toe to swing side-to-side so as to allow the gripping of moderate sized objects. As with a hinge, it is rigid in all other planes so that the great toe was as stiff in toe-off as that of humans. The pelvis, while human-shaped, is extraordinarily broad, with a birth canal that is quite wide from side to side, not only broader than necessary to give birth, but far broader than that. The femoral necks are longer than those of humans or chimpanzees, and more highly angled. The femur is valgus; that is, the femora angle inward giving australopiths a distinct knock-kneed appearance, whereas ape femora have no such angle, yielding a rather bow-legged appearance. The australopith femur is not just valgus, it is even more valgus than that of humans, a hyper-human condition.

The wide pelvis and short femur have been interpreted by Kevin Hunt as having evolved to lower the center of gravity thereby increasing balance on unstable substrates. The wide pelvis allows internal organs to ride lower in the body cavity, and short legs lower the center of mass still more. With short femora and long femoral necks, the knees must angle in more to reach the center of the body. Owen Lovejoy suggested that long femoral necks increase the mechanical advantage of muscles that stabilize the pelvis. These long necks are needed because the wide and unwieldy pelvis of australopiths requires more force to stabilize, and long femoral necks give hip musculature better leverage. The smaller angle of the femoral neck and the more valgus femur are insignificant consequences of short legs. Imagine the letter “Z” as a rather tall character. The upper horizontal represents the femoral neck, the lower the knee. If the “Z” is shorter, as the femur is in australopiths, the angle the top horizontal makes with the descending line is tighter, and the descending line makes a greater angle with the lower horizontal. The z is more valgus.

All australopith features considered together suggest a small robust-jawed, bipedal ape with considerable arboreal competence. Curved robust fingers function to reduce stress on the fingers during arm-hanging, and inferred large flexor tendons are required to grip branches during arm-hanging. Short fingers are an adaptation to foraging among small branches. Wide hips and short legs make balancing in trees easier. Tilted up shoulder joints give chimpanzees and australopiths a cranial set to the shoulder, meaning that they are more comfortable with their arms above their heads than at their sides, stressing the shoulder joint less during arm-hanging. Cone-shaped torsos evenly distribute stress on the ribcage during armhanging. Long, curved lateral toes are used for gripping branches while collecting fruits in trees bipedally. A large calcaneus, dual-function great toe, valgus femur, human-like hips, and long femoral necks suggest considerable terrestrial bipedal competence. Their adaptation was likely that of eating fruits in trees, supplemented with leaves and blossoms, and falling back on underground storage organs (like carrots or potatoes) during times of fruit scarcity. Given their small size and inferred arboreal competence, they likely slept in trees.

While these traits are rather consistent right through the lineage, each species has its peculiar adaptations.

Sahelanthropus tschadensis (6.5 Ma [6-7 Ma])

Sahelanthropus is represented by a well preserved skull and fragments from at least six individuals. Not surprisingly, this earliest (purported) hominin has the smallest australopith cranial capacity, 350 c.c.s. The brow ridge is similar in shape to that of later australopiths in lacking a chimpanzee-like depression or groove behind the browridge, but the brow is unusually thick. The zygomatics or cheek bones of Sahelanthropus recede from the face so that the center of the face is more prominent than the sides. Most other australopiths have laterally prominent zygomatics; in the more robust species as one traces the zygomatics from the nasal opening toward the side of the face they project ever farther forward, leaving the nose as the most depressed area on the face, and the outer margins of the zygomatics the most prominent. Sahelanthropus lacks this dish-shaped face, and has more receding but still robust zygomatics. The face is less prognathic than chimpanzees or later australopiths, more like that of later australopith-like habilines such as ER 1813. Molars are smaller and tooth enamel thinner than in A. afarensis and later australopiths, intermediate between them and chimpanzees. The foramen magnum, the opening for the spinal cord, is placed forward and the neck muscles were oriented downward, both evidence of bipedality. Though more ape-like than later australopiths, unlike apes the canines wear at the tip, have only minor honing morphology on the lower premolar, and lack a space between the canine and premolar. Some canines have shoulders or basal tubercles, resembling the later A. anamensis.

