

Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record

William H. Kimbel^{a,*}, Charles A. Lockwood^b, Carol V. Ward^c, Meave G. Leakey^d,
Yoel Rak^e, Donald C. Johanson^a

^a Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 80287-4101, USA

^b Department of Anthropology, University College London, London, UK

^c Department of Anthropology, Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, MO 65211

^d Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA

^e Department of Anatomy, Sackler School of Medicine, Tel Aviv University, Tel Aviv, Israel

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Abstract

We tested the hypothesis that early Pliocene *Australopithecus anamensis* was ancestral to *A. afarensis* by conducting a phylogenetic analysis of four temporally successive fossil samples assigned to these species (from earliest to latest: Kanapoi, Allia Bay, Laetoli, Hadar) using polarized character-state data from 20 morphological characters of the dentition and jaws. If the hypothesis that *A. anamensis* is ancestral to *A. afarensis* is true, then character-state changes between the temporally ordered site-samples should be congruent with hypothesized polarity transformations based on outgroup (African great ape) conditions. The most parsimonious reconstruction of character-state evolution suggests that each of the hominin OTUs shares apomorphies only with geologically younger OTUs, as predicted by the hypothesis of ancestry (tree length = 31; Consistency Index = 0.903). This concordance of stratigraphic and character-state data supports the idea that the *A. anamensis* and *A. afarensis* samples represent parts of an anagenetically evolving lineage, or evolutionary species. Each site-sample appears to capture a different point along this evolutionary trajectory. We discuss the implications of this conclusion for the taxonomy and adaptive evolution of these early-middle Pliocene hominins.

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Introduction

Recent debate concerning the shape of the hominin phylogenetic tree—the relative importance of anagenesis vs. cladogenesis in the generation of morphological diversity—has focused on early Pliocene and late Miocene discoveries that have extended the hominin fossil record back to the 5–7 Ma interval in which DNA evidence suggests chimpanzee and human lineages diverged (Stauffer et al., 2001). Much of the record prior to 3.5 Ma remains poorly sampled, however,

creating the opportunity for widely divergent interpretations of lineage diversity near the base of the hominin clade (e.g., Tattersall, 2000; Wood and Richmond, 2000; Senut et al., 2001; Leakey et al., 2001; Brunet et al., 2002; Wood, 2002; White, 2002; Haile-Selassie et al., 2004). A theoretical commitment to cladogenesis as the major, if not the only, basis for macroevolutionary change supports interpretations of recent discoveries as evidence of high taxonomic diversity early in the hominin fossil record, whereas the view that anagenesis is capable of generating species-level differences interprets the early record of hominins as supporting only one or at most two lineages prior to the widely accepted proliferation of lineages observed close to the Plio-Pleistocene boundary. Progress toward resolution will come from a more thoroughly sampled

* Corresponding author. Fax: +1 480 727 6582.

E-mail address: wkimbel.ih@asu.edu (W.H. Kimbel).

fossil record over time and space and more completely documented ranges of sample variation, accompanied by the rigorous testing of phylogenetic hypotheses.

One area where existing samples can already be examined in this context is the hypothesized ancestor-descendant relationship between *Australopithecus anamensis* (4.2–3.9 Ma) and its successor in eastern Africa, *A. afarensis* (3.6–3.0 Ma).¹ The *A. anamensis* hypodigm consists of approximately 80 (mostly craniodental) fossils from two Kenyan sites, Allia Bay and Kanapoi (Leakey et al., 1995, 1998; Ward et al., 2001). The *A. afarensis* hypodigm comprises more than 400 fossils, the great majority of which are from Laetoli, Tanzania, and Hadar, Ethiopia, with more than 90% of the total coming from the latter site (Johanson et al., 1982; Kimbel et al., 1994, 2004).² The two hypodigms contrast strikingly in comparable aspects of mandibular, maxillary, and dental anatomy (Ward et al., 2001), and there is little doubt that, on purely phenetic grounds, they can be distinguished effectively at the species level. This conclusion is underscored by the fact that morphological variation is well documented in the extensive Hadar sample, but this variation does not diminish the observed differences between *A. anamensis* and *A. afarensis* (Kimbel et al., 2004).

It is widely accepted that *A. anamensis* was directly ancestral to *A. afarensis* (e.g., Leakey et al., 1995; Wolpoff, 1999; Ward et al., 2001; Gibbons, 2002; White, 2002). This view is attributable to two factors: the known temporal range of *A. anamensis* completely antedates that of *A. afarensis*, and, insofar as the two differ anatomically, *A. anamensis* is described as the more plesiomorphic taxon (Ward et al., 2001). Each of these factors warrants closer scrutiny.

Although the temporal positions of the two species' hypodigms do not overlap, each hypodigm itself consists of two temporally disjunct site-samples (Fig. 1). The *A. anamensis* sample from Kanapoi (~4.20–4.17 Ma) predates that from Allia Bay (~3.9 Ma), while the Laetoli sample of *A. afarensis* (~3.7–3.5 Ma) predates the one from Hadar (~3.4–3.0 Ma). With the four site-samples thus ordered in time, it is possible to examine the sequence for temporally vectored morphological change. Leakey et al. (1995; see also Ward et al., 2001) initiated such an examination and found some differences among the samples, noting in particular that *A. anamensis* tends to resemble the older Laetoli sample of *A. afarensis* phenetically more than it does the younger Hadar sample. Lockwood et al. (2000) identified temporal trends in *A. afarensis* that lend statistical weight to the differences between the Laetoli and Hadar site-samples.

These observations constitute a testable hypothesis about ancestry and descent among the site-samples. To test this

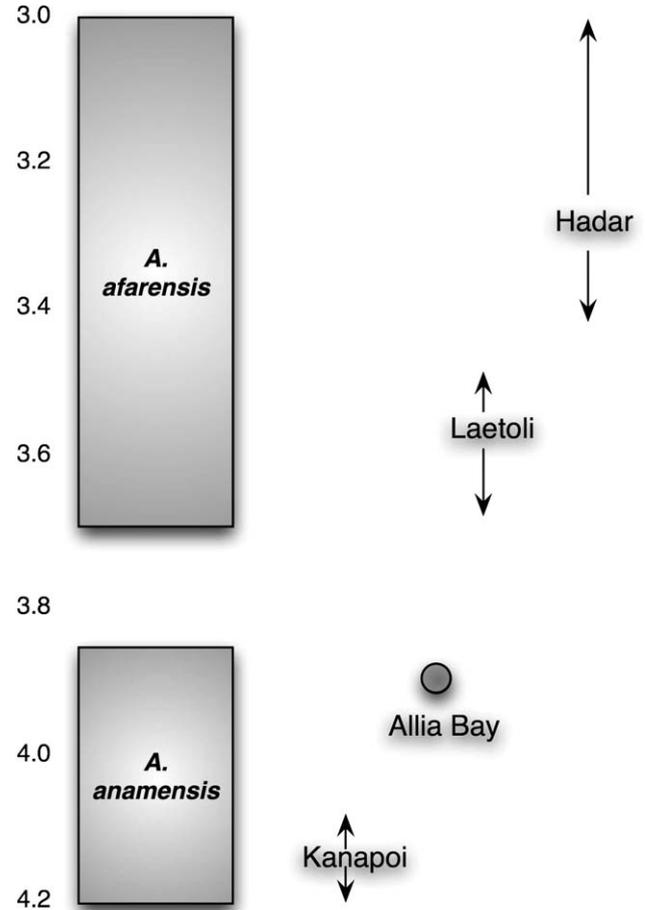


Fig. 1. Temporal relationships of *Australopithecus anamensis* and *A. afarensis* site-samples analyzed in this study.

hypothesis, we conducted a formal phylogenetic analysis that treated each site-sample as an operational taxonomic unit (OTU) bearing polarized morphological character-states. If the hypothesis that *A. anamensis* was ancestral to *A. afarensis* is true, then character-state changes between the temporally ordered site-samples should be congruent with hypothesized polarity transformations based on outgroup conditions. That is, when employing the site-samples as OTUs in a cladistic analysis, each of the three geologically older site-samples should have only younger samples in its sister group, and no sample save the terminal one, from Hadar, should have autapomorphic states.³ Nor should there be derived states shared by some of the in-group OTUs as homoplasies.

¹ The BEL-VP 1/1 partial frontal bone from ca. 3.8 Ma sediments at Belohdelie, Middle Awash, Ethiopia, has been likened to the frontal of *A. afarensis* (Asfaw, 1987; Kimbel et al., 1994, 2004). It is discussed below.

² *Australopithecus afarensis* is also definitively present in Tulu Bor member sediments at Koobi Fora (Kimbel, 1988), and in the Maka sands, Middle Awash, Ethiopia (White et al., 2000). In our opinion, the partial mandible attributed to *A. bahrelghazali* from Chad (Brunet et al., 1996) also represents this taxon. All of these samples are close to the Hadar assemblage in age, and, where data are available, they are here treated as part of the "Hadar" OTU.

³ One could argue that the trend toward large cranial and jaw size in the upper part of the Hadar Formation (Lockwood et al., 2000) implies that this site-sample should be divided into two OTUs. However, as we have shown elsewhere (Lockwood et al., 2000; Kimbel et al., 2004), these changes did not impact craniodental characters diagnostic of the species (including those examined in the present study). Because character-state coding would be identical for both earlier and later Hadar OTUs, we did not divide the sample for this analysis.

