

The Evolutionary History of the Australopiths

David S. Strait

Published online: 27 July 2010
© Springer Science+Business Media, LLC 2010

Abstract The australopiths are a group of early hominins (humans and their close extinct relatives) that lived in Africa between approximately 4.1 and 1.4 million years ago. Formerly known as the australopithecines, they are not a “natural” group, in that they do not represent all of the descendants of a single common ancestor (i.e., they are not a “clade”). Rather, they are grouped together informally because nearly all share a similar adaptive grade (i.e., they have similar adaptations). In particular, they are bipedal apes that, to a greater or lesser extent, exhibit enlarged molar and premolar teeth (postcanine megadontia) and other associated modifications to their feeding apparatuses. Dietary adaptations clearly played an important role in shaping their evolutionary history. They also are distinguished by their lack of derived features typically associated with the genus *Homo*, such as a large brain, a broad complement of adaptations for manual dexterity, and advanced tool use. However, *Homo* is almost certainly descended from an australopith ancestor, so at least one or some australopiths belong directly to the human lineage. Regardless, australopiths had a rich evolutionary history deserving of study independent of questions about our direct ancestry. They were diverse, geographically widespread, and anatomically derived, they lived through periods of pronounced climate change, and their story dominates the narrative of human evolution for millions of years.

Keywords *Australopithecus* · *Paranthropus* · Hominin · Human evolution

D. S. Strait (✉)
Department of Anthropology, University at Albany,
Albany, NY 12222, USA
e-mail: dstrait@albany.edu

History of Discovery

The first australopith fossil was discovered in 1924 in a South African limestone mine referred to now as Taung. The fossil had been deposited in a dissolution cavity (a cave or sinkhole) in the surrounding limestone and had been encased in a natural cement (breccia) formed by water, sediment that had been blown or washed into the cavity, and carbonates that had been leaching out of the surrounding rock. Workers had discovered a small skull (Fig. 1) encased in breccia, and this was brought to Raymond Dart, a professor of anatomy at the University of the Witwatersrand in Johannesburg. He carefully cleaned the specimen to reveal a face, mandible, partial braincase, and a beautifully preserved endocast (a fossilized imprint of the inside of the cranial cavity preserving some details of the morphology of the brain). Dart (1925) then made a series of observations that radically challenged the conventional wisdom of the time concerning human evolution.

The specimen’s morphology was broadly ape-like, and it was clearly a juvenile because it still possessed some of its milk (deciduous) teeth. However, its canine was slightly smaller and its face was slightly less projecting than one might have expected of a juvenile ape at a similar stage of development. Most importantly, its brain was small but appeared to be reorganized so that its spinal cord exited the cranial cavity through a hole (the foramen magnum) that was positioned farther forward on the skull than is typical in apes. This was a critical observation because an anteriorly positioned foramen magnum suggests that the vertebral column was vertically oriented and positioned directly beneath the skull, as in humans. In other words, it appeared to Dart as if the specimen had been bipedal. In contrast, the foramen magnum in nonhuman apes is positioned posteriorly on the skull and faces backward,

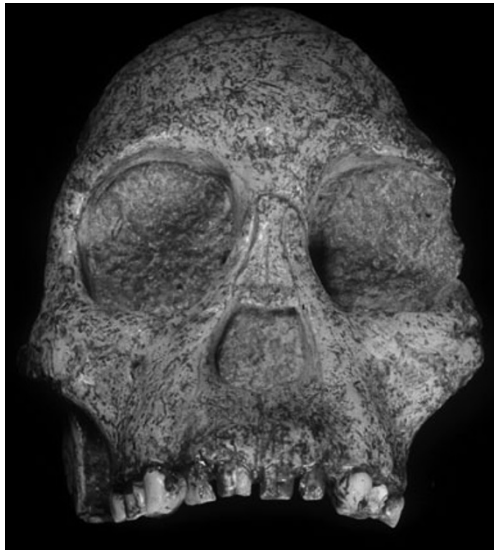


Fig. 1 The Taung child. This fossil was described in 1925 by Raymond Dart, who assigned it the name *A. africanus*. Image and copyright courtesy of Eric Delson

corresponding to an inclined vertebral column. Dart (1925) concluded that the specimen, now widely known as the Taung child, was an extinct human ancestor, and he assigned it the name *Australopithecus africanus*, meaning “southern ape of Africa.”

Dart’s (1925) conclusion was controversial. Up to that point, fossil hominins had been discovered only in Europe and Asia, and one species in particular, *Eoanthropus dawsoni* from Piltdown in England, suggested a scenario of human evolution that was completely at odds with that implied by the Taung child (Keith 1915; Boule 1921). The Piltdown specimen preserved a large braincase with very ape-like jaws and teeth. It implied that a large brain appeared at a very early stage of human evolution. In contrast, the Taung child implied that the earliest humans did not have large brains, and many authorities consequently dismissed the Taung child as an unusual ape (e.g., Keith 1925; Smith 1925). This controversy persisted for more than two decades, but subsequent discoveries (Broom 1938, 1949; Broom and Schepers 1946; Dart 1948; Broom and Robinson 1949, 1950) of australopiths at other South African cave sites (Kromdraai, Swartkrans, Sterkfontein, and Makapansgat; Fig. 2) firmly established the existence of small-brained fossil hominins in Africa. Eventually, the Piltdown skull was exposed as a hoax; fragments of a modern human braincase had been falsely associated with an ape mandible (see Spencer 1990 for review).

In the second half of the twentieth century, discoveries continued in southern Africa, but australopiths were also found in eastern Africa. The first notable such discovery was made in Olduvai Gorge in Tanzania (Leakey 1959). The Gorge is part of the East African Rift Valley system,

which is significant because the Rift preserves volcanic sediments that can be dated using radiometric methods. Australopiths from Olduvai are now known to be as old as approximately 1.8 million years ago (e.g., Leakey et al. 1961; Walter et al. 1991), which makes them much older than had originally been thought (e.g., Washburn 1960). Indeed, the dating of the Olduvai australopiths contributed to the idea that entire epochs of Earth’s history were older than previously surmised. Subsequent discoveries (e.g., Leakey and Walker 1976; Johanson and White 1979; Howell 1978; Walker et al. 1986) at other Rift Valley site complexes (e.g., Koobi Fora, West Turkana, Omo Shungura, Hadar) vastly expanded the number of australopith specimens and species, as well as the time range from which they were known to have existed. More recently, australopith fossils have also been discovered in both south and north central Africa (Brunet et al. 1996; Kullmer et al. 1999). Australopiths are currently unknown outside of Africa.

