

The New Hominid Species *Australopithecus anamensis*

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*Australopithecus anamensis*¹ is the earliest species of this genus to have been found. Fossils attributed to *A. anamensis* have been recovered from sediments dating to between 3.8 and 4.2 mya at the sites of Kanapoi and Allia Bay in northern Kenya. *A. anamensis* is still poorly known in comparison with other early hominid species, but the material discovered so far displays primitive features along with more derived characteristics typical of later *Australopithecus* species. This mix of features suggests that *A. anamensis* belongs near the ancestry of this genus. Indeed, it may eventually be determined that this was the earliest *Australopithecus* species.

HISTORICAL BACKGROUND

Bryan Patterson of Harvard University² found the first *A. anamensis* fossil, a distal humerus at Kanapoi in 1965. Patterson's expeditions were exploring the South Turkana localities of Lothagam, Kanapoi, and Ekora.^{3,4} In 1967, Patterson thought the Kanapoi fauna dated to about 2.5 mya, based on whole-rock potassium-argon dates on the capping lava. This date was uncertain, however, because K/Ar determinations on relatively young rocks were difficult in those days, whole-

rock determinations were even more so than those made on samples of sorted crystals. By 1970, the difficulty of dating the capping lava at Kanapoi, together with the early state of the development of a detailed paleomagnetic time scale, had created problems for Patterson's team. The later age determinations on the lava capping the sequence at Kanapoi had a wide spread, from greater than 2.9 ± 0.3 to 2.5 ± 0.2 mya, and thus could not be brought into concordance with the geomagnetic polarities then known. Luckily, however, the pioneering multidisciplinary program of deciphering the geological and faunal history of the Turkana Basin⁵ had by then begun to bear fruit. Using faunal correlation with other dated sites, Patterson was able to estimate the age of the Kanapoi fauna to be between 4.0 and 4.5 mya.⁴ The capping lava at Kanapoi is still recalcitrant to dating. McDougall¹ has carried out whole-rock ⁴⁰Ar/³⁹Ar dating and made determinations of 3.11 ± 0.04 and 3.41 ± 0.04 mya, which he regards as minima for the actual age.

The Kanapoi fossil humerus was mentioned occasionally in reviews of the forearm anatomy of early hominids, with some researchers claiming *Homo* status for the fossil.⁶ Still, the uncertainty about its geological age meant that the humerus re-

ceived little attention. Apart from a brief exploratory expedition led by Richard Leakey in the early 1980s, which was cut short for security reasons, Kanapoi was not surveyed again until recently. One of us (M.L.) has led a series of expeditions to Kanapoi during each of the past four years. These expeditions have produced important new hominid fossils, including the holotype of *A. anamensis*, as well as new faunal specimens. They have also been important in allowing our colleagues Craig Feibel, of Rutgers University, and Ian McDougall, of the Australian National University, to undertake new geological and geochronological investigations.

Work at Allia Bay, East Lake Turkana, was part of the East Turkana Project, which was run by Richard Leakey and Glynn Isaac from 1968 onward. The site of 261-1 was discovered by J. Kithumbi, Kamoya Kimeu's brother-in-law. He found a single hominid upper molar on the surface where a pavement of bone fragments marked the place where a bone bed was exposed. This site lies near a Neolithic burial site and so, over the years, students and staff from the Koobi Fora Field School searched the surface and found a few more hominid teeth. Subsequent sieving of surface material at the site produced additional isolated hominid teeth. A small test trench yielded a small piece of mandible with two teeth in situ. Coffing and coworkers⁷ described these early surface finds and attributed them to *Australopithecus* cf. *A. afarensis*. Still later, Musa Kyeva discovered a radius in beds that are laterally equivalent at the nearby Sibilot Hill. This radius was described and analyzed by Heinrich and colleagues,⁸ who noted

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its similarities to other *Australopithecus* radii. Excavations at the Allia Bay 261-1 site were carried out for three seasons, from 1995 through 1997, and resulted in the recovery of a maxilla, more isolated teeth, and a more complete fauna. Craig Feibel and Ian McDougall were also involved in explicating the geology and dating at this site.

The list of hominid specimens attributed to *A. anamensis* is growing every season. It now includes several maxillae and mandibles, more than 50 isolated teeth, a piece of temporal bone, and parts of the humerus, radius, capitate, manual phalanx, and tibia from different individuals.⁹

GEOLOGICAL AND PALEOECOLOGICAL BACKGROUND

The two sites at which *A. anamensis* has been found are united by their geological setting. They can be placed in solid geological and temporal contexts, thanks to the pioneering work of Frank Brown, Craig Feibel, and their students and colleagues.