Our combined stratigraphic-phylogenetic approach to testing a hypothesis of ancestry and descent derives from common principles underlying the identification of ancestors in a phylogenetic framework. Specifically, it is equivalent to the procedure outlined by Smith (1994: 131–132) for using cladistic practice to determine whether older, plesiomorphic phena in the fossil record can be considered to represent populations from which the ancestors of progressively younger, more derived phena were drawn. Some researchers might expect ancestors never to be identified if cladogenesis is the primary mechanism for generating macroevolutionary change, but if that is true in this case, we would expect to see evidence in the form of autapomorphic traits in older OTUs.

Failure to reject the hypothesis would support the view that anagenetic change in a lineage is sufficient to explain morphological differences among these site-samples. On the other hand, the discovery of autapomorphic (or homoplastic) states in older, putatively ancestral site-samples would suggest a more complex, “bushy” evolutionary history. Either result is important for determining the appropriate taxonomy for these samples, for resolving the relationships of *A. anamensis* and *A. afarensis* to other hominins, and for interpreting the process of adaptive evolution in these Pliocene hominins.

Materials and methods

The choice of characters was determined by the anatomy preserved on specimens in the Kanapoi, Allia Bay, and Laetoli samples, which are smaller and less representative of the entire skull than is the Hadar sample. The small Allia Bay sample is especially problematic in this regard, as it lacks some key regions (such as the nasoalveolar region of the maxilla and symphyseal part of the mandible) containing morphology diagnostic of *A. anamensis* (see Ward et al., 2001). The Laetoli sample, too, is smaller and less representative than one would prefer, though it does include at least one specimen representing each of the dentognathic regions that differentiate *A. anamensis* from *A. afarensis*. The large Hadar collection serves as a useful reference point for the expected magnitude of individual variation in the jaws and teeth of the smaller samples.

We examined all characters that were documented in at least three of the samples. Twenty characters, representing the maxilla, the mandible, and the dentition, effectively discriminate among the fossil OTUs (see Appendix). Five of these are from the mandible, three are from the maxilla, and 12 are from the dentition. The characters comprise a combination of discrete traits, qualitative expressions of a continuum of morphological variation, and polymorphisms (cases in which a site-sample has multiple character-states). The latter type of character is consistent with treating variable states as intermediate character-states (see Strait et al., 1997, for an example of this in hominins). In the Appendix we provide the results of our character analysis; character evolution and possible effects of character correlation are discussed in detail following the phylogenetic analysis presented below.

To polarize the character-states we employed chimpanzees and gorillas as outgroups. *Australopithecus africanus*, whose teeth and jaws are universally interpreted as derived relative to those of *A. anamensis* and *A. afarensis*, was included to illustrate the apomorphic end of the polarity scale. Other hominin taxa are omitted from this analysis because our goal is not to broadly reconstruct early hominin phylogenetic relationships. We seek instead to address questions concerning the fit of stratigraphic and character-state data to a specific, narrowly drawn hypothesis of phylogenetic relationships among four time-successive site-samples. Previous analyses of early hominin phylogeny have strongly supported successive branches for *A. anamensis* and *A. afarensis* basal to all other *Australopithecus* and *Homo* species, without a hint of homoplasy involving the dental and jaw morphology studied for this project (Strait et al., 1997; Strait and Grine, 2004; Kimbel et al., 2004). Moreover, for the characters included here, later hominin species are either similar to *A. africanus* or possess character-states more derived in relation to outgroup conditions than those observed in *A. anamensis*, *A. afarensis*, or *A. africanus*. This pattern underlies the consensus conclusion that *A. afarensis* and *A. anamensis* are basal to later hominin taxa. Including these more apomorphic taxa in the analysis would therefore not affect results pertaining to the hypothesis tested by this analysis.

A more significant concern is the presence of *Kenyanthropus* at 3.5 Ma. *Kenyanthropus* may demonstrate cladogenesis prior to this time, but this taxon is only directly relevant to the analysis if any of the samples share derived character-states with it. At present, the *Kenyanthropus* hypodigm does not match the others in the availability or quality of character data for the mandible and anterior teeth, while the evidence that exists (from the maxilla, for example) does not suggest a close relationship of *Kenyanthropus* to any of the phena considered here (Leakey et al., 2001).

To conduct the phylogenetic analysis, we entered the character-state data in MacClade 4.07 (Maddison and Maddison, 2005) and searched for most parsimonious trees using the branch-and-bound algorithm of PAUP 4.0b10 (Swofford, 2002). Character-state changes were mapped using PAUP with the delayed transformation option (this option affects only one character and not the main conclusions). As implied by the null hypothesis of ancestry and descent, all characters were assumed to be ordered. Because the Allia Bay sample lacked information for 13 of the 20 characters (see Appendix), PAUP reconstructed the states for the ancestral node leading to the Allia Bay OTU based on the states in its sister-group OTUs. This does not affect the phylogenetic position of the Allia Bay OTU, which is determined by the seven characters preserved in that sample.

Results

The most parsimonious reconstruction of character-state evolution suggests that each of the hominin OTUs shares apomorphies only with geologically younger OTUs, as predicted

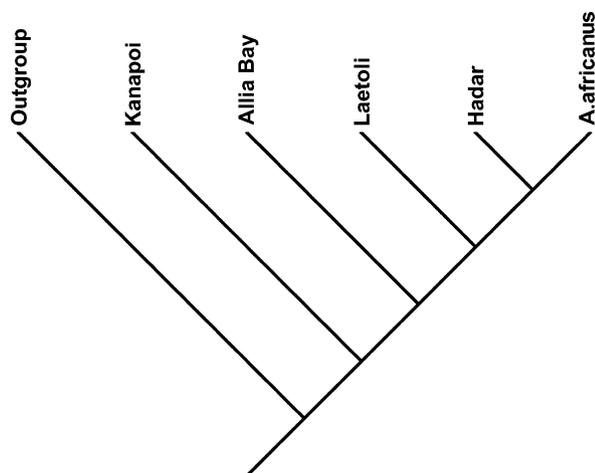


Fig. 2. The most parsimonious cladogram of relationships among the four OTUs and *Australopithecus africanus* (tree length = 31; CI = 0.903), corresponding to the null hypothesis.

by the null hypothesis (Fig. 2: tree length = 31; Consistency Index [CI] = 0.903). With one exception (lateral incisor placement beneath the nasal aperture of the Garusi I maxilla in the Laetoli sample), autapomorphies or homoplasies are not present in any fossil site-sample except the “terminal” branch of Hadar (i.e., the sharp corner of the nasal aperture, which is a derived state shared homoplastically with *Gorilla*; see Appendix).⁴ In other words, the Kanapoi sample of *A. anamensis* is more plesiomorphic than the Allia Bay one, and the Laetoli sample of *A. afarensis* retains more primitive characteristics than do the Hadar fossils. The hypothesis of ancestry and descent between *A. anamensis* and *A. afarensis* is supported by our analysis. The differences among the four temporally successive site-samples—even those between samples of the same nominal species—appear to be phylogenetically significant in that each sample shows more derived features than its predecessor.

The next two most parsimonious trees have three more steps (34) and lower CIs (0.824). One of these trees links the Allia Bay and Laetoli OTUs as a sister clade to a Hadar–*A. africanus* clade, an arrangement that is consistent with the relative geological ages of the site-samples. The other tree places the Laetoli OTU as the basal unit in a (Laetoli, (Allia Bay, (Hadar, *A. africanus*))) clade, which is inconsistent with temporal ordering of the samples (the younger Laetoli OTU is basal to the older Allia Bay OTU). Uncertainty surrounding the assignment of character-states to the node that joins the Allia Bay OTU to the Laetoli, Hadar, and

A. africanus OTUs lies behind these less parsimonious alternatives. However, these trees agree in the placement of Kanapoi as the sister OTU to a clade containing all later samples. Given the small number of characters, a three-step difference between the primary tree and the less parsimonious trees is substantial, and therefore we focus subsequent discussion on the most parsimonious arrangement of taxa.

In the following sections, we analyze character evolution by discussing some of the morphological differences between sites in more detail.

Allia Bay vs. Kanapoi

In our analysis the Allia Bay sample differs from the Kanapoi sample in five of seven comparable characters. These characters distinguish the former as more derived and likely the sister group to the Laetoli and Hadar samples (Table 1).

Lateral corpus contour

One of the distinctive characteristics of the *A. anamensis* mandible is the inferomedial sweep of the lateral corpus contour to the base, inferior to the level of the mental foramen beneath C to P₄. This is best seen in transverse cross sections of the corpus, for example at mid-P₃ (Fig. 3). The three Kanapoi specimens clearly demonstrate this feature (KNM-KP 29281, KNM-KP 29287, and KNM-KP 31713), which contrasts with the homologous anatomy of *A. afarensis* mandibles, especially those from Hadar (we discuss the comparison between Laetoli and Hadar specimens below). In the mandibles of the Hadar sample this contour descends along a straight, much more vertical path toward the basal margin. Examination of the Kanapoi specimens in basal view demonstrates that the inferomedial inclination of this lower portion of the lateral corpus represents a posterolateral extension of the convex, posteroinferiorly retreating basal segment of the anterior corpus (as seen in symphyseal cross section). Indeed, in the Hadar mandible sample the lateral corpus contour is straighter and more vertical than in the Kanapoi sample, and the anterior corpus (symphyseal) contour is straighter and fuller down to the midline basal margin.