Pre-australopiths

The australopiths were not the first hominins. They were preceded by earlier taxa which are generally not assigned either a formal or informal group name, but which are referred to here as pre-australopiths. One might also refer to them as basal hominins. There are four such species assigned to three genera. *Sahelanthropus tchadensis* is the earliest known putative hominin and is derived from sediments that are approximately seven million years old from Chad (Brunet et al. 2002). *Orrorin tugenensis* is dated to six million years ago from Kenya and is the earliest known hominin to preserve compelling postcranial evidence that it walked bipedally (Senut et al. 2001; Galik et al. 2004; Richmond and Jungers 2008). *Ardipithecus kadabba* is a poorly-known species



Fig. 2 Fossil cranium of an adult *A. africanus*. This specimen, known as Sts 5, was discovered in the Sterkfontein cave in South Africa. Note that the teeth were not preserved in the fossil and thus are missing. Image and copyright courtesy of Eric Delson

appearing at 5.7 million years ago from Ethiopia (Haile-Selassie et al. 2004) that may be ancestral to the better known *Ardipithecus ramidus* (White et al. 1994). This latter species, known from Ethiopia and, possibly, Kenya at 4.4 million years ago, is the best known of the four and is represented by more than 100 specimens, including a partial skeleton (e.g., White et al. 2009). Interestingly, that skeleton preserves an unexpected combination of primitive traits. It has almost none of the derived traits typically associated with bipedalism, and it is said to lack many of the traits seen in the extant apes associated with suspension and vertical climbing (modes of locomotion that rely heavily on the upper limbs for propulsion and support; Lovejoy et al. 2009a, b, c). Accordingly, although all of these species share a small number of derived cranial traits with later hominins (including a reduced canine and, in some species, an anteriorly positioned foramen magnum; White et al. 1994, 2009; Senut et al. 2001; Brunet et al. 2002; Haile-Selassie et al. 2004; Strait and Grine 2004), there is a reasonable possibility that some of them (particularly *Ardipithecus*) may not be hominins. If so, then the derived traits they share with later hominins must have evolved in parallel (i.e., independently). Evaluating the hominin status of the pre-australopiths will be a major priority of paleoanthropology in the coming years.

Australopith Taxonomy, Distribution, and Chronology

Australopiths were once known as australopithecines, and the latter is the name that is probably most familiar to students, educators, or casual readers. However, this name is now used less and less frequently because the term australopithecine implies the existence of a formal taxonomic group, the Australopithecinae, that is no longer recognized. In contrast, the term australopith does not relate to any formal taxonomic group and thus is a more convenient shorthand label for these species.

As recently as 1994, there were relatively few australopith species known to science. At present, there are at least eight and perhaps as many as ten such species that have been recovered from the Plio-Pleistocene of southern, eastern, and central Africa (Table 1). This pattern tells us that these hominins diversified across, in some cases, relatively modest geographical and temporal spans. However, the large number of species also makes it difficult for students to keep track of them. Key details of each species are presented below, but it is helpful to contextualize these facts by first offering some broad generalizations. Australopiths are usually divided into two informal groups, the gracile and the robust australopiths. The robust species are often attributed to the genus *Paranthropus* (although some researchers retain them in *Australopithecus*) and generally have more massive jaws, crania, and molar and premolar (cheek) teeth than the gracile species, but all

australopiths have more heavily built skulls than living apes. The gracile species appear earlier in the fossil record than the robust species, and the latter are, in a general sense, descended from the former. As the number of known australopith species has grown, the boundary between gracile and robust has blurred (see below), but these terms nonetheless provide a useful shorthand for categorizing these hominins.

In eastern Africa, the first known australopith appears in the fossil record at 4.1 million years ago as *Australopithecus anamensis* (Leakey et al. 1995). This species is relatively poorly known but preserves evidence of postcanine megadontia and bipedal locomotion. It disappears at 3.9 million years ago but is replaced in the record either immediately or shortly thereafter by *Australopithecus afarensis* (Kimbel and Deleuzene 2009). Some workers believe that *A. anamensis* is the direct ancestor of *A. afarensis* and that the two form a phyletic lineage (i.e., the former was transformed into the latter; Kimbel et al. 2006). *A. afarensis* is known from multiple sites throughout eastern Africa ranging from Tanzania to Ethiopia and may extend deep into central Africa if specimens from Chad attributed to *Australopithecus bahrelghazali* (Brunet et al. 1996) in fact represent *A. afarensis*. *A. afarensis* (see review in Kimbel and Deleuzene, 2009) is known from hundreds of specimens, and these preserve large jaws, large molar teeth with thick enamel, a massive but projecting face, and a brain that is small but nonetheless slightly larger than that predicted for an ape of its body mass. The postcranial skeleton is well known in this species, and it preserves evidence that *A. afarensis* walked bipedally on the ground but may have retained an aptitude for climbing in the trees (e.g., Stern and Susman 1983). Among the specimens known from this species is the partial skeleton nicknamed Lucy (Fig. 3). Lucy was short and weighed perhaps only 30 kilograms (66 pounds), but males in her species may have been substantially larger in body mass. Famously, there are footprints presumed to have been made by *A. afarensis* preserved at the site of Laetoli in Tanzania (Leakey and Hay 1979), and these provide clear evidence that this species walked on two legs.

A. afarensis is broadly contemporaneous with *Kenyanthropus platyops*, a species known primarily from a single, badly damaged cranium derived from sediments on the western side of Lake Turkana in Kenya (Leakey et al. 2001). This specimen possesses small molar teeth, and in this respect it differs from most other australopiths (indeed, some workers would not classify it as such). It also exhibits craniofacial features that appear to resemble those in certain much later specimens of the genus *Homo*, although its brain is small. However, the poor condition of the specimen has led some to speculate that it is distorted and in fact represents simply a cranium of *A. afarensis* (White 2003). Alternatively, some workers see this species as the phyletic ancestor of certain members of the genus *Homo* (Leakey et al. 2001), but there