Orrorin tugenensis (~6 Ma)

There is no braincase or face for this species. There are, however, teeth from both the upper and lower jaws, and fragments of mandible. As with Sahelanthropus, the cheek teeth are smaller than later australopiths. Dental enamel is thicker than that in either Sahelanthropus or the later Ardipithecus. A humerus is unremarkable and like other australopiths. A finger bone is curved, or typical for an australopith. Most remarkable is the femur, for which there are two specimens, one rather complete. The femoral head is small and the femoral neck long compared to humans, but both are more human-like than they are in A. afarensis. The angle of the femoral neck is great, though this trait is ambiguous since it is shared by humans and chimpanzees. This upward orientation reduces the effective femoral neck length. Long femoral necks offset the stresses of a very wide pelvis, and low shaft-neck angles in most australopiths are interpreted as related to more valgus femora, which is in turn a consequence of short legs. Chimpanzees have short legs, but because they do not walk upright, they have neither the valgus femur, the tight angle of the neck, nor the long femoral neck of australopiths. The morphology of Orrorin therefore suggests that if it is a biped, its pelvis is narrow, its legs are long, or both. Although other features are human-like, interpretation is complicated by short femoral necks and upward angled necks in chimpanzees. Although unlikely, it is possible Orrorin is not a biped.

Ardipithecus kadabba (5.2-5.8 Ma)

The species is defined by fragments of a mandible, clavicle, ulna, and humerus. All are quite similar to earlier and later hominins. A complete toe bone and fragments of hand phalanges are curved, robust and indistinguishable from other australopiths. Loose teeth include incisors, canines, premolars and molars. Canines differ in some minor details from other early hominins and retain some elements of a canine/P3 honing complex that sharpens the back side of ape upper canines. This feature is variable in early hominins, leaving the A. kadabba similar to other species. The cheek teeth are the size of other early hominins, if not slightly larger. The cheek teeth have slightly thicker enamel than Sahelanthropus, Orrorin, and the later A. ramidus.

Ardipithecus ramidus (4.2-4.4 Ma)

The cheek teeth of A. ramidus are small--as are other early australopiths--but are largely within the range of the later A. afarensis. The enamel is intermediate between chimpanzees and A. afarensis. The canines are similar to A. afarensis but slightly more chimpanzee-like. Postcrania have not yet been described, but are said to differ in significant ways from A. afarensis. Perhaps they resemble Orrorin.

Australopithecus anamensis (3.9-4.2 Ma)

This species has many more specimens than earlier australopiths. The canines, though within the range of A. afarensis, can be placed between Ardipithecus and A. afarensis in a graded series from slightly chimpanzee-like to less chimpanzee-like. As in Sahelanthropus, some canines have shoulders or basal tubercles that are uncommon in A. afarensis. The mandible is quite robust, but the left and right cheek teeth rows are parallel to one another, as is the case in chimpanzees, whereas A. afarensis has slightly divergent tooth rows. In profile the chin is straighter and more receding than that of A. afarensis or the earlier Sahelanthropus. Cheek teeth are the size of A. afarensis, but the deciduous molars and premolars are distinctly smaller and more ape-like. That is, adults are like later species, juveniles like earlier species. Specimens discovered earlier had more vertically implanted upper canines than A. afarensis, but later finds differ less. This species has a smaller and therefore more ape-like ear opening than later hominins, though this feature likely varies more than appreciated at first. The postcranial skeletal elements are indistinguishable from A. afarensis.

Australopithecus afarensis (2.9-3.6 Ma)

A. afarensis is the exemplar of early hominins, as described above. Its zygomatics protrude forward laterally more than Sahelanthropus, but less than the later A. africanus. Cranial capacity is near 400 cc, the slightest of increases from 350 cc in Sahelanthropus. Canines and first lower premolars are more ape-like characters than later australopiths, but the trait varies, with some individuals ape-like, and others not at all. Incisors are smaller and cheek teeth larger than early australopiths. Enamel is thick.