The present-day Lake Turkana lies in a basin that has had a varied history. There was a lake in this basin for only a small fraction of the last four million years.¹⁰ Between 4.2 and 4.0 mya, a lake called Lonyumun filled the basin. The ancestral Kerio River drained into lake Lonyumun from the south, over time building a delta out into the lake. The fossiliferous sediments at Kanapoi are from channel deposits of this river, including those filling the dissected Miocene volcanics and those associated with the Kerio river delta. Three tuffaceous horizons were dated by the single-crystal laser fusion ⁴⁰Ar/³⁹Ar method. The upper and lower of these dates bracket all but one of the Kanapoi hominid fossils to between 4.17 ± 0.03 and 4.07 ± 0.02 mya.⁹ A presumed male mandible recovered from sediments immediately above the 4.07 mya tuff cannot be much younger than it is. Most of the fossil hominids are bracketed by the lower two of these dated tuffs, and so are dated to between 4.17 ± 0.03 and 4.12 ± 0.02 mya.¹

The 261-1 site at Allia Bay was formed after the filling of Lonyumun lake. By about four million years ago, sediments from the ancient Omo, Turk-

wel, Kerio, and smaller rivers had filled the basin, and these rivers continued to flow over their extensive floodplains. The ancestral Omo was then, as it is now, the dominant river.¹⁰ The Allia Bay site is associated with a channel of this great river, and is probably a meander-splay concentration of bones. The bone bed itself consists primarily of bones of aquatic species, mainly fish and reptiles. Many of the fossils in this bed are rolled and weathered, indicating transport from a distance, reworking from older sediments, or both. At the top of the bed there are better-preserved fossils, including those of mammals, which probably are from animals that lived close to the channel.

The mainly fluvial sedimentary sequences at Allia Bay have tuffs in them. A thick outcrop of the Moiti Tuff

As far as can be determined, the riverine woodlands and gallery forest habitats sampled at Kanapoi and Allia Bay are similar to those reconstructed for *A. afarensis* sites.

is exposed in the hill just above the site and about 5 m stratigraphically above the bone bed. This has been dated elsewhere in the basin and near the source in the Ethiopian highlands to about 3.9 mya.¹¹ The age of the bone bed can be extrapolated, assuming uniform sedimentary rates, to 3.95 ± 0.05 mya. Thin tuffaceous horizons beneath the bone bed do not have crystals suitable for dating, but may provide correlative power through chemical fingerprinting (Craig Feibel, personal communication) and thus give a maximum age for the site.

The strata at Sibilot, where the radius was found,⁸ are clearly bracketed by the Moiti and Lokochot Tuffs and are, therefore, between 3.92 ± 0.3 and $3.50 \pm .10$ mya. Further, Craig Feibel (personal communication) places the radius site below the Topernawi Tuff

($3.75 \pm .25$ mya) and estimates by stratigraphic extrapolation that it is about 3.8 mya. Thus, all *A. anamensis* fossils come from sites dated to between 3.8 and 4.2 mya.

Reconstructing the habitat preferences of *A. anamensis* is difficult because the relationship between a death assemblage and the habitat preferences of animals is a complex one. Even assuming that the hominids from Kanapoi and Allia Bay once lived near the areas where their bones are found, it is by no means certain that they preferred to live near the depositional environment itself. Also, habitat changes can be sudden in the East African Rift. A large river such as the Omo can dominate an otherwise arid environment to the point at which only narrow ecotone exists between desert and forest. Seasonal flooding can lead to habitats that support a large mammal biomass without much local rainfall. As far as we can tell, all Kanapoi hominid fossils have been damaged by carnivores, and the Allia Bay ones also may have been. These carnivores may have carried dead hominids or parts of them for a considerable distance before discarding them. Therefore, the fact that the hominids have been found in fluvial and deltaic deposits in the ancient Turkana Basin does not mean that they lived in a riparian environment, although it is possible that they did. We know from the micromammals that dry woodland and bushland conditions existed close to the river that deposited the sediments, and we can be reasonably sure that the river would have supported a gallery forest. The Allia Bay hominids are among the fossils that are unrolled and so probably did come from environments more proximal to the ancient river.

As far as can be determined, the riverine woodlands and gallery forest habitats sampled at Kanapoi and Allia Bay are similar to those reconstructed for *A. afarensis* sites. Laetoli probably had open grassland with scattered trees and nearby woodland.¹² Hadar ranged from open and closed woodland to bush and grassland.¹³ All of these sites contrast with the paleoenvironmental reconstruction of the *A. ramidus* site of Aramis, which is interpreted as having been closed woodland.¹⁴