Table 1 Australopith species

Species	Key sites	Temporal range (million years)	Other key facts
<i>Australopithecus anamensis</i>	Kanapoi, Kenya Allia Bay, Kenya	4.1–3.9	The first known hominin species to exhibit enlarged molar and premolar teeth (postcanine megadontia) Evidence from the knee joint indicates bipedal locomotion
<i>Australopithecus afarensis</i>	Hadar, Ethiopia Maka, Ethiopia Laetoli, Tanzania	3.9 (or 3.7)– 3.0	Called <i>Praeanthropus afarensis</i> by some workers One of the best known fossil hominin species. The species to which the partial skeleton nicknamed “Lucy” belongs Associated with fossilized footprints from Laetoli indicating bipedalism
<i>Australopithecus bahrelghazali</i>	Koro Toro, Chad	~3.6	Poorly-known species represented by only fragmentary specimens. Attributed by some workers to <i>A. afarensis</i> . One of only two hominin species known from north central Africa
<i>Kenyanthropus platyops</i>	West Turkana, Kenya	3.5~3.3	Poorly-known species best represented by a damaged cranium that preserves small molar teeth and facial morphology resembling that of some specimens of the genus <i>Homo</i>
<i>Australopithecus africanus</i>	Taung, South Africa Sterkfontein, South Africa Makapansgat, South Africa	~3.0–2.1	The first australopith species to be discovered and one of the best known of all such species
<i>Paranthropus aethiopicus</i>	West Turkana, Kenya Omo Shungura, Ethiopia	2.7–2.3	The earliest known robust australopith Possesses some but not all of the derived craniofacial traits characteristic of the other robust species
<i>Australopithecus garhi</i>	Bouri, Ethiopia	~2.5	Possesses huge molar and premolar teeth but lacks the derived craniofacial morphology characteristic of the robust australopiths. Known from only a single specimen, a partial cranium
<i>Paranthropus boisei</i>	Olduvai Gorge, Tanzania Koobi Fora, Kenya Konso, Ethiopia Omo Shungura, Ethiopia Peninj, Tanzania	2.3–1.4	The first australopith discovered in eastern Africa A robust australopith originally attributed to the genus <i>Zinjanthropus</i> but now commonly attributed to the genus <i>Paranthropus</i> Well known from jaws, crania, and teeth, but poorly known from postcrania
<i>Australopithecus sediba</i>	Malapa, South Africa	1.95–1.78	Newly discovered species preserving an intriguing mix of australopith-like and <i>Homo</i> -like traits
<i>Paranthropus robustus</i>	Drimolen, South Africa Kromdraai, South Africa Swartkrans, South Africa	~1.8–1.5	The only robust australopith known from southern Africa. Well known from jaws, teeth, and crania but, although postcranial remains are known from the same sites, these are not firmly attributed to the species

are other ways of interpreting the morphological evidence (Strait and Grine 2004; see below).

A. afarensis disappears at around three million years ago, but the eastern African fossil record is poor following that time, so the precise date at which the species goes extinct is not known with certainty. Hominins reappear starting at approximately 2.7 million years ago in the Omo Shungura site complex (Suwa et al. 1996), and these seem to represent multiple distinct species. Among them is the first of the taxa known as the robust australopiths, *Paranthropus aethiopicus* (Arambourg and Coppens 1967). The robust species are all characterized by enlarged cheek teeth, massive chewing muscles, and modifications to their facial skeleton that are thought to either increase the leverage of those muscles or to buttress the face against the loads imposed by high or repetitive bite forces that would have been applied to the teeth (e.g., Rak 1983). *P. aethiopicus*

has these traits but, unlike the other robust species, combines them with large anterior teeth (incisors and canines), a highly projecting face, and a small brain (Walker et al. 1986).

P. aethiopicus is broadly contemporaneous with *Australopithecus garhi* (Asfaw et al. 1999), a species that blurs the distinction between robust and gracile australopiths. This species resembles the gracile taxa in that it preserves a broadly *A. afarensis*-like craniofacial skeleton, but it resembles robust taxa in that it possesses absolutely massive molar and premolar teeth. However, the details of the surface anatomy of these teeth appear to differ from those of *P. aethiopicus* and the later robust australopiths. The species is known from only a single specimen from Ethiopia, and it is dated to approximately 2.5 million years ago. Interestingly, the specimen derives from strata that also preserve stone tools and animal bones with cut marks (de

Fig. 3 Lucy. Partial skeleton of *A. afarensis*. This specimen, AL 288-1 (nicknamed “Lucy”), is more than three million years old and up until recently was the oldest reasonably complete hominin skeleton known to science. During life, she would have stood about three feet tall and weighed approximately 30 kilograms. Image and copy-right courtesy of Eric Delson



Heinzelin et al. 1999), but there is no way of firmly associating these finds with *A. garhi*. Some workers imply that *A. garhi* is a suitable ancestor of *Homo* (Asfaw et al. 1999), but there is no direct evidence suggesting this to be the case (Strait and Grine 1999, 2004). It is equally or more likely that *A. garhi* represents a terminal descendant of *A. afarensis* that evolved massive cheek teeth in parallel with the robust australopiths (Strait et al. 2007).

P. aethiopicus is succeeded in the eastern African fossil record by *Paranthropus boisei* (Leakey 1959) at 2.3 million years ago (Suwa et al. 1996; although a fragmentary fossil from south central Africa may belong to this species and may be as old as 2.5 million years ago; Kullmer et al. 1999). This species (see review in Constantino and Wood 2007), discovered by Mary Leakey in 1959, is known from multiple localities across eastern Africa, and its disappearance after 1.4 million years ago marks the end of the australopith fossil record. *P. boisei* is in many respects the most derived of the australopiths. It has the largest molar and premolar teeth, the thickest tooth enamel, the most massive jaw (Fig. 4), the most derived facial skeleton (including cheek bones that are swept out to the side and pulled so far forward that they resemble a bony visor), and extraordinarily reduced incisor and canine teeth. They also have huge chewing muscles that have been repositioned so

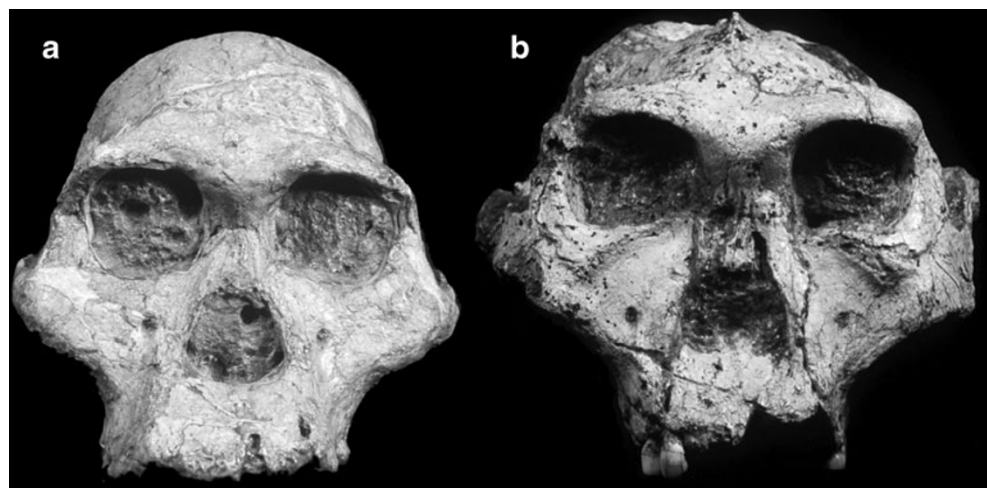
as to maximize their leverage. Interestingly, its brain appears to be slightly larger than that of the earlier robust australopith, *P. aethiopicus*.