This species alone of the early hominins discussed so far gives us information on ribcage shape, base of great toe morphology, pelvic shape, arm to leg length comparisons, calcaneus (heel) shape, scapula shape and sexual dimorphism.

#### Australopithecus aethiopicus (2.7-2.3 Ma)

This robust australopith was a shock when it was discovered in the mid-1980s. It combines enormous cheek teeth with incisors and canines that are unreduced from the presumably ancestral A. afarensis condition. Although the lateral zygomatics are so prominent the face is dished, the face is as prognathic (protruding) as any previous australopith, if not more so, and is quite ape-like. The preserved skull has a crest on the top, a condition present when chewing muscles are larger than the area of the braincase can accommodate. Previously, large cheek teeth had been expected in species that specialized on grinding, which meant small incisors and retracted faces. In life the species presumably subsisted on piths, roots and seeds. Its cranial capacity is 400 cc, the same as A. afarensis. Large incisors and prognathic faces are interpreted as adaptations to stripping, or pulling the hard outer layer off piths. Postcrania are unknown.

#### Australopithecus boisei (2.3-1.4 Ma)

The most classic of robust australopithecines has, compared to its presumed ancestor A. aethiopicus, smaller incisors and canines, a bizarrely robust mandible, and a considerably more orthognathic (pulled back) face. The main chewing muscle, temporalis, is more vertical and larger anteriorly, presumably oriented to maximize chewing power and endurance. The small incisors suggest stripping was not significant, that food items were small, or at least small before they entered the mouth. There are no known postcranial bones.

#### Australopithecus africanus (2.5 Ma [2-3 Ma])

Long the prototype for australopiths, this species from South Africa was first named by Raymond Dart in 1925. It varies from A. afarensis in some of the same ways A. boisei varies from A. aethiopicus. Compared to A. afarensis, its incisors are smaller and its cheek teeth larger. The canine has lost nearly all ape features, and resembles the incisors. Studies of wear on the teeth suggest A. africanus was a fruit eater that supplemented its diet with pith, leaves and seeds. Cranial capacity is 450 cc, or still quite ape-like. The face is more dished than A. afarensis, and exhibits canine pillars, ridges that pass from the canines up to either side of the nose, and are believed to reinforce the face from the forces of chewing. Whatever their function, such reinforcements are not found in A. afarensis, despite its robust mandible and large cheek teeth. Postcranially, A. africanus has longer arms and shorter legs than A. afarensis, and a scapula that is quite ape-like, probably more ape-like than Lucy. The pelvis is broad but not quite as broad as that of Lucy. A. africanus retains all other

features of the hand, arm, legs and feet found in A. afarensis. That is, it is a terrestrial biped and an arboreal arm-hanger/biped.

#### Australopithecus garhi (~2.5 Ma)

A. garhi has a robust face like that of other non-robust australopiths, a more projecting jaw than typical. Molars and premolars are huge, of A. boisei proportions. Canines are very broad and appear to function as premolars. An associated femur fragment is suggested by the discoverers to suggest the hindlimbs are long for an australopiths, though not human-like. The claim is controversial because the forearm is also extraordinarily long, perhaps indicating the individual is merely large, rather than possessing human-like limb proportions, the femur is incomplete and its length therefore uncertain, and there is no comparable male complete femur for A. afarensis to compare. Other postcrania are similar to those of other australopiths. Cranial capacity is estimated at 450 cc, or at the A. africanus mean. Its discoverers argue that nearby tools and cut marked animal bone belong to A. garhi, suggesting it is in the Homo lineage. Others argue it is a unique offshoot unrelated to later hominins.