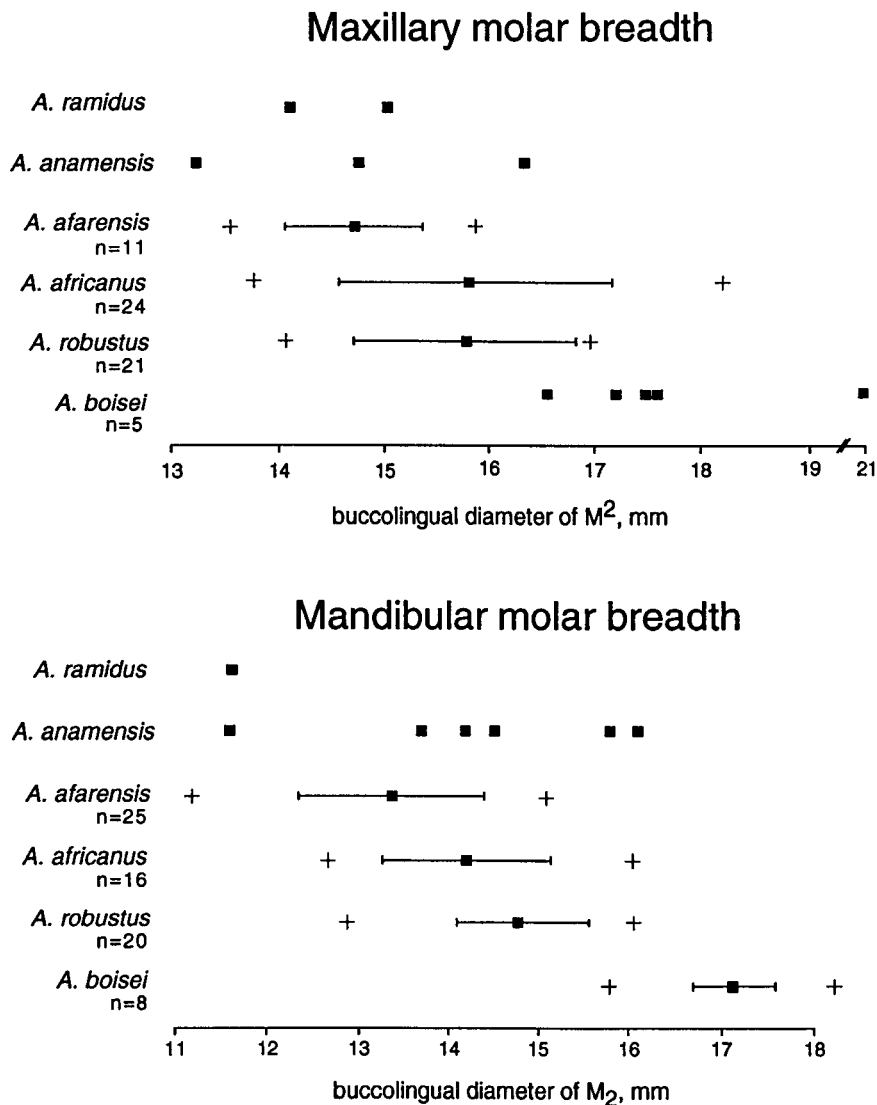


Figure 1. Maximum buccolingual breadths of mandibular and maxillary second molar crowns for several *Australopithecus* taxa. Sample means, standard deviations, and ranges are indicated for most taxa. Individual data points are shown for *A. ramidus*, *A. anamensis*, and maxillary specimens of *A. boisei*. Comparative data for *A. africanus*, *A. robustus*, and *A. boisei* from⁵¹⁻⁵², *A. ramidus* data from¹². *A. afarensis* data kindly provided by William H. Kimbel. *A. anamensis* teeth are comparable in size to those of *A. afarensis*, but have a slightly greater observed size range.

COMPARATIVE ANATOMY

A. anamensis is intermediate in time between *Ardipithecus ramidus* and *Australopithecus afarensis*, and is morphologically distinct from both in several ways. The new genus and species *Ardipithecus ramidus* was named for fossils from horizons at Aramis in Ethiopia that have been securely dated by single-crystal ⁴⁰Ar/³⁹Ar laser fusion dating to just less than 4.4 mya.¹⁴⁻¹⁶ So far, the brief publications regarding the fossils have not allowed a detailed comparison between the two species, but *A. ramidus* clearly is distinguished

from all *Australopithecus* species in that it has 1) absolutely and relatively thinner tooth enamel; 2) canines larger relative to the postcanine teeth; 3) a distinctively small deciduous first molar resembling that of *Pan paniscus*; 4) a marked inclination of the distal radial articular surface; 5) a strong lateral condylar ridge on the distal humerus; and 6) an elongate, superoposteriorly extended lateral humeral epicondyle.¹⁵ Because *A. anamensis* had not been named in 1994, there were a few features, such as lack of a clearly defined articular eminence on

the temporal bone, that were originally thought to differentiate *A. ramidus* from all *Australopithecus* species, but that we now know probably do not.

Australopithecus afarensis is perhaps the best-known species of its genus. It has been found in Tanzania, Ethiopia, and Kenya in deposits ranging in age from about 3.7 mya to 3.0 mya (see Kimbel et al.¹⁷ for recent discoveries, dates, and references). The large collections of *A. afarensis* fossils give a picture of this species as a habitually bipedal hominid with body size and sexual dimorphism at the levels seen in *Gorilla gorilla*.^{18,19} All parts of the skeleton known for *A. anamensis* are also known for *A. afarensis*, so comparisons are easily made between these species.

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spects. Both species exhibit thick tooth enamel, as do all *Australopithecus* species, with that in robust species being especially thick. This appears, on the basis of comparisons with living African apes and *Ardipithecus*, to be a shared derived feature of the genus *Australopithecus*, although it must be noted that many, if not most, Miocene hominoids also had thick enamel.

A. anamensis and *A. afarensis* are similar in their degrees of postcanine megadontia, although the range of size variation in the sample of *A. anamensis* molars is just slightly larger than that in *A. afarensis*. There also is considerable overlap between size distributions of molars in these two species (Fig. 1). Tooth size variability was at least as great in *A. anamensis*, if not greater. Given that molar size is generally related to body size, this may