In southern Africa, the hominin fossil record preserves much less species diversity. Only two species are well established (Fig. 5), although there is a possibility that others are represented among the known fossils, and an additional new species has just been described (Berger et al. 2010). The earliest well-known species is *A. africanus*, the species named by Dart (1925), which appears at approximately three million years ago and persists until approximately 2.1 million years ago (e.g., Vrba 1995; Walker et al. 2006). It is known from hundreds of cranial and postcranial specimens. Its jaws and teeth are generally considered to be more derived than those of *A. afarensis* but less so than the robust australopiths (e.g., Rak 1983; Lockwood and Tobias 2002). A partial skeleton and many isolated postcranial fossils are known of this species, and, like *A. afarensis*, it seems to have been capable both of terrestrial bipedalism and arboreal climbing. Interestingly, its limb proportions may indicate that it was slightly more adept in the trees than *A. afarensis* (McHenry and Berger 1998; Green et al. 2007). Notably, a nearly complete hominin skeleton has been discovered and is in the process of being extracted from Sterkfontein, the cave in which most *A. africanus* specimens have been found, but its taxonomic affinities have yet to be established (Clarke 2002). That same site also preserves unattributed hominin fossils that may substantially predate the *A. africanus* specimens found elsewhere in the cave (Partridge et al. 2003).



Fig. 4 Mandible of *P. boisei*. Seen from the top, this specimen, from Lake Natron in Tanzania, preserves molar teeth that are each approximately as large as a thumbnail. Note that the premolar teeth (in this view, above the three molar teeth on each side of the jaw) are nearly as large as the molar teeth. In comparison, the incisor and canine teeth towards the front of the jaw are tiny. The body of the mandible holding the molars and premolars is extremely thick and robust. Image by Bob Campbell, courtesy of Bernard Wood

Fig. 5 Early hominins from South Africa. **a** *A. africanus* from Sterkfontein. **b** *P. robustus* from Swartkrans. The sites from which these fossils are found are approximately only a mile from each other. *A. africanus*, a gracile australopith, predates *P. robustus*, a robust australopith. Note the more massive cheekbones and the sagittal crest (a ridge of bone on the braincase from which large chewing muscles arise) in *P. robustus*. Image and copyright courtesy of Eric Delson



A. africanus is succeeded in the southern African fossil record by a robust australopith, *Paranthropus robustus*. This species is said to have appeared at approximately 1.8 million years ago (e.g., Vrba 1995). It is likely to have persisted for at least a few hundred thousand years. Like *P. boisei*, it has derived craniodental features associated with generating and withstanding high or repetitive bite forces, although the expression of these traits is not as extreme as is seen in the eastern African species (Rak 1983). Interestingly, *P. robustus* is derived from sediments that also preserve postcranial remains that may indicate a more advanced degree of bipedalism and manual dexterity than is seen in *A. afarensis* and *A. africanus* (Susman 1988a, b, 1994). However, these fossils cannot be assigned to *P. robustus* with certainty because individuals of the genus *Homo* are also found in those layers (e.g., Trinkaus and Long 1990).

A new southern African australopith, *Australopithecus sediba*, has just been described from the site of Malapa. It is currently known from two partial skeletons, although future work may reveal more specimens. This species preserves an interesting mix of anatomical traits that include some australopith-like features (including a small brain) and some *Homo*-like features. It appears to either slightly predate or be roughly contemporaneous with *P. robustus*.

Phylogeny

Phylogeny refers to the pattern of evolutionary relationships between species. Phylogeny, broadly speaking, is usually depicted in either of two ways. A cladogram is a branching diagram that illustrates the recency with which taxa share a common ancestor, but it provides no specific information about time or whether or not the species in question are direct ancestors or descendants of each other or are simply “cousins.”

A cladogram of early hominin relationships (Fig. 6a) suggests that the pre-australopiths diverged, in succession, from the clade of australopiths and later hominins early in human evolution (Strait and Grine, 2004). Recall, however, that the hominin status of these pre-australopiths is likely to be a source of debate in the coming years. Most gracile australopiths, including *A. anamensis*, *A. afarensis*, *A. garhi*, and *A. africanus*, then branch off the tree, but these species do not form a natural group insofar as they are not all more closely related to each other than they are to other species. In contrast, the robust australopiths appear to form a natural group that shares an exclusive, recent common ancestor. Among australopiths, the robust species appear to be more closely related to *Homo* than the other well-known taxa, although *Kenyanthropus* may be a close relative of both *Homo* and *Paranthropus*. *Australopithecus sediba* is not included in this cladogram, but Berger et al. (2010) have hypothesized that it is more closely related to *Homo* than are the other australopiths.

Note that debate persists regarding the precise cladistic relationships of early hominins, and the cladogram depicted in Fig. 6a represents only one of several phylogenetic hypotheses. However, most workers would probably accept some form of the simplified cladograms shown in Fig. 6b, c.

Cladistic relationships can be used to make informed guesses about ancestor–descendant relationships, and these can be depicted on a phyletic tree, which also provides information about time (Fig. 7). Hominins are likely to have originated prior to seven million years ago. *Sahelanthropus* is unlikely to be a direct ancestor of other known hominins because its facial skeleton exhibits unusual traits not expected to be present in the last common ancestor of the hominins. It has been suggested elsewhere (White et al. 2006) that *Ardipithecus* may have been a suitable ancestor of the australopiths, but recent analyses and descriptions of pre-australopith postcranial anatomy (Richmond and Jungers 2008; Lovejoy et al. 2009a, b, c) make *Orrorin* just as, or