Table 1
Comparison of character-states for Kanapoi and Allia Bay OTUs

OTU	Lateral mandibular corpus	Lower canine distal cingulum	Lower P3
Kanapoi	strongly sloping inferomedially beneath premolars, reflecting strong symphyseal retreat	strong (heel or tubercle)	anterior fovea larger than posterior; ant. fovea open to CEJ; low, thin dmr
Allia Bay	more vertical, implying less symphyseal retreat	weak	posterior fovea larger; ant. fovea sealed by mmm; higher, wider dmr

Note: mmm = mesial marginal ridge; dmr = distal marginal ridge.

⁴ As shown by Ward et al. (2001), the Kanapoi mandibular lateral incisors have plesiomorphically large mesiodistal dimensions compared to Hadar homologues. However, *A. africanus* also appears to share a mesiodistally elongated I₂ with the Kanapoi sample (see Appendix). Accordingly, the Hadar sample ($n = 6$, including one Maka tooth) may be apomorphic for this character, although the dearth of data for Allia Bay ($n = 0$) and Laetoli ($n = 1$) OTUs leaves the reconstruction of this character's phylogenetic history in early *Australopithecus* an unresolved question. The single Laetoli value falls within the Hadar sample range, but below those for Kanapoi ($n = 3$) and *A. africanus* ($n = 9$). See Appendix.

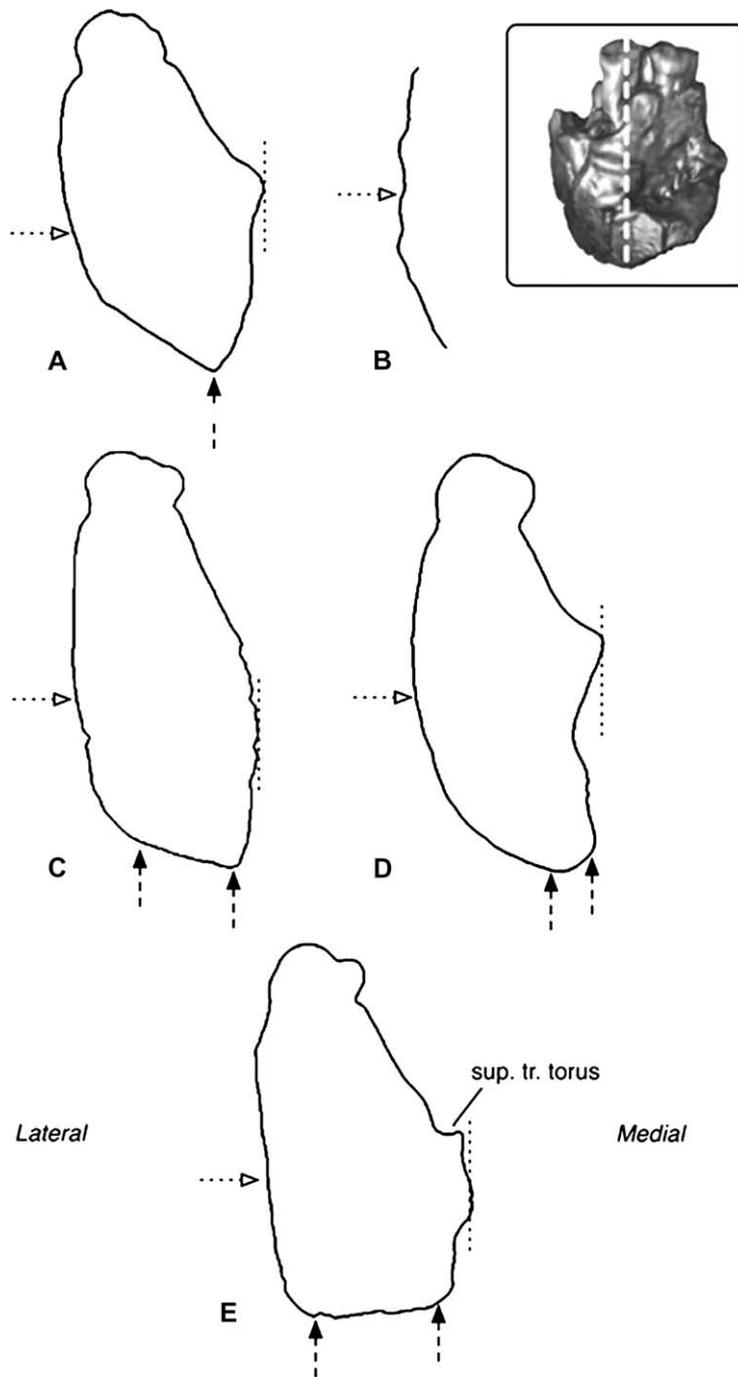


Fig. 3. Cross sections of hominin left mandibular corpora at distal P_3 (approximately natural size): *Australopithecus anamensis*, A. KNM-KP 29281; B. KNM-ER 20432. *A. afarensis*, C. A.L. 277-1; D. A.L. 400-1a (right side reversed); E. A.L. 417-1a. Cross sections were acquired by 3-D laser scanning of casts and the resulting images processed in Photoshop[®]. Each cross section was taken across the P_3 talonid, perpendicular to the mesiodistal postcanine axis (occlusal view) and the external alveolar line (lateral view). Vertical dashed line indicates the midline; horizontal white arrows indicate the approximate level of the mental foramen (projected anteriorly from P_4); vertical black arrows indicate the boundaries of the basal margin. In B, the cortical surface is not anywhere preserved on the medial aspect of the specimen, the contour of which is thus not shown. Some of the variation evident in the figures reflects the degree to which the corpus cross sections on the plane of P_3 intersect structures in the midline, such as the transverse tori and the genioglossal fossa. In the *A. anamensis* mandible from Kanapoi, KNM-KP 29281, the abrupt deviation of the lateral corpus to the base is apparent; in this mandible, the plane of the cross section meets the midline at the most posteroinferior point on the symphyseal plane (indicated by the single black arrow in A). Note the more vertical lateral and broader basal contours of the *A. afarensis* mandibles, with A.L. 400-1a (D) coming closest morphologically to the Kanapoi specimen (though without the abrupt inferomedial deviation evident in the latter). This Hadar specimen is more similar to the Kanapoi mandible in the external convexity of its symphyseal profile, as well, though not in its pronounced symphyseal inclination. The other Hadar mandibles depicted here (C, E) have more vertical lateral contours at P_3 , as well as more upright and straighter symphyseal cross sections; they are, in fact, more typical of the Hadar mandible sample of *A. afarensis* as a whole (Kimbel et al., 2004). The Allia Bay mandibular fragment (B) is not well preserved (no medial cortex remains, for example), but the lateral contour, while abraded, appears to preserve original cortical contours below C and P_3 (see image inset). In comparison to the Kanapoi specimen, note the more vertical lateral contour, with much less inferomedial deviation at comparable positions below the projected level of the mental foramen. This difference is also evident below the canine alveolus, supporting the inference of a less convex and retreating symphyseal area for the Allia Bay fragment. See text for further discussion.

Unfortunately, the Allia Bay mandible KNM-ER 20432 is imperfectly preserved in this region: the anterior corpus and most of the base are lost, and most of the buccal cortical plate is damaged. However, a segment of the buccal cortical plate is present beneath the canine and P₃, and this permits the observation that the inferior portion of the lateral corpus contour did not sweep inferomedially to the mandible's base as strongly as it does in the Kanapoi sample. In fact, the preserved (and partly reconstructed) path of this contour on the Allia Bay mandible can be matched in at least one Hadar jaw (A.L. 330-5), whereas no Hadar mandible approaches the condition characteristic of the three Kanapoi mandibles. This implies that the symphyseal cross-sectional contour in the Allia Bay specimen may likewise have been less retreating than in the Kanapoi mandibles, although direct evidence for this is lacking.

Cingulum development of the lower canines

The lower canines in the Kanapoi sample ($n=4$ completely formed adult crowns) feature a pronounced distal basal heel or cingulum (especially well developed in KNM-KP 29281, KNM-KP 29284, and KNM-KP 29286, though less so in KNM-KP 31727, in which there is a strong distal basal tubercle; see Ward et al., 2001), but in the two known Allia Bay lower canines (KNM-ER 30750, KNM-ER 30731) the distal cingulum is less developed than in any of the four Kanapoi teeth (character #10; Fig. 4). The Allia Bay condition is the more derived state shared with the large majority of Laetoli and Hadar canines of *A. afarensis*. This canine character-state is also similar in *A. afarensis* and *A. africanus*, with the exception of *A. afarensis* teeth LH-3 and A.L. 198-1, whose relatively pronounced cingula define the more primitive extreme of variation in the Laetoli and Hadar samples,

respectively (the MAK-VP 1/12 lower canine also has a relatively large basal cingulum).