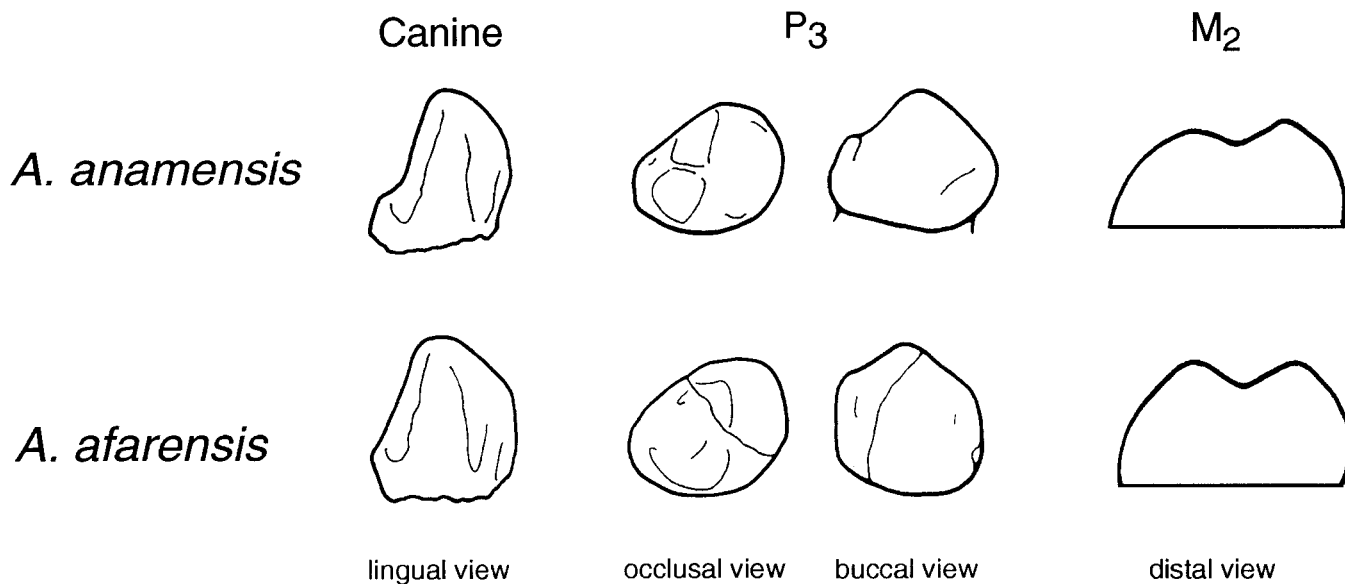


Figure 2. Mandibular canine, third premolar, and second molar crowns of *Australopithecus anamensis* compared with those of *A. afarensis*. Canines (*A. anamensis* KNM-KP 29286 and *A. afarensis* LH 3) are shown in lingual view. Third premolars (*A. anamensis* KNM-KP 29286 and *A. afarensis* LH 3, the latter reversed for comparison) are shown in occlusal and buccal views. Molars (composite outlines from Hlusko⁵³) are shown in distal view. *A. anamensis* canines are more asymmetrical than those of *A. afarensis*. *A. anamensis* premolars have larger buccal cusps with very little lingual cusp development; and molar crowns are lower with more sloping sides.

mean that body size variability in *A. anamensis* was also considerable.

The teeth of *A. anamensis* and *A. afarensis* differ in several aspects of morphology. Both the upper and lower molars of *A. anamensis* have lower crowns with more sloping buccal and lingual sides (Fig. 2). The lower third premolars of *A. anamensis* are more asymmetrical than are those of *A. afarensis* (Fig. 2). They have a large, centrally placed buccal cusp that occupies most of the crown surface area in occlusal view. The lingual cusp is considerably smaller, and is barely distinguishable from the distal marginal ridge. *A. afarensis* lower third premolars, on the other hand, have much greater lingual cusp development, so that the two cusps are more equal in size. The lower fourth premolars are similarly more asymmetrical in *A. anamensis* than in *A. afarensis*.

A. anamensis canines are similar to those of *A. afarensis* in size and shape, but their crowns tend to be more asymmetrical (Fig. 2). Relative to the size of the postcanine teeth, however, the lower canines of *A. anamensis* are slightly larger, on average, than those of *A. afarensis* (Fig. 3). Despite the slightly larger canines of *A. anamensis*, the ranges of variation are similar for both species, demonstrating that they most likely had a similar pattern

of canine size dimorphism. An index of largest to smallest canine crown area is 1.35 for *A. anamensis*, about the same as that for *A. afarensis* and less than that in African apes.

There is some evidence, however, that male canine size in *A. anamensis* was greater than we have estimated. A mandibular fragment from Allia Bay has a very large canine root. In addition, a new presumed male mandible from Kanapoi has a large left canine alveolus, although the fact that a piece of the lateral alveolar wall is missing makes it possible that the alveolus appears larger now than it was in life. The alveolus on the right has the lower part of the canine root still in place. CT scans taken by Fred Spoor through both bodies at the level of the mental foramina show that the large left alveolus is not distorted. It seems, then, that male *Australopithecus* canines were sometimes much larger in the earlier species.