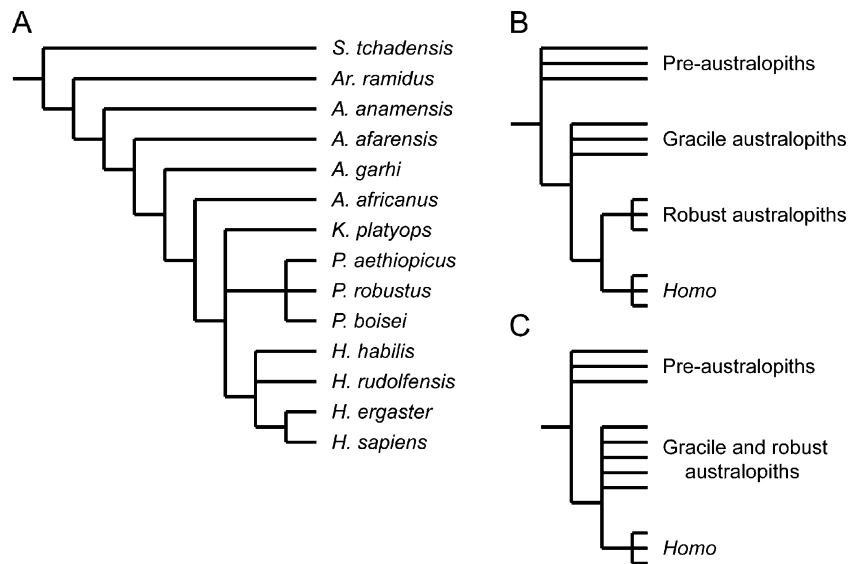


Fig. 6 Early hominin cladistic relationships. **a** Cladogram derived from the phylogenetic analysis of Strait and Grine (2004). **b** Simplified cladogram suggesting that robust australopiths and *Homo* are closely related to each other. **c** Simplified cladogram suggesting

that robust and gracile australopiths have complex and unresolved relationships but that they are all more closely related to *Homo* than they are to any of the pre-australopiths

more, likely to play that role. The first australopith, *A. anamensis*, is likely to be the phyletic ancestor of *A. afarensis* (Kimbel et al. 2006), and this latter species may in turn have given rise to a diversity of hominin lineages and/or clades. One such lineage may be represented by *A. africanus*. Another may be represented by *A. garhi* and yet another by *A. bahrelghazali*. Finally, *A. afarensis* may have been ancestral to the clade that ultimately gives rise to *Homo* and *Paranthropus*. It is possible that *Kenyanthropus* lies near the base of that clade and that it may be ancestral to some or all of the later taxa in that group. *Homo* and *Paranthropus* diverge

at some point prior to 2.7 million years ago. Within *Paranthropus*, *P. aethiopicus* predates *P. boisei* and *P. robustus*, but although the former may be ancestral to one or both of the latter two, this may not necessarily be the case. The relationships of *A. sediba* require further study, but it has been suggested (Berger et al. 2010) that this species pertains to the origin of *Homo*. Regardless, although the robust australopiths are close relatives of *Homo*, they are not ancestral to our genus. The ancestor of *Homo* was almost certainly a gracile australopith. It is possible that *A. sediba* and/or *K. platyops* resemble that ancestor morphologically.

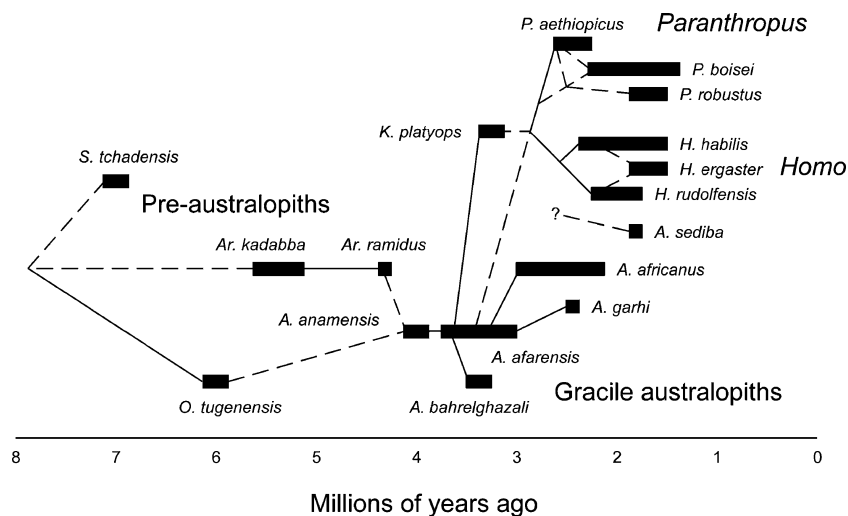


Fig. 7 Early hominin phyletic relationships. Phyletic tree based on cladistic relationships depicted in Fig. 6a. The pre-australopiths give rise to the gracile australopiths, which in turn give rise to both the robust australopiths (*Paranthropus*) and *Homo*. The approximate time

ranges of hominin species are shown as black bars. Solid lines represent likely ancestor–descendant relationships. Dashed lines represent possible ancestor–descendant relationships

Naturally, phyletic trees are like cladograms in that they represent hypotheses, and the phylogenetic hypothesis depicted in Fig. 7 is only one of several that might explain the pattern of early human evolution.

Australopith Paleoenvironments

The australopiths lived during a period of pronounced climatic change. During the late Miocene and into the Pliocene, African climates became cooler and dryer. Over time, this led to a fragmentation of African forests that almost certainly played a role in hominin origins and the evolution of both bipedalism and the pre-australopiths. Then, between three and two million years ago, the onset of northern hemisphere glaciation led to increased climatic variability as climates shifted strongly back and forth from cool and dry to warm and wet over relatively short time periods (Potts 1998). This pattern continued throughout the Pleistocene. Although most australopiths are associated with so-called mosaic environments in which multiple types of habitat were present (e.g., woodland, savannah, gallery forest, bushland, etc.), the earlier australopiths are generally associated with habitats that were more heavily wooded than those associated with later australopiths (e.g., Reed 1997). In order to cope with changing and unstable habitats, it is generally thought that many of the derived anatomical traits seen in australopiths are adaptations that enabled them to be behaviorally flexible, particularly concerning their diet (e.g., Wood and Strait 2004).

Paleobiology

Locomotion: Most of what we know about australopith locomotion derives from postcranial fossils of two species, *A. afarensis* and *A. africanus*. These species were bipedal when traveling on the ground (e.g., Lovejoy et al. 1973; Lovejoy 1988) but appear to have retained adaptations for climbing in trees (e.g., Stern and Susman 1983; McHenry and Berger 1998; Green et al. 2007). They both exhibit valgus knee joints, meaning that their knees were closer together than their hip joints and nearly underneath the center of the body, which facilitated balance during walking (Fig. 8). They also both had low, bowl-shaped pelvises that also aided balance when standing upright. The toe bones of *A. afarensis* were shorter than those of modern apes, meaning that it was comparatively easier and more efficient for them to swing their feet forward during bipedal walking. However, their toes were nonetheless longer than those of modern humans, meaning that their mode of locomotion was less efficient than ours because they would have had to have adopted a somewhat high-stepping gait to clear their toes above the



Fig. 8 The knee joint and bipedalism. The part of the thigh bone (femur) that contributes to the knee joint is shown in chimpanzees (*Pan troglodytes*), *A. africanus*, and humans (*Homo sapiens*). Note how the shaft of the femur approaches the horizontal plane of the knee joint at a more acute angle in *A. africanus* and *H. sapiens* than in *P. troglodytes*. This is known as having a valgus knee, and it is functionally important because this angulation allows the knee joints to be positioned closer together than the hip joints. This facilitates balance and enhances energetic efficiency during bipedal walking and running. A valgus knee joint is also present in *A. afarensis*

ground with each step. Moreover, their finger and toe bones retained a degree of curvature that is consistent with the possibility that they were used during arboreal climbing (Stern and Susman 1983; Richmond 2007). They lacked the unusually long hind limbs of modern people, meaning that they covered less distance with each stride (Jungers 1982), and their shoulder joints were oriented more superiorly than ours, which would have made them more adept in the trees (Stern and Susman 1983). An important difference between *A. afarensis* and *A. africanus* is that the forelimbs in the latter species might have been proportionally larger, meaning that the arms of *A. africanus* may have been more effective at climbing in trees (McHenry and Berger 1998; Green et al. 2007).