Occlusal morphology of the mandibular third premolars

Three characters that separate the Allia Bay from the Kanapoi sample relate to lower P₃ morphology (#s 6, 17, 20). In the Kanapoi sample, the P₃ is strongly plesiomorphic: unicuspid, though with an incipiently developed lingual cusp (manifested as a small pyramid of enamel arising from the transverse crest); mesiodistally elongated; strongly asymmetric; and obliquely oriented in the postcanine tooth row. The size of the anterior fovea on these Kanapoi teeth dominates the posterior fovea (character #16; e.g., KNM-KP 29286, KNM-KP 28287, KNM-KP 30500, KNM-KP 34725; see Fig. 5 and Deluzene, 2004), a condition similar to that of the great apes. In addition, the anterior fovea deeply invaginates the mesiolingual face of the crown such that the fovea remains “open” as far rootward as the thin, linear enamel bulge immediately above the cervicoenamel junction (character #17). Distally, the distal marginal ridge in the Kanapoi P₃s is a basally set, very thin enamel wrinkle (character #20) that virtually disappears with moderate occlusal wear (e.g., KNM-KP 29281, KNM-KP 31730). While the single Allia Bay P₃, KNM-ER 20432, bears most of the primitive, apelike hallmarks of Kanapoi homologues, including the mesiodistally elongate, skewed asymmetry of the crown in occlusal view, it differs from the Kanapoi condition in these three characters:

1. the transverse crest is shifted mesially such that the posterior fovea dominates the occlusal aspect of the crown;
2. the anterior fovea, though “open” anteriorly by Plio-Pleistocene and later hominin standards, is sealed mesially by a prominent enamel rim (mesial marginal ridge) well

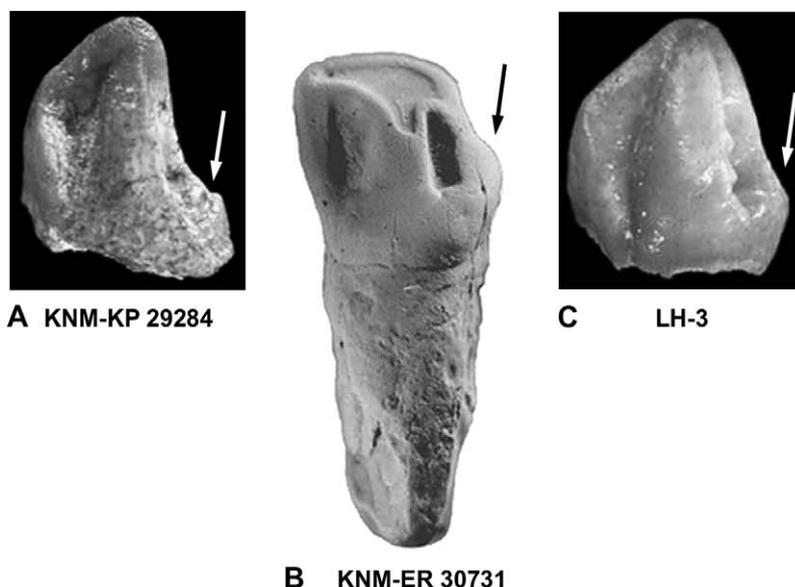


Fig. 4. Lingual views of right lower canines scaled to same mesiodistal (MD) length. A. KNM-KP 29284 (actual MD = 9.8); B. KNM-ER 30731 (actual MD = 8.3); C. LH-3 (actual MD = 11.7). Note the large distal cingulum (arrow) in the Kanapoi tooth (A), and compare it to the reduced cingula in the Allia Bay (B) and Laetoli (C) specimens, which are similar to canines in the Hadar sample in this respect.

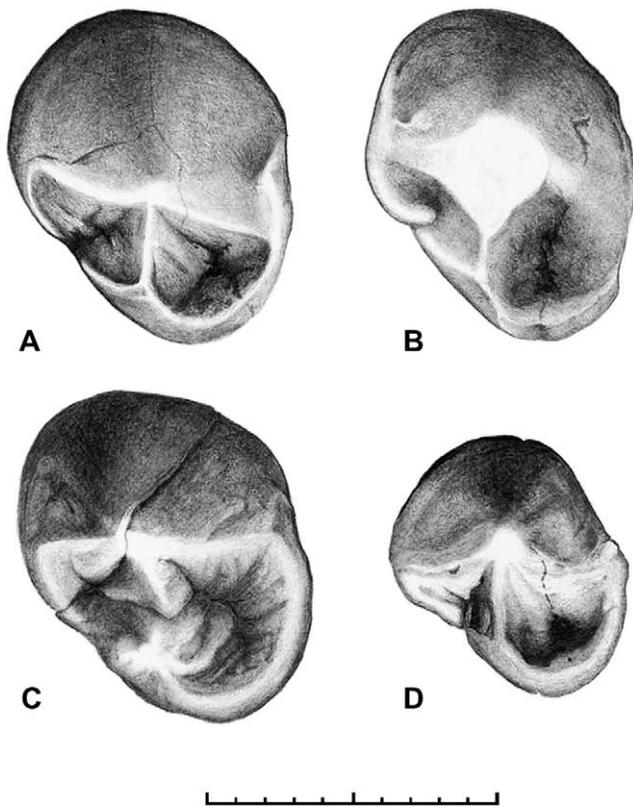


Fig. 5. Artist's renderings of occlusal views of hominin right P_3 s. *Australopithecus anamensis*, A. KNM-KP 27286; B. KNM-ER 20432. *Australopithecus afarensis*, C. LH-3; D. A.L. 128-23. Although phenetically similar to the Kanapoi tooth, KNM-ER 20432 shares with *A. afarensis* homologues a relatively large posterior fovea, a wide distal marginal ridge, and a prominent, elevated mesial marginal ridge that seals the anterior fovea mesiolingually. Scale equals 1 cm. Drawings by Denise To.

above the level of the cervicoenamel junction of the tooth. In occlusal view, this is manifested as a fuller, less indented mesiolingual profile than in the Kanapoi teeth;

- the distal marginal ridge resides higher on the crown (despite moderate occlusal wear), is broader mesiodistally, and is worn occlusally to a flat platform.

In all three of these characters, the Allia Bay P_3 is like the P_3 s from Laetoli and Hadar. Indeed, whereas in their total morphological pattern the Kanapoi P_3 s are quite distinctive compared to the *A. afarensis* condition, the Allia Bay specimen falls well within the *A. afarensis* range of expression for all three of these P_3 characters (it is especially similar to the P_3 s of A.L. 277-1 and A.L. 400-1a, though the latter have a better developed lingual cusp). Significantly, the similarities between the Allia Bay and *A. afarensis* P_3 s are derived relative to those in the Kanapoi and outgroup samples.

Laetoli vs. Hadar

In our analysis, the Laetoli and Hadar samples differ from one another in eight of 20 (40%) characters; in all but one of these the Laetoli specimens bear the more plesiomorphic state

(Table 2). The finding of differences between the Hadar and Laetoli samples is not unexpected. Comparing the 1970s Hadar collection with the much less extensive Laetoli dental samples of *A. afarensis* in 1985 (p. 138), White noted “minor metric and morphological differences” that distinguish the teeth from the two site-samples, “attributable to both intra-specific variation and/or sampling error.” However, different interpretations are suggested by two recent advances: (1) an increase in the Hadar sample to sizes permitting statistical assessment of some of these differences, and (2) discovery of the older jaws and teeth of *A. anamensis* from Kanapoi and Allia Bay. Together, these discoveries have shown that the differences between the Laetoli and Hadar samples cannot be explained entirely by sampling error (Lockwood et al., 2000) and that they have phylogenetic significance, by virtue of the similarity between Laetoli and *A. anamensis* samples (Leakey et al., 1995; Ward et al., 2001).

Inclination and contour of the anterior mandibular corpus

In terms of corpus size, shape, cortical contouring, and dental arch form, LH-4, the type-specimen of *A. afarensis*, closely resembles the Hadar mandibles attributed to this taxon (e.g., A.L. 400-1a). The morphology of the Laetoli mandible does differ from that of the Hadar sample in at least one important respect, however. In Hadar mandibles preserving the symphyseal cross section intact, as well as in the Maka mandible MAK-VP 1/12, the external contour is usually straight, though receding, with a filled-out (slightly bulbous) basal segment (character #2). As discussed elsewhere (Kimbel et al., 2004), this cross-sectional shape is independent of the inclination of the symphyseal axis. In contrast, the anterior outline of the symphyseal cross section in the Laetoli mandible is strongly convex and retreating (“cut away”) inferiorly such that the most inferior point on the external midsagittal basal contour is more posterior—closer to the posterior boundary of the cross section—than in Hadar mandibles. While some Hadar mandibles hint at the Laetoli morphology (A.L. 207-13, A.L. 330-5), none show it as fully developed as LH-4. Importantly, the LH-4 morphology closely resembles that observed in the several mandibles of *A. anamensis*, whose symphyseal cross section has been characterized by Ward et al. (2001: 334) as “unique among hominoids and fossil hominids in its smooth convexity across this contour.”