Several maxillae and mandibles are known for *A. anamensis*, and they also differ morphologically from those of *A. afarensis*. They have a striking primitive feature not found in *A. afarensis*: Their postcanine tooth rows are set parallel to one another (Fig. 4). Living apes have postcanine maxillary tooth rows that converge slightly posteriorly; in contrast, those of humans

diverge strongly posteriorly. *A. anamensis* postcanine tooth rows are roughly parallel, while those of *A. afarensis* are more derived, ranging from nearly parallel to slightly divergent. In addition, the *A. anamensis* palate is narrower and shallower than that of *A. afarensis*, although it must be noted that the original Garusi maxillary fragment from Laetoli has also been reconstructed as having been narrow and shallow.²⁰

The narrow, parallel tooth rows in all three mandibles of *A. anamensis* are correlated with the characteristic oblique long axes of the symphyseal cross-sections (Fig. 5).²¹ This leads to *A. anamensis* mandibles having a strongly receding symphyseal contour, a feature that distinguishes both of these mandibles from those of all other *Australopithecus* species.²¹

A left temporal fragment of *A. anamensis* is instructive in that it shows extensive pneumatization of the squame, a barely definable articular eminence, and a tiny external acoustic meatus.²² These three primitive features are found also in *A. ramidus*.¹⁵ The articular eminence is more pronounced and the acoustic meatus larger, however, in *A. afarensis* and other species of *Australopithecus*. It is almost certain that the small acoustic

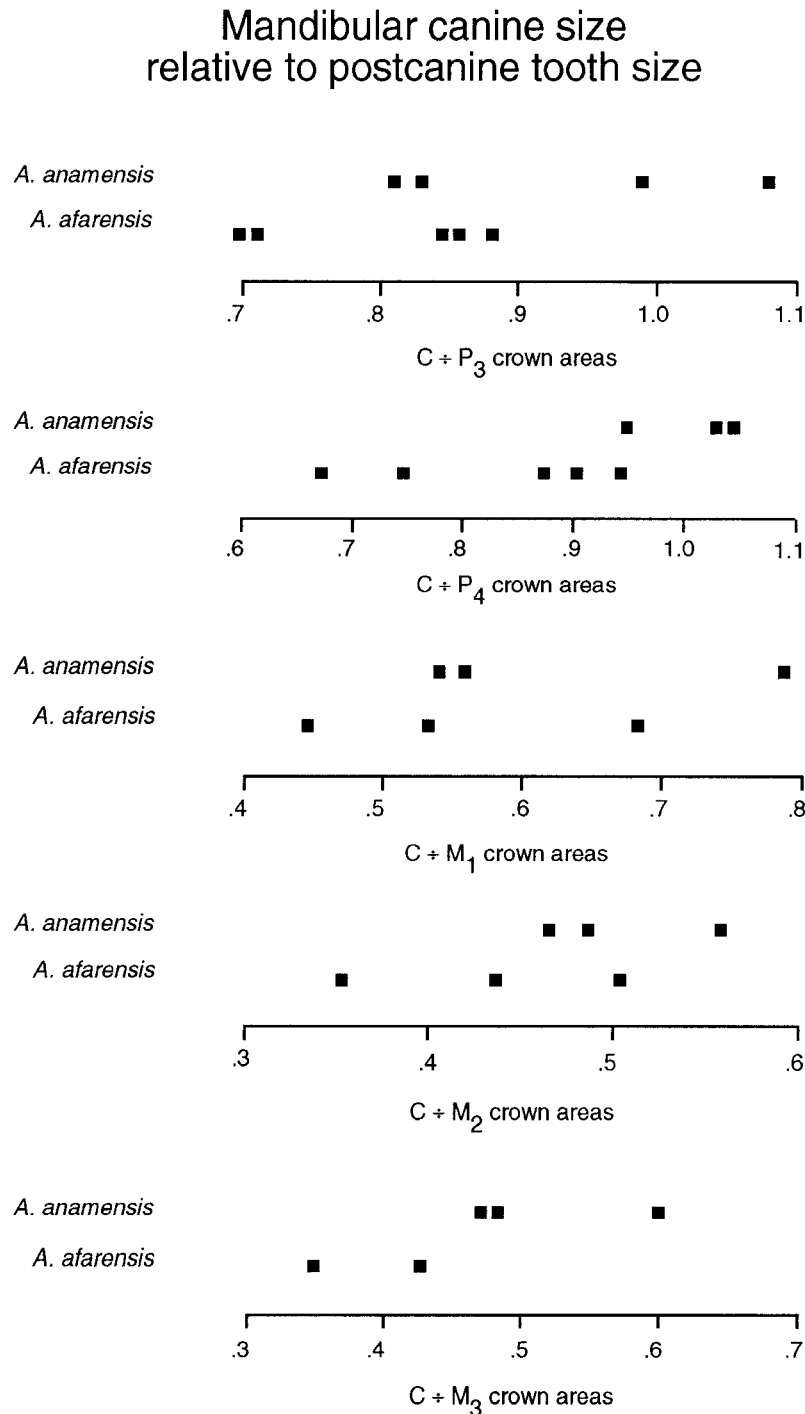


Figure 3. Mandibular canine occlusal area, calculated as crown breadth times length, compared with crown areas, breadth times length, of each mandibular postcanine tooth. Data are presented as ratios of canine area to the area of each of the postcanine teeth. Only associated specimens are included. Individual values for *A. anamensis* and *A. afarensis* are shown. Sample ranges of both species overlap in all comparisons. In all cases, *A. anamensis* canines are slightly larger relative to the postcanine teeth than is the case in *A. afarensis*, although the magnitude of size variation is similar in both species.

meatus has nothing to do with hearing or the size of the pinna.