Less is known about locomotion in other australopith species, but based on the fossils that are preserved, there is nothing to indicate that locomotion in them would have been fundamentally different from that of *A. afarensis* and *A. africanus*. One exception might be that some modern-appearing fossils from the southern African cave site of Swartkrans might indicate that *P. robustus* had a more human-like mode of locomotion than the gracile australopiths (Susman 1988a), but this possibility cannot be established with certainty because fossils of the genus *Homo* are also known from this cave. Moreover, postcranial fossils derived from the same site complex as *A. garhi* appear to exhibit longer hind limbs than *A. afarensis*, but these fossils have not been attributed to *A. garhi* or any other australopith (Asfaw et al. 1999). Aspects of the australopith proximal femur (the part of the thigh bone that contributes to the hip joint) appear to

have been highly conservative and were present in at least one pre-australopith, *Orrorin*. These traits pertain to maintaining balance while shifting weight from one limb to another during bipedalism. This suggests that components of australopith locomotor behavior persisted for over four million years (Richmond and Jungers 2008). However, other pre-australopiths, particularly *Ardipithecus*, had radically different postcranial skeletons that exhibit barely any adaptations for bipedalism (Lovejoy et al. 2009a, b, c). If *Ardipithecus* is a hominin, then it appears as if the evolution of locomotion was complex during the earliest third of human evolution.

Diet: Unlike postcranial anatomy, aspects of craniodental morphology are known for every australopith species. With the exception of *Kenyanthropus* (Leakey et al. 2001) and *A. sediba* (Berger et al. 2010), all australopiths exhibit postcanine megadontia (e.g., McHenry 1984). This megadontia is initially expressed primarily in the molars, but in later species it is expressed to a high degree in the premolars as well. Relative to living chimpanzees and gorillas, all australopith species also exhibit thick enamel (the highly mineralized outer coating of the tooth crowns) on their postcanine teeth (e.g., Martin 1985; Olejniczak et al. 2008). As megadontia increases, so too does the size and robusticity of the mandible. Simultaneously, the chewing muscles become proportionally larger and their positions on the skull shift so as to maximize their leverage. Finally, several of the australopiths exhibit derived traits on their facial skeletons that act to withstand high stresses imposed by feeding (e.g., Rak 1983). Collectively, all of these adaptations point to the probability that australopiths had the ability to process foods that were mechanically resistant (e.g., Jolly 1970; Peters 1987).

Like most apes, australopiths undoubtedly would have preferred to eat soft, sweet, fleshy fruit, but when those resources were not available, they would have had the ability to “fall back” on foods that were less desirable and more difficult to process (e.g., Marshall and Wrangham 2007). In this manner, they were likely to have been ecological generalists well suited to respond to changes in their habitats (Wood and Strait 2004). Indeed, analyses of stable (nonradioactive) isotopes preserved in the tooth enamel of *P. robustus* indicate that at least this species shifted its diet seasonally (Sponheimer et al. 2006). The precise nature of the fallback foods eaten by australopiths is a matter of debate. On mechanical grounds, some workers suggest that australopith facial traits are adaptations for feeding on large, hard objects like large nuts and seeds (e.g. Peters 1987; Strait et al. 2009). However, studies of dental microwear (the microscopic damage done to teeth by food and grit) suggest that few australopiths routinely fed on hard objects and that some may have fallen back on tough, rather than hard, vegetation (Scott et al. 2005; Grine et al. 2006a, b; Ungar et al. 2008). The mechanical and microwear data are compatible if large hard

objects were selectively very important but consumed very rarely or if large hard objects do not tend to leave microwear signals (as has been suggested; Lawn and Lee 2009). Regardless, it seems evident that selective pressures related to diet and feeding profoundly influenced the evolution of australopiths.

Sexual dimorphism: Sexual dimorphism refers to the phenomenon in which males and females of a species differ with respect to size and/or shape. The most common manifestation of dimorphism among anthropoid primates is when males have a larger body mass and larger, more projecting canine teeth than females (e.g., Plavcan 2001). Dimorphism in these traits is, in turn, correlated with social behavior insofar as highly dimorphic primates tend to be polygynous such that social groups are centered around several breeding females, one breeding male, and their offspring. This is a simplification, and polygynous groups can take multiple forms, but the single male–multifemale organization is a component of most such groups. Dimorphism in body mass and canine size is thought to have evolved due to sexual selection because large body and canine size are advantageous for males as they compete with each other to become the breeding male in a group and because females may preferentially select those traits in their breeding partners. Several, although not all, australopiths appear to be highly dimorphic with respect to both cranial and postcranial dimensions (e.g., Plavcan 2001, 2003; Gordon et al. 2008), and these data may suggest that several of these species were highly dimorphic in body mass as well, although this latter point is disputed (e.g., Reno et al. 2003). Interestingly, hominins appear to be unique among anthropoids in that canine and body size dimorphism appear to have been decoupled (Plavcan 2001). Thus, although several australopiths may have been quite dimorphic in body mass, they exhibit reduced dimorphism in canine size. One possible explanation for this unique pattern is that hominins were polygynous, but that canine size was no longer a target of sexual selection. If true, the reason why canine size was no longer being selected remains unclear. However, those workers that challenge the notion that australopiths, particularly *A. afarensis*, were dimorphic in body mass (e.g., Reno et al. 2003) suggest that these species may have been monogamous (i.e., their social groups were centered around a single male and a single female; e.g., Lovejoy 1981). However, this hypothesis is very difficult to test.