Distinctions between the morphologies of juvenile Hadar and Laetoli mandibles highlight the differences observed in the adults. In the LH-2 mandible (M_1 just erupted and in occlusion), damage to the cortical plate of the anterior corpus has removed much of the bone surface in the midline, but the basal component of the external symphyseal contour can be securely reconstructed from the morphology immediately adjacent to the midline on both sides of the jaw. As in the LH-4 adult mandible, the inferior segment of the LH-2 contour curves posteroinferiorly from the straighter, more vertical upper part of the corpus to give the median profile a basally retreating appearance. In this configuration the most inferior and

Table 2
Comparison of character-states for Laetoli and Hadar OTUs

OTU	Mandibular symphysis	Lateral mandibular corpus	Nasal aperture margins	Upper canine length and shape	Lower P3 shape	Position of upper I2
Laetoli	adult and juvenile jaws with convex, basally “cut away” profile	deviates medially at C/P ₃	dull corner with smooth transition to nasal cavity	mesiodistally elongated, symmetrically placed distal and mesial crown shoulders	mesiodistally elongated	below nasal aperture
Hadar	adult and juvenile jaws with straighter and basally full profile	deviates medially at P ₃	sharp corner with abrupt transition	mesiodistal length reduced, mesial crown shoulder more apical than distal shoulder	mesiodistal length reduced	partly or wholly lateral to nasal aperture

posterior points on the symphyseal cross section nearly coincide. The inferior view reveals that the convex surface of the posteroinferiorly retreating basal portion of the anterior corpus extends posterolaterally from the midline along the base at least as far posteriorly as mid-dm₁ level (posterior to which damage precludes observation) such that coronal cross sections at dc and dm₁ show marked inferomedial inclination of the lateral corpus contour below the level of the mental foramen. This is precisely what is observed at homologous points (beneath C-P₄) on the LH-4 mandible’s lateral corpus, which, as already noted, recalls the morphology of the *A. anamensis* adult mandible series in this respect.

Although a juvenile mandible has previously been available in the A.L. 333 assemblage from Hadar (A.L. 333-43), the anterior corpus is not preserved on this specimen, and so a comparison of this region with that in LH-2 has not been possible. However, recent field work has led to the discovery of a second juvenile mandible from A.L. 333, which does preserve much of this region (A.L. 333n-1; M₁ unerupted). The contrast with the anatomy of LH-2 is pronounced. The symphyseal cross section, which is best preserved toward the corpus base, is moderately inclined (as in LH-2), but straight and full down to the lowest point on the basal margin, which is distinctly anterior to the most posterior point on the midsagittal cross section (corresponding to the inferior transverse torus). Vertical cross sections at di₂, dc, and dm₁ show that the anterior and lateral corpus contours descend vertically to the base, without a hint of the inferomedial angulation observed in the Laetoli mandible; wherever it is observed in A.L. 333n-1, the external corpus contour meets the base abruptly, essentially at a 90° angle (this morphology is also suggested by the lateral corpus of A.L. 333-43).

That the differences between the Laetoli and Hadar juvenile mandibles parallel those that distinguish the adult jaws from these two sites suggests a distinction of biological significance, rather than one due to sampling error.

Buccal contour of the mandibular alveolar process

One of the distinctive characteristics of the *A. anamensis* mandible in relation to those of later hominins is the alignment of the lower canine crown on the anteroposterior axis of the postcanine toothrow (character #4). This creates a sharp corner in the buccal contour of the mandibular alveolar process at the

canine position (Ward et al., 2001). In the Hadar sample of *A. afarensis*, the canine is offset medially so that the postcanine axis passes mostly lateral to the crown and the anteromedial turn of the buccal alveolar plate begins at the mesial P₃ position (compare, for example, KNM-KP 29281 and KNM-KP 29287 with A.L. 400-1a and A.L. 417-1a); this is the derived state shared with all subsequent hominins. However, in contrast to the Hadar condition, in the Laetoli mandible of *A. afarensis*, LH-4, the remnants of the right canine crown clearly lie on the postcanine axis. In addition, the buccal alveolar plate at C/P₃ deviates only slightly anteromedially from the straight margin external to P₃, P₄, and M₁. In this respect, LH-4 is intermediate between Hadar mandibles of *A. afarensis* and the *A. anamensis* mandibles from Kanapoi.

Morphology of the nasal aperture margins

The Garusi I maxillary fragment preserves the only adult facial morphology in the Laetoli sample of *A. afarensis*. The morphology around the lower part of the nasal aperture differs between Garusi I and the Hadar maxillae, as previously noted by Puech et al. (1986). In all Hadar maxillae with the relevant area preserved, the bony surface immediately lateral to the nasal aperture is a thin, flat-to-slightly-convex plate whose horizontal cross section tapers medially to a sharp crest forming the lateral margin of the nasal aperture (e.g., A.L. 200-1a; character #6). The morphology of this region is not directly influenced by the canine root (even when this root is large, as, for example, in A.L. 333-1 and A.L. 444-2), which is manifested as a topographically distinct entity in the midface (e.g., A.L. 200-1a, A.L. 333-1, A.L. 417-1d, A.L. 427-1). Inferiorly, the lower margin of the nasal aperture in Hadar maxillae usually is a well-defined, sometimes raised, marginal crest (character #7). The nasal aperture in *A. afarensis* is thus bounded by a continuous rim constituting the thin lateral and marginal crests that meet in sharp inferolateral corners.

The Garusi I specimen shows a different morphological pattern (Kimbel et al., 2004). Here, the surface lateral to the nasal aperture is a stout column with a tightly curved horizontal cross section that passes medially into the nasal cavity without interruption by a distinct margin. In contrast to the solid anterior pillar in the face of *A. africanus* (Rak, 1983), however, the bony column alongside the nasal aperture in Garusi I is hollow, faithfully reflecting the considerable size of the

missing canine root. Thus, in contrast to Hadar maxillae, the canine root in Garusi I directly shapes the morphology of the face lateral to the nasal aperture (Ward et al., 2001). At the lower margin of the nasal aperture in Garusi I, the strongly projecting, convex subnasal surface grades insensibly into the anterior floor of the nasal cavity; there is no hint of a marginal crest separating these surfaces from one another.

Some Hadar maxillae do lack the raised marginal crest inferiorly, but in full adults there is always an abrupt contour change at the nasal cavity entrance that indicates where the subnasal surface ends and the nasal floor begins. Such an abrupt transition is not present in Garusi I. In this respect, the nasal aperture/cavity morphology of Garusi I is very similar to that of *A. anamensis* maxilla KNM-KP 29283 (Ward et al., 2001).

Thus, Garusi I resembles *A. anamensis* specimens in the form of both lateral and inferior nasal margins. In the context of the small sample of *A. afarensis* maxillae known in the 1970s, the importance of Garusi I's morphological distinction from Hadar was difficult to evaluate. However, with the enlarged Hadar sample and the discovery of the more plesiomorphic *A. anamensis* maxillae, the significance of these distinctions is more evident (Kimbel et al., 2004).

Crown shape index and lingual profile of the maxillary canine

Ward et al. (2001) described *A. anamensis* maxillary canines as mesiodistally longer than those of *A. afarensis* (character #11; MD/LL crown shape indices are 1.04 for each of two Kanapoi teeth and a mean of 0.91 for 15 *A. afarensis* teeth [including the Hadar sample through 2002]). The crown shape indices for *A. afarensis* are variable, however, ranging from 0.81 to 1.01. As White (1985) noted, two of three teeth from Laetoli (LH-5, LH-6) stand above the upper end of the Hadar sample range (this remains true with the addition of five upper canines to the Hadar sample since 1990; Table 3); the mean shape-index value for the Laetoli sample is 0.97, which indicates a longer mesiodistal dimension (in relation to breadth) than in the Hadar sample (0.89 ± 0.05).

Figure 6 illustrates these differences in a plot of MD length vs. LL breadth for maxillary canines in the Kanapoi, Laetoli, and Hadar samples. A sample of *A. africanus* from Sterkfontein Member 4 is included for comparison. The Kanapoi canines are clearly the most MD elongate, with the Laetoli teeth intermediate between the Kanapoi and Hadar samples.

Table 3
Maxillary canine metrics for hominin samples examined in this study

Sample/Taxon (n)	Mesiodistal (mean \pm SD)	Labiolingual (mean \pm SD)	MD/LL*100 (mean \pm SD)
Kanapoi (2) ^a	11.2	10.7	104.0
Laetoli (3)	10.4	10.8	97.3
Hadar (12)	9.6 \pm 0.6	10.8 \pm 0.9	89.1 \pm 4.7
<i>A. africanus</i> (13)	9.9 \pm 0.7	10.4 \pm 1.0	95.5 \pm 6.4

^a The Kanapoi values represent the mean of the right tooth of KNM-KP 35839 and KNM-KP 30498.

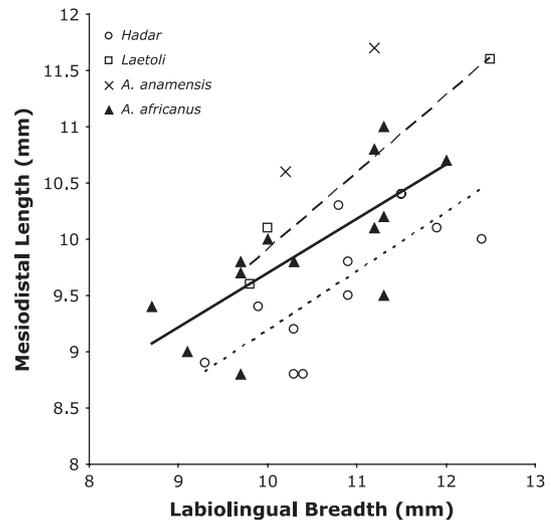


Fig. 6. Bivariate plot of mesiodistal crown length vs. labiolingual crown breadth for maxillary canines in the Kanapoi, Laetoli, and Hadar samples. A sample of *A. africanus* from Sterkfontein Member 4 is included for comparison. Trend lines are provided for (from above) the Laetoli ($n = 3$), *A. africanus* ($n = 13$), and Hadar ($n = 11$) samples.