Postcranially, *A. anamensis* is very like *A. afarensis*, despite some workers seeing derived human-like features in

the humerus^{2,6,23,24} and tibia.^{25,26} The humerus, radius, and tibia can be almost exactly matched in size and morphology to the *A. afarensis* collections from Hadar.^{27–29} These elements are as

large as and sometimes a little larger than any known for *A. afarensis*. This suggests that some *A. anamensis* individuals may have had body sizes exceeding those of the largest *A. afarensis* individuals, which are estimated to have weighed about 45 kg^{30,31} or even up to 80 kg.³²

The radius of *A. anamensis*⁸ is too long to fit the longest ulna from Hadar, A.L. 438-1a.¹⁷ However, this radius is morphologically very similar to others of *A. afarensis*, down to the unusual division of the lunate and scaphoid surfaces, where the lunate area rather than the scaphoid predominates, as in African apes and humans.⁸ If the long radius is a guide, at least the largest of this species had forearms as long as those of human males over six feet tall. We think this suggests that *A. anamensis* had relatively long forearms compared with humans, a conclusion also reached by Kimbel, Johanson, and Rak¹⁷ about the arm proportions of *A. afarensis*.

The humerus does not show the extant African ape-like conditions in the distal articular surface and epicondyle to the degree seen in *A. ramidus*.¹⁵ The phenetic affinities of the *A. anamensis* humerus are with other *Australopithecus* distal humeri. However, some authors^{23,24} also have found similarities between *A. anamensis* and *Homo* distal humeri, raising potentially interesting questions about relations among these taxa. But because many of these features are quite variable, with poorly understood functional and developmental bases, their value as taxonomic indicators is uncertain.

The partial phalanx is as large as the largest of the Hadar specimens and is similar in shape, curvature, and degree of development of the flexor sheath ridges. The capitate is damaged, but enough detail is preserved to say that it lacked a facet for the third metacarpal styloid process, and in this is similar to apes and all other *Australopithecus* capitates. It still, however, retains the primitive condition of having the facet for the second metacarpal facing directly laterally, and in this it is unlike *A. afarensis*,^{33,34} *Australopithecus africanus*,^{35,36} and *Homo sapiens*, including Neandertals.^{37,38}

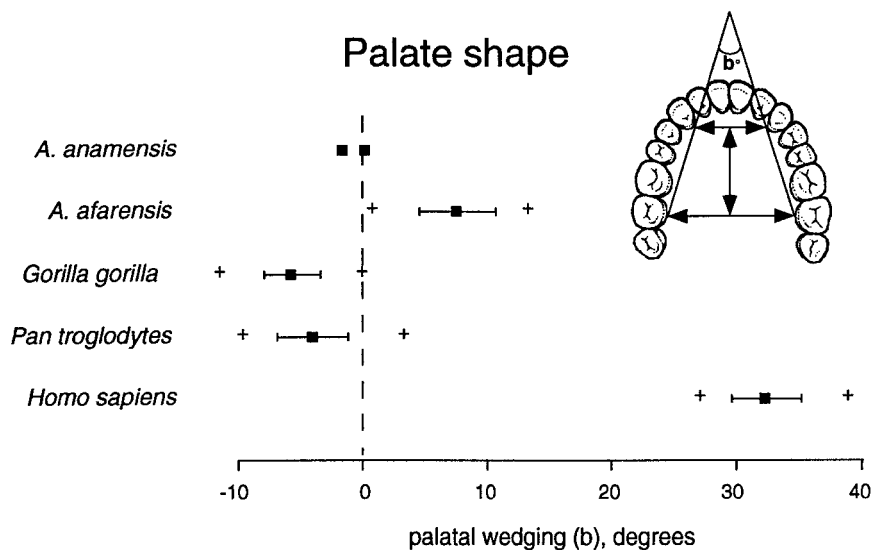


Figure 4. Shape of the maxillary dental arcade computed as the angle of tooth row divergence between minimum distances between canine and second molar crowns, calculated using formula published by Digiovanni, Scoles, and Latimer⁵⁴ and considering anteroposterior distance between canines and second molars. Equivalent results can be obtained by using distances between P³s instead of canines, or by computing a simple ratio between anterior and posterior breadths. Sample means, standard deviations, and observed ranges are depicted for comparative taxa and individual data points for *A. anamensis*. Extant taxa are represented by 20 individuals each and *A. afarensis* by 8 specimens from Hadar (data provided by W. H. Kimbel). *A. anamensis* maxillary dental arcades have roughly parallel sides, retaining an ape-like condition, while those of *A. afarensis* have postcanine tooth rows that diverge posteriorly. (The only exception is the Garusi specimen, which is not included here but appears to have parallel postcanine tooth rows). The same pattern is seen in mandibular shape. Canine size does not affect these results; there are no differences between male and females of any species.

The tibia is matched closely in morphology by the largest Hadar tibia, A.L. 333-42, although it is a little larger than that one. It also shows unequivocal adaptations to habitually bipedal gait. The tibial shaft is oriented orthogonally relative to the talar joint surface, placing the knee directly over the foot in bipedal stance.³⁹ This vertical reorientation of the long axis of the tibia, which is found in all bipedal hominids, contrasts markedly with the varus angle of the shank in apes (Fig. 6). The *A. anamensis* tibial metaphyses are markedly flared proximally and distally, another feature found only in hominid bipeds. The Kanapoi tibia also displays a reduced fibular articulation,¹ but is still lunate in shape, as in other *Australopithecus* tibias. The clear adaptations to bipedal posture and locomotion seen in the Kanapoi tibia indicate that terrestrial bipedality had been selectively advantageous for *A. anamensis* and its immediate ancestors, beginning some time prior to 4.2 mya.