Extinction

Australopiths disappear after 1.4 million years ago. The last surviving species are *P. boisei* in eastern Africa and *P.*

robustus in southern Africa. Unfortunately, the African fossil record is poor after this point, so we cannot rule out the possibility that australopiths persisted for some time before eventually going extinct. However, at some point, they eventually succumbed. The reason for their extinction is unclear. During the time in which both they and *Homo* existed, fossils of australopiths were much more numerous at most sites (e.g., Wood and Strait 2004), yet it is only *Homo* that survived. Moreover, australopiths were probably ecological generalists that were capable of living in different types of habitats and consuming different types of food, and this flexibility ought to have made them resistant to extinction (Wood and Strait 2004), although all species, regardless of their adaptations, eventually go extinct at some time. One might point to any number of factors to explain their demise (predation, competition with other hominins, competition with nonhominin mammals; Klein 1988; Wood and Strait 2004), but it is proposed here that the reason concerns dietary ecology. It is evident from their craniodental morphology that australopiths were under intense selection pressure to modify their feeding apparatus, and strong selection carries with it a strong risk of extinction. Two hypotheses are posed here to explain their disappearance. First, the critical resources that australopiths fell back on during periods of resource scarcity may have themselves disappeared, perhaps as a result of climate change. Without these key fallback foods, australopiths might have been unable to survive. Alternatively, the fallback foods might have evolved to become so mechanically resistant that not even robust australopiths could access them. This, too, might have led to australopith extinction. Unfortunately, these hypotheses are difficult to test and, at the present time, must be considered mere conjecture.

Conclusion

The australopiths are gone, but in much the same way that birds are dinosaurs, we are australopiths in that we are almost certainly descended from one of them. It is possible that the australopiths on our direct lineage are not yet known to science, but it is highly unlikely that australopiths represent an entirely distinct clade whose evolutionary history is completely independent from ours. Interestingly, members of our own genus (*Homo*) appear to have succeeded by abandoning the adaptations that made australopiths successful (e.g., large jaws, massive cheek teeth, huge chewing muscles). In their place, early members of the genus *Homo* may have become behaviorally flexible by evolving large brains, more dextrous hands, and advanced tool use. This strategy evidently proved to be more successful in navigating the vicissitudes of the Pleistocene.

Acknowledgements I thank Will Harcourt-Smith and Niles Eldredge for the invitation to submit this article. Eric Delson and Bernard Wood kindly provided images for some of the figures. This paper was improved considerably by comments by the editors, Eric Delson, and an anonymous reviewer.

References

- Arambourg C, Coppens Y. Sur la decouverte, dans la Pleistocene inferieur de la vallee de l'Omo [Ethiopie], d'une mandibule d'australopieciens. CR Acad Sci Paris. 1967;265:589–90.
- Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. *Australopithecus garhi*: a new species of early hominid from Ethiopia. Science. 1999;284:629–35.
- Berger LR, de Ruiter DJ, Churchill SE, Schmid P, Carlson KJ, Dirks PHGM, et al. *Australopithecus sediba*: a new species of Homo-like australopith from South Africa. Science. 2010;328:195–204.
- Boule M. Les homes fossils: elements de paleontology humaine. Paris: Masson; 1921.
- Broom R. The Pleistocene anthropoid apes of South Africa. Nature. 1938;142:377–9.
- Broom R. Another type of fossil ape-man. Nature. 1949;163:57.
- Broom R, Robinson J. A new type of fossil man. Nature. 1949;164:322–3.
- Broom R, Robinson J. Further evidence of the structure of the Sterkfontein ape-man *Plesianthropus*. Mem Transv Mus. 1950;4:7–84.
- Broom R, Schepers GWH. The South African fossil ape-men: the Australopithecinae. Mem Trans Mus. 1946;2:1–272.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam DR. *Australopithecus bahrelghazali*, une nouvelle espece d'Homínide ancien de la region Koro Toro. C R Acad Sci Paris. 1996;322:907–13.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, et al. A new hominid from the Upper Miocene of Chad, Central Africa. Nature. 2002;418:145–51.
- Clarke RJ. Newly revealed information on the Sterkfontein Member 2 *Australopithecus* skeleton. S Afr J Sci. 2002;98:523–6.
- Constantino P, Wood B. The evolution of *Zinjanthropus boisei*. Evol Anthropol. 2007;16:49–62.
- Dart RA. *Australopithecus africanus*: the man-ape of South Africa. Nature. 1925;115:195–9.
- Dart RA. The Makapansgat protohuman *Australopithecus prometheus*. Am J Phys Anthropol. 1948;6:259–83.
- de Heinzelin J, Clark JD, White T, Hart W, Renne P, Woldegabriel G, et al. Environment and behavior of 2.5-million-year-old Bouri hominids. Science. 1999;284:625–9.
- Galik K, Senut B, Pickford M, Gommery D, Treil J, Kuperavage A, et al. External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. Science. 2004;305:1450–3.
- Gordon AD, Green DJ, Richmond BG. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. Am J Phys Anthropol. 2008;135:311–28.
- Green DJ, Gordon AD, Richmond BG. Limb size proportions in *Australopithecus afarensis* and *Australopithecus africanus*. J Hum Evol. 2007;52:187–200.
- Grine FE, Ungar PS, Teaford MF. Was the Early Pliocene hominid '*Australopithecus*' *anamensis* a hard object feeder? S Afr J Sci. 2006a;102:301–10.
- Grine FE, Ungar PS, Teaford MF, El-Zaatari S. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time