Analysis of covariance (ANCOVA) shows that the separate slopes for Laetoli, Hadar, and Sterkfontein are not statistically distinguishable ($p = 0.396$; Kanapoi was excluded from statistical tests because its sample size is too small). In other words, there is a consistent scaling pattern within each sample. On the other hand, significant differences do exist in the elevations of within-sample regression lines ($p < 0.0001$). Comparisons of samples using t -tests of y -intercepts (Sokal and Rohlf, 1995) indicate that Laetoli is significantly different from Hadar ($p = 0.0015$) but not significantly different from Sterkfontein ($p = 0.28$). (The raw value for mesiodistal length in the Sterkfontein sample is actually much closer to that of Hadar than to that of Laetoli, but the South African teeth are narrower labiolingually than in either of these samples, so the mean crown shape index value is intermediate between those of the Laetoli and Hadar samples. See Table 3.) Thus, the intermediate shape of the Laetoli upper canines, compared to the older Kanapoi and younger Hadar conditions, is of statistical as well as potential phylogenetic significance. Owing to the lack of data for the Allia Bay OTU, the state of this character is ambiguous at the nodes connecting both the Allia Bay and Laetoli OTUs to their respective sister groups.

Maxillary canines in *A. anamensis* are more symmetric (in lingual profile) than in *A. afarensis* (Ward et al., 2001) (character #12). This is due to the subequally basal position of the mesial and distal crown shoulders on the Kanapoi upper canines (no Allia Bay upper canine preserves relevant crown anatomy). Ward et al. (2001) pointed out that, while the crown shoulders in *A. afarensis* maxillary canines are placed further apically than in *A. anamensis*, the Hadar *A. afarensis* canines are more asymmetrical than those from Laetoli because the mesial crown shoulder occupies a more apical position than the distal shoulder in the Hadar teeth. This asymmetry is observed in both unworn (A.L. 333x-3, A.L. 763-1) and worn

(e.g., A.L. 199-1) specimens, which contrast with Laetoli teeth in similar stages of wear (unworn: LH-3, the slightly damaged LH-6; worn: LH-5; see Ward et al., 2001: Fig. 29; Kimbel et al., 2004).⁵ The conical great ape maxillary canines are asymmetric in outline, due to the sectorial C/P₃ complex. They have a concave distal margin and a convex mesial margin, but the crown shoulders are symmetric in that both are basally set (positioning the axis of the maximum mesiodistal length at or close to the cervicoenamel junction). The Kanapoi symmetry is similar to the outgroup condition and thus we consider it plesiomorphic. This morphology is retained in the Laetoli canines even though in the latter specimens the crown shoulders are both shifted apically as in Hadar canines.

Shape of mandibular third premolar crown

As evident from the data in White's (1985) early survey (see also Blumenberg and Lloyd, 1983), and substantiated statistically in Lockwood et al.'s (2000) temporal-trends analysis using augmented Hadar samples, Laetoli lower third premolars are significantly longer mesiodistally than the P₃s from Hadar (character #15; Table 4, Fig. 7). Figure 7, a bivariate graph plotting the P₃ crown shape index (MD/BL × 100) against P₃ breadth, demonstrates that at given crown breadths Laetoli P₃s ($n = 5$) tend to be relatively long compared to Hadar homologues. Of interest is the fact that the *A. anamensis* P₃ sample ($n = 5$) shares this tendency. Including chimpanzees⁶ and *A. africanus* ($n = 15$) in the analysis places these comparisons in a phylogenetic perspective (Fig. 7). Chimpanzees exhibit mesiodistally elongated P₃ crowns, as represented graphically in the location of the chimpanzee regression line above that for the Hadar sample in Fig. 7. Mesiodistal elongation is undoubtedly the primitive condition—the gorilla data occupy an even more elevated position in the graph (not shown here). In contrast, the *A. africanus* sample broadly overlaps the Hadar distribution, showing a tendency toward relative mesiodistal compression. These differences are further revealed in analysis of covariance (ANCOVA). The slopes of linear regression lines for each group are not significantly different from one another (ANCOVA, $F = 1.42$, $p = 0.24$). However, the elevations of the lines are significantly different ($F = 5.83$, $p = 0.019$). In other words, the Laetoli, *A. anamensis*, and chimpanzee samples have high y-intercepts, while those of the Hadar and *A. africanus* samples are lower. Even when unicuspid (as in A.L. 128-23, A.L. 288-li, and A.L. 417-la), Hadar P₃s tend to be less asymmetric in occlusal outline and less obliquely oriented in the postcanine tooththrow than are P₃s in the earlier *Australopithecus* samples (Fig. 5); this morphological difference most likely explains the metrical distinctions highlighted here (see also Deleze, 2004).

⁵ In Ward et al.'s (2001) Figure 29, the labels for the LH-6 and A.L. 333x-3 canines were reversed.

⁶ A mixed-sex sample of 19 *Pan troglodytes troglodytes* from the Hamann-Todd Osteological Collection, CMNH. Measurements were taken on high-quality casts for the present study in order to ensure consistency of measurement technique with the data collected for the fossil samples.

Table 4
Mandibular P₃ metrics for hominid samples examined in this study^a

Sample/Taxon (n)	Mesiodistal length (mean ± SD)	Buccolingual breadth (mean ± SD)	MD/BL*100 (mean ± SD)
<i>Pan troglodytes</i> (19)	9.7 ± 0.7	8.1 ± 0.7	119.6 ± 8.8
<i>A. anamensis</i> (6)	9.9 ± 0.6	10.9 ± 1.0	93.4 ± 13.5
Laetoli (5)	10.7 ± 1.1	10.7 ± 0.5	100.3 ± 12.4
Hadar (21)	9.2 ± 0.8	10.4 ± 0.9	88.6 ± 9.2
<i>A. africanus</i> (15)	9.5 ± 0.5	11.5 ± 0.8	83.2 ± 6.7

^a P₃ measurements taken as follows: length is the mesiodistal dimension on or parallel to the long axis of the postcanine tooth row; breadth is perpendicular to length at the mesiodistal crown midpoint. These are not the same as the maximum and minimum dimensions of the crown.

Position of the maxillary incisors beneath the nasal aperture

In the Garusi maxilla from Laetoli, the alveolus of the lateral incisor is positioned directly inferior to the nasal aperture (i.e., medial to an imaginary vertical line dropped inferiorly from the inferolateral corner of the aperture). This is a derived condition (character #8) compared to what is observed in chimpanzees, the Kanapoi maxilla KNM-KP 29283 (Ward et al., 2001), and the Hadar maxillary sample of *A. afarensis*, in which the lateral incisor root is almost always lateral to the nasal aperture's inferiorly projected margin (Kimbel et al., 1982). Thus, the distribution of this character in the hominin OTUs runs counter to the null phylogenetic hypothesis because a geologically older OTU (Laetoli) bears an apomorphic state relative to the state in a younger OTU (Hadar). It is the only one to do so in our analysis. One caveat pertaining to this character is that gorillas also possess what we here interpret as the derived condition of medially positioned maxillary lateral incisor roots, which implies that the chimpanzee morphology may not be the plesiomorphic one. However, as gorillas have a unique nasal region morphology among hominoids (e.g., Shea, 1983), and as the chimpanzee condition is shared with orangutans, we are comfortable with the inference that the latter state is the primitive one for hominins.

Discussion

Systematic implications

The distribution of character-states among the ingroup OTUs highlights the fact that the four fossil samples differ from one another morphologically, even in comparisons of samples assigned to the same nominal species. Moreover, the polarity of character-state differences is consistent with the chronological ordering of the site-samples, and the high consistency index supports the fit between the character-state assignments and the hypothesis of anagenetic change. Together, these findings confirm Leakey et al.'s (1995) observation that Laetoli specimens are morphologically intermediate between *A. anamensis* samples and Hadar, strengthen the hypothesis that *A. anamensis* was ancestral to *A. afarensis*,