EVOLUTIONARY PERSPECTIVE

Several other hominid fossils that date to this period were previously referred to *Australopithecus afarensis*. With the discovery of *A. anamensis* and the earlier discovery of *A. ramidus*, however, it is now not easy to decide to which species they belong. These fossils include the femur from Maka,⁴⁰ the frontal bone from Belohdelie,⁴¹ and the teeth from Fejej,⁴² all in Ethiopia. There are, as yet, no femora known from *A. anamensis*, but in view of the fact that the *A. anamensis* tibia resembles those of *A. afarensis* in some detail, it would not be surprising to find that the femora of these two species were also similar. The frontal bone of *A. anamensis* is also unknown. Until one is found, there is really no way of determining if the Belohdelie frontal really belongs to *A. afarensis* or *A. anamensis*, or whether these species had equivalent frontal bone morphology.

The case of the 4.00 to 4.18 mya teeth from Fejej^{42,43} is not much easier, as only one tooth in the sample has much of its crown left. Fejej is also less than 100 miles from Allia Bay. Tooth size ranges of *A. anamensis* and *A. afarensis* overlap considerably. The crown of the Fejej P₄ can be matched easily in size and morphology with some of those from Allia Bay and Kanapoi. The Fejej teeth also have thick enamel, which, as noted earlier, is a derived trait shared by all *Australopithecus* species, but not the earlier *Ardipithecus ramidus*.^{15,16} Thus, we cannot be certain whether these specimens should be attributed to *A. afarensis* or *A. anamensis*.

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There is no temporal overlap between *A. anamensis* and *A. afarensis*. Consequently, we feel that it is premature to decide that more than one hominid species necessarily existed around 4 mya,⁴³ even though there is no theoretical reason for only one hominid species to have existed at any one time. If these few earlier *A. afarensis* examples are later shown to belong to *A. anamensis*, then an ancestor-descendent relationship between *A. anamensis* and *A. afarensis* might explain their distribution in time.

The simplest hypothesis that can be made to accommodate the new early hominid fossils is that there was one

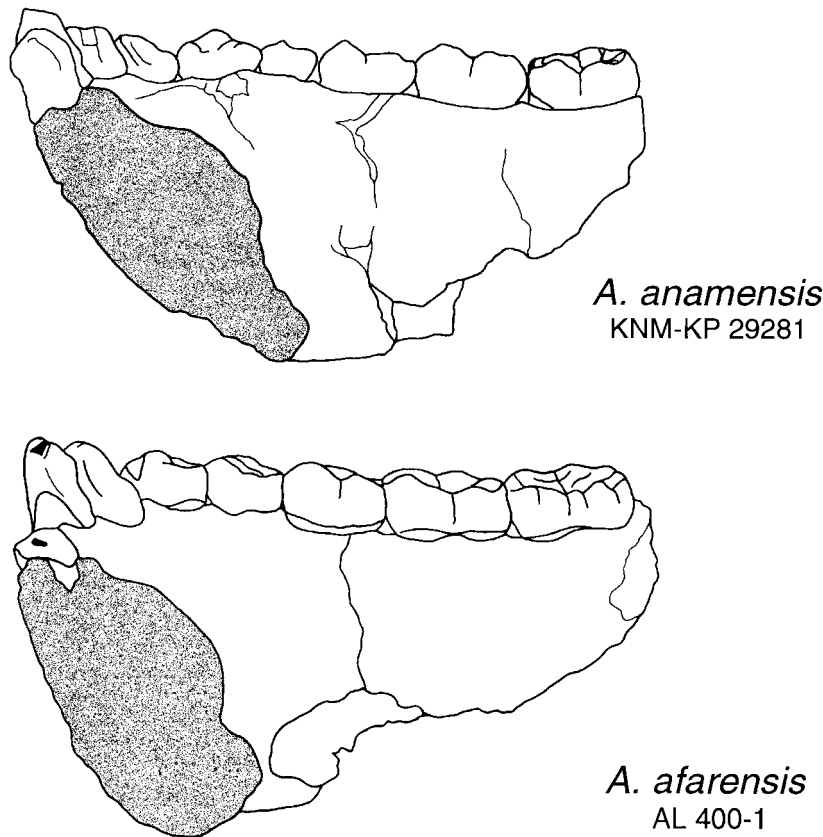


Figure 5. Medial views of mandibles of *A. anamensis* and *A. afarensis*, with symphyseal cross-sections stippled. Both sufficiently well-preserved *A. anamensis* mandibles have more sloping symphyses than any known for *A. afarensis*, and correspondingly long postincisive plana.²¹

evolving lineage of hominids. Future fossil discoveries may reveal a bushier phylogenetic tree, but currently there is no data that supports such a hypothesis. At present, we believe that no compelling evidence rules out the phylogenetic position of *A. anamensis* as intermediate between *A. ramidus* and *A. afarensis*. If we could be certain that these three taxa represent a single evolving lineage that was the result of a single splitting event, it would not be necessary to designate *A. anamensis* as names a new species. But this has not yet been demonstrated, so placing the *A. anamensis* fossils in either of the other taxa on the basis that they might be from an intermediate part of a single lineage would obscure and restrict any other possible phylogenetic interpretations.