#### Australopithecus robustus (~1.5-1.9 Ma)

This South African species appears to have evolved from A. africanus, and it differs from it as A. boisei differs from A. afarensis. Despite facial similarity to A. boisei, studies suggest it had a different growth pattern, and its teeth are dramatically smaller. Its closest relative was more likely A. africanus than A. boisei. Compared to A. africanus, it has a more dished face, smaller incisors, larger molars, more vertical chewing muscles, a more robust face, larger zygomatics and the presence of a sagittal crest to anchor huge chewing muscles. Cranial capacity is reported at 475 cc. Since Homo also occurs at the same site, postcranial attributions are difficult. However, most craniodental fossils are A. robustus, meaning postcranials probably are, too. The femoral head and neck and pelvic fragments are much like A. afarensis and A. africanus. Fingers are straight, less robust, and finger tips are broad, all as in humans; the elbow joint is not topographically distinct, suggesting it less often bore body weight. The toes are much more human-like than A. afarensis and A. africanus.

#### Australopithecus “habilis” (1.4-1.9 Ma)

A number of specimens in East Africa are too small to be Homo, but have been pooled with Homo habilis for want of a better solution. The type specimen of Homo habilis is OH 7, which has a cranial capacity 700-750 cc's, or similar to that of ER 1470 at 780 cc. If ER 1470 is the same species as OH 7, which the cranial capacity and other features suggest, Homo habilis retained the large teeth and flat face of its australopith forebears. Often associated with ER 1470 is a long ER 1472 femur, as long as that of later humans. These large-bodied, robust-faced, large-brained hominins may have evolved into Homo erectus. Persisting during the time of both H. habilis and Homo erectus are fossils of a smaller-brained, smaller-



toothed, often more delicate-faced species. Some skulls are quite similar to A. africanus, particularly OH 24 with its distinct canine pillars and flat face. Others, e.g. ER 1813, have reduced zygomatics and the first hint of an external nose. Their cranial capacities range from 500 to 600 cc's. Similar to these is another small specimen, OH 62. This specimen has postcrania that display the classic australopith features associated with a partly arboreal lifeway. Because most paleontologists placed these fossils in Homo habilis, they have no official species name of their own. All are too small to be in the genus Homo, but they are different enough they may ultimately be placed in more than one species. For now, they are left as the still-australopith-like last hangers-on of the glorious australopith tradition that began 6.5 Ma and ends with the extinction of A. "habilis" and A. boisei at 1.4 Ma.

To simplify, australopiths can be divided into roughly seven groups based on current knowledge. Sahelanthropus, Orrorin, and early Ardipithecus are all fragmentary, all share somewhat small cheek teeth, somewhat large incisors, somewhat thin enamel, and more ape-like canine/lower premolar honing complex than later australopiths. They may be all closely related, and in fact one describer of Ardipithecus kadabba has suggested they all belong to a single species. If so, all were bipedal in a way that is significantly different from the bipedalism of later hominins. We can add Ardipithecus ramidus to this group and label them Poorly Known Early Probable australopiths, PKEPs.

PKEPs likely gave rise to a second group, the A. anamensis and A. afarensis lineage, which are similar enough to one another to suggest they are a single, evolving lineage. Compared to PKEPs, they have larger cheek teeth, thicker enamel, smaller incisors, and less ape-like canines.

Presumably branching off the A. anamensis/afarensis lineage was an East African lineage that evolved a more robust face, more muscular jaws and much larger cheek teeth very rapidly, and then slowly evolved smaller incisors and a more retracted face. This group began with A. aethiopicus at 2.7 Ma, evolved into A. boisei near 2.3 Ma, and persisted well into the reign of Homo erectus, going extinct only at 1.4 Ma, and perhaps even later.

In South Africa a descendent of A. afarensis evolved slightly larger cheek teeth, slightly smaller incisors, and slightly more reinforced faces. A. africanus not only retained all the ape-like characters of Lucy, but likely even converged on apes slightly, evolving longer arms and shorter legs. A. africanus had a South African robust offshoot, A. robustus, that evolved even more robust faces. Despite a superficial resemblance to A. boisei, evidence suggests it grew differently than A. boisei, and its molars are considerably smaller, suggesting it is not related to the East African robusts.

In East Africa at 2.5 Ma A. garhi shows only equivocal evidence of more human-like postcrania, and its specialized teeth leave its role in human evolution ambiguous. The last hanger-on among the australopiths was the variable A. "habilis." It retained small brains and more ape-like bodies, and persisted until 1.4 million years ago.

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