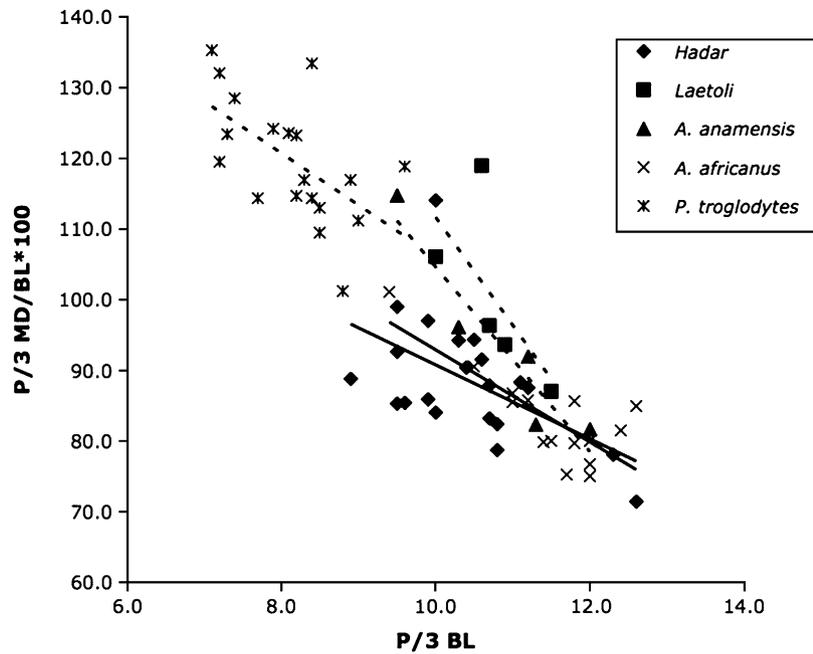


Fig. 7. Bivariate plot of P_3 crown shape index ($MD/BL \cdot 100$) vs. buccolingual crown breadth for *A. anamensis*, Hadar, Laetoli, *A. africanus*, and *Pan troglodytes* samples. Trendlines are, clockwise from above left, for chimpanzee ($n = 19$), Laetoli ($n = 5$), *A. anamensis* ($n = 6$), *A. africanus* ($n = 16$), and Hadar ($n = 21$) samples.

and also suggest that the four site-samples represent an evolving lineage across 1.2 million years of time.

From a critical standpoint, one may ask how strong a test of anagenesis this case represents. We have relied on a short list of known characters, and given the small and anatomically limited samples from Kanapoi, Allia Bay, and Laetoli, the possibility that at least one of these OTUs represents an apomorphy-bearing terminal population cannot be entirely ruled out (this possibility is hinted at by the derived, homoplastic position of the maxillary lateral incisor alveolus medial to the nasal aperture corner in Garusi I, representing the Laetoli condition). Small sample sizes are a difficulty for any analysis of fossil evidence, but this problem should only introduce random error into the analysis. Given the number of characters (20) and site-samples (4) in our analysis, it is improbable that random error could produce an orderly pattern in which younger site-samples consistently have more derived character-states than older ones. Strong correlation among characters could produce such a pattern, regardless of sample size, but this would weaken the argument rather than undermine it. It may be that further sampling of relevant time periods will yield fossils preserving characters that conflict with and overturn the hypothesis of lineage continuity. Nevertheless, it is significant, given current data, that precisely the same phylogenetic signal is given by the C/P_3 complex, the juvenile and adult mandibles, and the adult maxillae. The finding of high levels of consistency among characters suggests that the signal from jaw and dental structure is a robust one.

Stratigraphic data can influence these alternative hypotheses. As we have noted, at present there is no evidence for the temporal overlap between *A. anamensis* and *A. afarensis*. A key specimen in this regard is the Belohdelie frontal bone

(BEL-VP 1/1) from ca. 3.9-million-year-old deposits in the Middle Awash basin, Ethiopia, which has been likened to the frontal bone of *A. afarensis* (Asfaw, 1987; Kimbel et al., 1994, 2004). With the discovery of *A. anamensis* of approximately the same antiquity, it is possible that the Belohdelie frontal belongs to this species rather than to *A. afarensis*. Of course, until a frontal bone is recovered in association with fossils bearing anatomy diagnostic of *A. anamensis*, this alternative remains conjectural. But if the frontal bone of *A. anamensis* turns out to be morphologically distinctive compared to that of *A. afarensis*, then the affinity of the Belohdelie specimen to *A. afarensis* would demonstrate geological contemporaneity between these species and thus reduce the likelihood that the two taxa are related to one another anagenetically. In a similar vein, if it were to be demonstrated that one or both of the temporally intermediate OTUs (Allia Bay, Laetoli) bears an exclusive cladistic relationship to another hominin taxon, then the hypothesis of an anagenetic relationship between *A. anamensis* and *A. afarensis* would effectively be falsified. *Kenyanthropus* represents another potential test case, but, as we pointed out above, the limited character data now available for this species does not suggest a close relationship between it and any of the OTUs analyzed herein (Leakey et al., 2001).

Until future discoveries rule more decisively on these issues, we adopt the conclusion that *A. afarensis* was the descendant of *A. anamensis* via phyletic transformation within an unbranched lineage. These taxa would thus constitute an “evolutionary species” in the sense of Simpson’s original formulation of the concept (1951: 295, quoted in Krishtalka, 1993: 337): “The whole sequence of populations ... is genetically continuous and it fulfills the conditions of both genetical and

evolutionary definitions of a species. By these concepts, it is a single taxonomic group, defined as a species.”

This conclusion does not imply a direct ancestor–descendant relationship among the actual *samples* recovered from the four sites discussed here. Each of these samples represents one or more populations that were parts of a geographically diverse, temporally extended species. Many, perhaps most, of these populations probably did not leave descendants over geological time; those that did so were the source of character-state frequency distributions for populations on succeeding time planes. Thus, anagenesis does not entail the wholesale transformation of an *entire* ancestral species into a new descendant species (Archibald, 1993). By anagenesis we mean evolutionary change along a lineage without a concomitant increase in lineage diversity through speciation.

In our analysis, the *A. anamensis*–*A. afarensis* lineage is paraphyletic because, according to a strict reading of the cladogram in Fig. 2, the youngest sample—Hadar—represents the sister-group to *A. africanus* and so would be more closely related to this species than to the samples representing the geologically older populations within its lineage (Figs. 8, 9). This paradox is more apparent than real, however, because ancestral species are *by definition* paraphyletic with respect to those populations that give rise to nascent daughter species but with which they were (originally) conspecific. From the point of view of speciation, ancestral species are not equivalent to monophyletic higher taxa. Indeed, one can see in our approach a test of the *potential* ancestral status of a species–lineage in the fossil record. We stress “potential” because we do not think it is necessary to conclude from this result that the population represented by the Hadar sample was itself ancestral to *A. africanus*, only that *A. africanus* evolved from a population more similar to that from which the Hadar sample was drawn than from a population similar to those represented by the Laetoli, Allia Bay, and Kanapoi samples. To identify the Hadar sample as representing the actual ancestor of *A. africanus* would require a far better understanding of the chronological and geographic relationship between eastern and southern African middle Pliocene hominin lineages than currently exists.⁷

The classic paleontological conundrum of classifying chronologically and morphologically intermediate samples of populations thought to constitute an evolutionary species has been discussed extensively in the literature (see Rose and Bown, 1993, and Krishtalka, 1993, for recent arguments). Well known practical concerns for the taxonomy of such populations suggest several alternative outcomes for the classification of the hominin OTUs examined here: (1) maintaining the current specific distinction between the OTUs, with the Kanapoi and Allia Bay samples assigned to *A. anamensis* and the Laetoli and Hadar samples assigned to *A. afarensis*; (2) classifying all OTUs as *A. afarensis*, in which case *A. anamensis* would become a junior subjective synonym of *A. afarensis*; (3) assigning each of the four OTUs to a different species taxon;

(4) classifying the Allia Bay OTU together with the Laetoli and Hadar OTUs as *A. afarensis*; and (5) establishing a new multiple species classification, the most likely entailing the classification of Kanapoi, Allia Bay, and Laetoli OTUs in one species (necessarily *A. afarensis*, as the Laetoli sample includes the type-specimen LH-4) and the naming of a new species for the Hadar sample.⁸ Of these, we consider the first two alternatives to be the most sound.

Classifying the Kanapoi–Allia Bay–Laetoli–Hadar sequence as a single species was previously suggested by Senut (1996) and Wolpoff (1999), though not as the outcome of explicit phylogenetic analyses like those conducted here. Based on our results, this option represents the current state of knowledge about the chronologic, phenetic, and phylogenetic relationships among the relevant fossil samples. It is superior to the division of the lineage into four “chronospecies,” which, given the imperfect fossil record in the 3.9–3.5 Ma time interval, would most likely be the least stable taxonomic solution for these hominins (it would necessitate proposing several new species names for possibly arbitrary taxonomic units). Adopting the single name for the evolutionary species presents the option of using informal stage names to designate the phenetically distinct lineage segments (see Krishtalka, 1993, for further discussion and justification).

The principal argument for maintaining the taxonomic status quo rests on the ability of the differential diagnosis published by Leakey et al. (1995) to distinguish *A. anamensis* from *A. afarensis*. Although some of the features included in the original diagnosis currently apply only to the more comprehensive Kanapoi and Hadar samples (e.g., temporal bone morphology), and at least one appears to be unsuccessful in discriminating between the two species (inclination of the upper canine root and mid-face; see Kimbel et al., 2004), it is nevertheless clear that the two hypodigms can be sorted on a combination of morphological characters, including those of the capitate and the dm_1 , which have not been discussed here (Leakey et al., 1998; Ward et al., 2001). However, the conventional idea that an evolutionary species should be divided into two or more chronospecies (separated by a pseudo-extinction event), using a phenetic yardstick based on the degree of divergence between closely related extant species, demands that we recognize fossil species thus individuated as purely phenetic constructs, rather than as the historical-genetical “individuals” embodied in almost all modern concepts of the species category (see discussion in Kimbel and Rak, 1993). Thus, according to this argument, the continued use of the name *A. anamensis* to refer to the geologically early part of the evolutionary species *A. afarensis* helps localize and communicate about the clustering of morphology in time and space. It also recognizes that the information available for Allia Bay and Laetoli, and to a lesser extent Kanapoi, is based on limited sample sizes. Discovery of other skeletal elements, or larger samples, could change the way this lineage is perceived.