SUMMARY

The following scenario can be constructed from the available evidence,

and might have taken place. *Ardipithecus ramidus* is known from relatively high altitude, closed-canopy woodlands of Ethiopia. This species may have been ancestral to *A. anamensis*, known from riverine woodlands and gallery forests of the Turkana Basin. *A. anamensis*, in turn, preceded the ecologically widespread species *A. afarensis*, known from forest, woodlands, and more open country across East Africa, and possibly Central Africa. This scenario would accord with the changes in the teeth in these successive species. The dentition, tooth row, palate and temporal bone of *A. anamensis* suggest a change in diet and chewing mechanism from the primitive African ape-like ones in *A. ramidus*. With its primitive dentition and thin enamel, *A. ramidus* was probably much like a chimpanzee in diet, an omnivore that relied heavily on fruit. A shift appears to have been made first to thicker tooth enamel in *A. anamensis*, perhaps indicating a dietary shift

to harder foods.^{44,45} Later, changes occurred in the geometry of the mandible and maxilla in *A. afarensis*, along with heightened molar tooth crowns. These traits were carried to extremes in the later species *A. aethiopicus* and *A. boisei*.

We do not yet know how long before 4.2 mya the shift to habitual bipedality was made. Little has been published about the postcranial skeleton or locomotor adaptations of *Ardipithecus ramidus*. The postcranial fossils of *Australopithecus anamensis* show that it was a habitually bipedal species that still retained some primitive features of the upper limb skeleton, perhaps even more so than did *A. afarensis*.

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Controversy exists, and will not easily be resolved, about whether these primitive retentions were adaptive and thus indicate that arboreality was a significant part of *Australopithecus* locomotion, or whether they were merely the result of differential rates of adaptive change between the fore and hindlimbs (see reviews in Latimer⁴⁶ and Susman, Stern, and Jungers⁴⁷).

Molecular estimates for the divergence time of chimpanzees and humans range from 15 to 2.5 mya, but converge on 5 mya.⁴⁸⁻⁵⁰ Because of the early date of *A. anamensis*, its craniodental and postcranial skeletal mor-

Inclination of tibial shaft

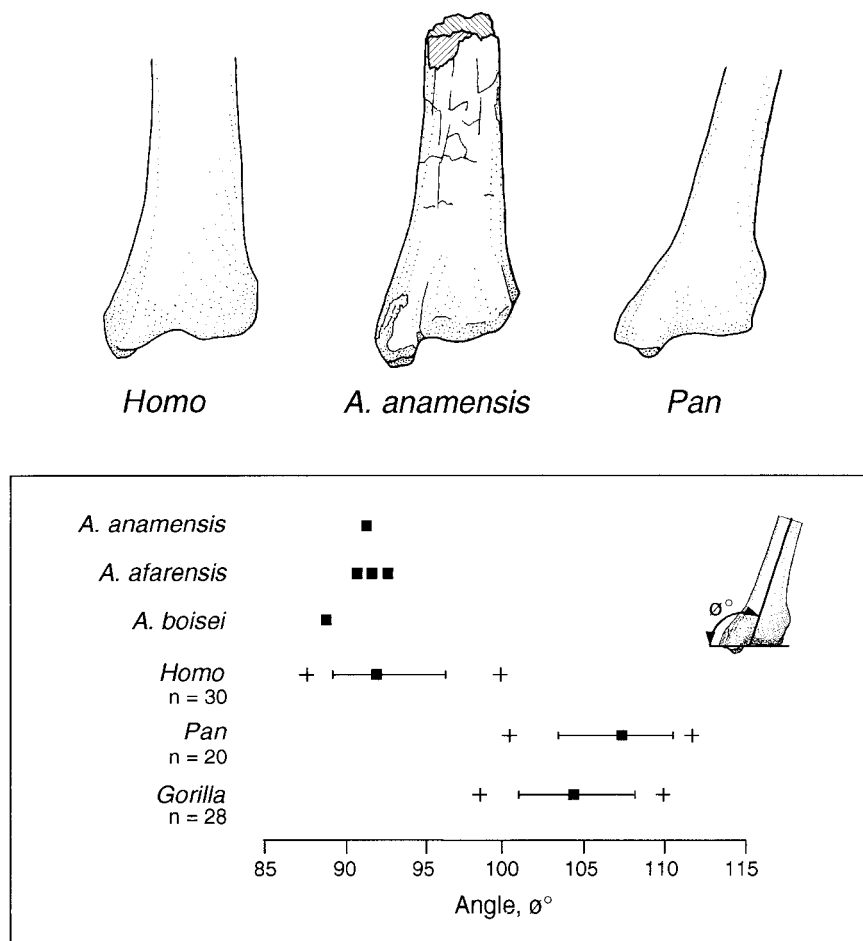


Figure 6. Top, posterior views of a distal tibia of *Homo sapiens* (KNM-KP 29285), and *Australopithecus anamensis* (KNM-KP 29285), and *Pan troglodytes* oriented so that the talocrural joint surfaces are horizontal. Bottom, graph of angles of inclination relative to the talar surface in extant and fossil taxa (adapted from Latimer, Ohman, and Lovejoy³⁹). Hominids have vertically oriented tibial shafts relative to the talar joint surface, whereas chimpanzees and gorillas have sharply inclined tibial shafts that place the knee well lateral to the ankle in plantigrade posture. The Kanapoi tibia resembles that of all other hominids and differs from those of all African apes in having its knee placed directly over its ankle joint.

phology is providing new and much-needed clues to the origin of our lineage.

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