- and under diverse paleoecological conditions. *J Hum Evol.* 2006b;51:297–319.
- Haile-Selassie Y, Suwa G, White TD. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science.* 2004;303:1503–5.
- Howell FC. Overview of the Pliocene and earlier Pleistocene of the lower Omo Basin, southern Ethiopia. In: Jolly C, editor. *Early hominids of Africa.* London: Duckworth; 1978. p. 85–130.
- Johanson DC, White TD. A systematic assessment of early African hominids. *Science.* 1979;202:321–30.
- Jolly CJ. Seed-eaters—new model of hominid differentiation based on a baboon analogy. *Man.* 1970;5:5–26.
- Jungers WL. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature.* 1982;297:676–8.
- Keith A. The antiquity of man. London: Williams & Norgate; 1915.
- Keith A. The fossil anthropoid ape from Taung's. *Nature.* 1925;115:234–5.
- Kimbel WH, Deleuzene LK. "Lucy" redux: a review of research on *Australopithecus afarensis*. *Am J Phys Anthropol.* 2009;140:2–48.
- Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC. Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis on the hominin fossil record. *J Hum Evol.* 2006;51:134–52.
- Klein RG. The causes of "robust" australopithecine extinction. In: Grine FE, editor. *Evolutionary history of the "robust" Australopithecines.* New York: Aldine de Gruyter; 1988. p. 499–505.
- Kullmer O, Sandrock O, Abel R, Schrenck F, Bromage TG, Juwayeyi YM. The first *Paranthropus* from the Malawi Rift. *J Hum Evol.* 1999;37:121–7.
- Lawn BR, Lee JJW. Analysis of fracture and deformation modes in teeth subjected to occlusal loading. *Acta Biomater.* 2009;5:2213–21.
- Leakey L. A new fossil skull from Olduvai. *Nature.* 1959;184:491–3.
- Leakey MD, Hay R. Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature.* 1979;232:308–12.
- Leakey REF, Walker A. *Australopithecus, Homo* and the single species hypothesis. *Nature.* 1976;261:572–4.
- Leakey LSB, Evernden JF, Curtis GH. Age of Bed I, Olduvai Gorge, Tanganyika. *Nature.* 1961;189:649–50.
- Leakey MG, Feibel CS, McDougall I, Ward C, Walker AC. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature.* 1995;376:565–71.
- Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, et al. New hominid genus from eastern Africa shows diverse middle Pliocene lineages. *Nature.* 2001;410:433–40.
- Lockwood CA, Tobias PV. Morphology and affinities of new hominin cranial remains from member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *J Hum Evol.* 2002;42:389–450.
- Lovejoy CO. The origin of man. *Science.* 1981;211:341–50.
- Lovejoy CO. Evolution of human walking. *Sci Am.* 1988;256:118–25.
- Lovejoy CO, Heiple KG, Burstein AH. The gait of *Australopithecus*. *Am J Phys Anthropol.* 1973;38:757–80.
- Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science.* 2009a;326:72e1–8.
- Lovejoy CO, Simpson SW, White TD, Asfaw B, Suwa G. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science.* 2009b;326:70e1–8.
- Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. *Science.* 2009c;326:71e1–6.
- Marshall AJ, Wrangham RW. Evolutionary consequences of fallback foods. *Int J Primatol.* 2007;28:1218–35.
- Martin LB. Significance of enamel thickness in hominoid evolution. *Nature.* 1985;314:260–3.
- McHenry HM. Relative cheek-tooth size in *Australopithecus*. *Am J Phys Anthropol.* 1984;64:297–306.
- McHenry HM, Berger L. Body proportions in *Australopithecus afarensis* and the origins of the genus *Homo*. *J Hum Evol.* 1998;35:1–22.
- Olejniczak AJ, Smith TM, Skinner MM, Grine FE, Feeney RNM, Thackeray JF, et al. Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biol Letters.* 2008;4:406–10.
- Partridge TC, Granger DE, Caffee MW, Clarke RJ. Lower Pliocene hominid remains from Sterkfontein. *Science.* 2003;300:607–12.
- Peters CR. Nut-like oil seeds—food for monkeys, chimpanzees, humans, and probably ape-men. *Am J Phys Anthropol.* 1987;73:333–63.
- Plavcan JM. Sexual dimorphism in primate evolution. *Yrbk Phys Anthropol.* 2001;44:25–53.
- Plavcan JM. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: implications for the fossil record. *Am J Phys Anthropol.* 2003;120:38–60.
- Potts R. Environmental hypotheses of hominin evolution. *Yrbk Phys Anthropol.* 1998;41:93–136.
- Rak Y. *The Australopithecine face.* New York: Academic; 1983.
- Reed KE. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J Hum Evol.* 1997;32:289–322.
- Reno PL, Meindl RS, McCollum MA, Lovejoy CO. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc Natl Acad Sci U S A.* 2003;100:9404–9.
- Richmond BG. Biomechanics of phalangeal curvature. *J Hum Evol.* 2007;53:678–90.
- Richmond BG, Jungers WL. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science.* 2008;319:1662–5.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, et al. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature.* 2005;436:693–5.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. First hominid from the Miocene (Lukeino formation, Kenya). *C R Acad Sci Paris Sci Terre Plan.* 2001;332:137–44.
- Smith GE. The fossil anthropoid ape from Taung's. *Nature.* 1925;115:235.
- Spencer F. *Pittdown: a scientific forgery.* Oxford: Oxford University Press; 1990.
- Sponheimer M, Passey BH, de Ruiter DJ, Guatelli-Steinberg D, Cerling TE, Lee-Thorp JA. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science.* 2006;314:980–2.
- Stern JT, Susman RL. The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol.* 1983;60:279–317.
- Strait DS, Grine FE. Cladistics and early hominid phylogeny. *Science.* 1999;285:1210.
- Strait DS, Grine FE. Inferring hominoids and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J Hum Evol.* 2004;47:399–452.
- Strait DS, Grine FE, Fleagle JG. Analyzing hominid phylogeny. In: Henke W, Tattersall I, editors. *Handbook of paleoanthropology*, vol. 3. Berlin: Springer; 2007. p. 1781–806.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, et al. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci U S A.* 2009;106:2124–9.
- Susman RL. New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus*. In: Grine FE, editor. *Evolutionary history of*

- the “robust” Australopithecines. New York: Aldine de Gruyter; 1988a. p. 149–72.
- Susman RL. Hand of *Paranthropus robustus* from member 1, Swartkrans: fossil evidence for tool behavior. *Science*. 1988b;240:781–4.
- Susman RL. Fossil evidence for early hominid tool use. *Science*. 1994;265:1570–3.
- Suwa G, White TD, Howell FC. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations and Plio-Pleistocene hominid evolution. *Am J Phys Anthropol*. 1996;101:247–82.
- Trinkaus E, Long J. Species attribution of the Swartkrans member 1 first metacarpals: SK 84 and SKX 5020. *Am J Phys Anthropol*. 1990;83:419–24.
- Ungar PS, Grine FE, Teaford MF. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE*. 2008;3:e2044.
- Vrba ES. On the connections between paleoclimate and evolution. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. *Paleoclimate and evolution with emphasis on human origins*. New Haven: Yale University Press; 1995. p. 24–45.
- Walker A, Leakey REF, Harris J, Brown F. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*. 1986;322:517–22.
- Walker J, Cliff RA, Latham AG. U–Pb isotopic age of the StW 573 hominid from Sterkfontein, South Africa. *Science*. 2006;314:1592–4.
- Walter RC, Manega PC, Hay RL, Drake RE, Curtis GH. Laser-fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Bed I, Olduvai Gorge, Tanzania. *Nature*. 1991;354:145–9.
- Washburn SL. Tools and human evolution. *Sci Am*. 1960;203:63–75.
- White TD. Early hominids—diversity or distortion? *Science*. 2003;299:1994–7.
- White TD, Suwa G, Asfaw B. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*. 1994;371:306–12.
- White TD, WoldeGabriel G, Asfaw B, Ambrose S, Beyene Y, Bernor RL, et al. Asa Issie, Aramis and the origin of *Australopithecus*. *Nature*. 2006;440:883–9.
- White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, et al. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*. 2009;326:75–86.
- Wood BA, Strait DS. Patterns of resource use in early *Homo* and *Paranthropus*. *J Hum Evol*. 2004;46:119–62.