⁷ In addition, the Hadar cranial sample may be too autapomorphic to represent the population ancestral to *A. africanus* (Kimbel et al., 2004).

⁸ We do not here consider alternatives that entail the designation of subspecies, a taxonomic category with ambiguous meaning in paleontology.

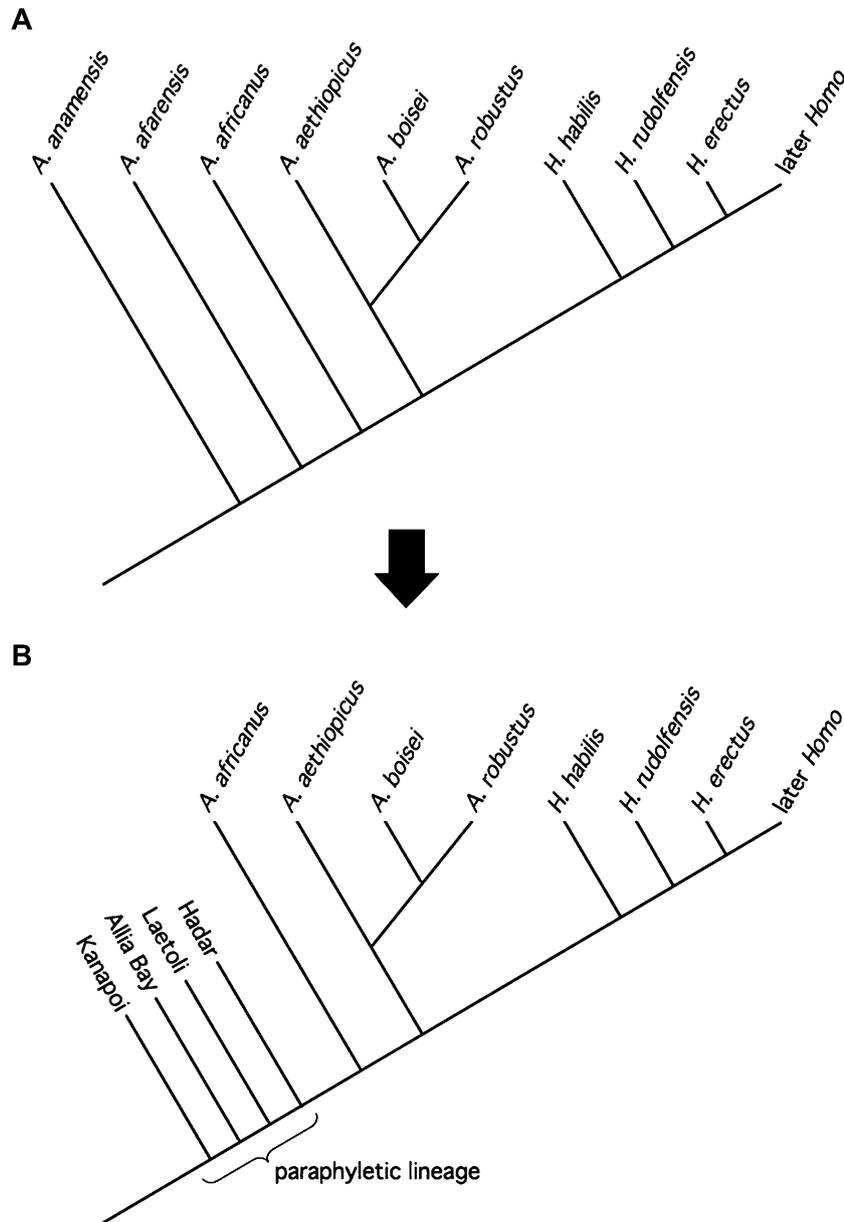


Fig. 8. Interpretation of results in the context of early hominin phylogeny. Cladogram A is shown for illustrative purposes only but is consistent with results from Kimbel et al. (2004) and Strait and Grine (2004). Cladogram B illustrates that the four site-samples analyzed herein form a paraphyletic lineage. See the text for further discussion.

The other multiple-species alternatives are each misleading regarding the pattern of affinities. While the overall pattern of comparable morphology demonstrates phenetic similarity between the Laetoli hominins and *A. anamensis* (anterior mandible corpus shape, nasal region morphology, upper canine crown shape, P₃ crown length), these groups are not isomorphic (for example, the lingual cusp on Laetoli P₃s is more pronounced than in the Kanapoi P₃s, the enamel shoulders of the maxillary canines are shifted away from the crown base as in Hadar canines). Thus, grouping the Laetoli specimens with those from Kanapoi and Allia Bay in a species taxon to the exclusion of the Hadar sample would arbitrarily emphasize the Laetoli-Hadar differences. The same objection would apply to a taxonomy that groups the Allia Bay OTU, to

the exclusion of the Kanapoi OTU, with Hadar and Laetoli in *A. afarensis*.

In sum, we think that the most appropriate taxonomic solution for these four site-samples is either the recognition of a single evolutionary species or the maintenance of the status quo: a two-species classification, with Kanapoi and Allia Bay samples assigned to *A. anamensis*, and Laetoli and Hadar samples classified as *A. afarensis*. Among the authors of this paper there is disagreement as to which taxonomy is best, and our discussion has shown that, on the available evidence, a good case can be made for either solution. The more important conclusion is the pattern of affinities itself and the support for evolutionary change across a 1.2-million-year period of time.

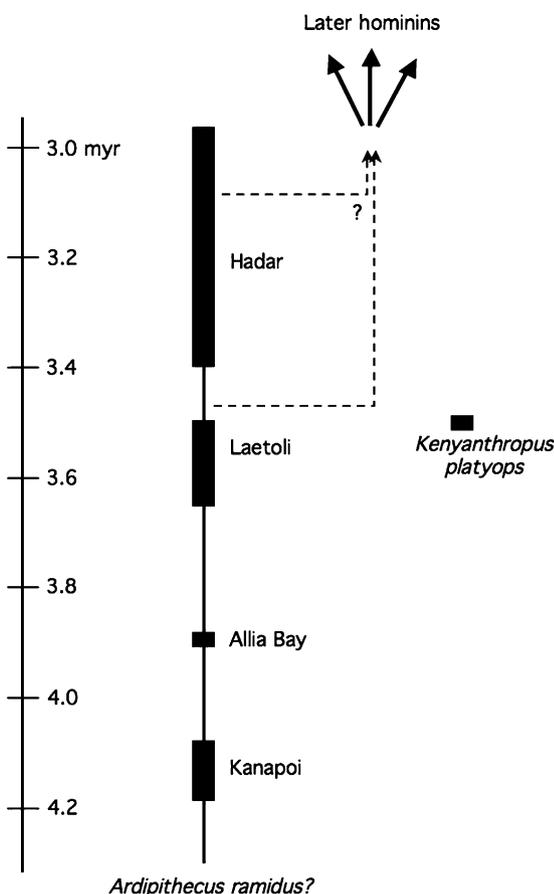


Fig. 9. A lineage view of the relationship between *A. anamensis* and *A. afarensis*. While we consider this lineage to be paraphyletic, and therefore a viable ancestor for later hominins, it is possible that the Hadar segment of the lineage is too autapomorphic to represent the ancestor of *A. africanus* or other hominins (Kimbel et al., 2004). There is currently no evidence that the presence of *Kenyanthropus* at 3.5 Ma indicates cladogenesis within the *A. anamensis*–*A. afarensis* lineage.

Adaptive evolution in the *A. anamensis*–*A. afarensis* lineage

The hypothesis that *A. anamensis* and *A. afarensis* constituted a single evolutionary species has implications for the adaptive evolution in early australopiths. So far as is known, the majority of the characters that demonstrate change along the chronocline connecting the Kanapoi sample with the Hadar sample are concerned with the snout (anterior mandible, nasal region of the maxilla) and the C/P₃ complex (Fig. 10).⁹ These anatomical sites underwent dramatic structural modification during the course of hominin evolution. Whether these modifications were the result of change in a functionally integrated character complex or were achieved in a mosaic fashion is not known at this time, although our results (Fig. 10) suggest that change in P₃ characters was at least partly mosaic (e.g., crown

shape, relative fovea size, and cusp number did not all change states together across the four site-samples). Indeed, the C/P₃ region was a locus of pronounced change, from the ancestral shearing (sectorial) complex functionally linked to intrasexual competition for mates (common to many catarrhine primates) to the derived condition in which the P₃ was progressively molarized and co-opted for postcanine food processing and the canine crown became smaller and more incisiform. This pattern was the template for both the severely reduced condition of the modern human C/P₃, on the one hand, and the exaggerated metrical disproportion and morphological differentiation of the “robust” *Australopithecus* anterior/posterior dentition on the other. Derived hominin morphology is already glimpsed by at least ca. 5.5 Ma in *Ardipithecus* (Haile-Selassie, 2001; Haile-Selassie et al., 2004), and geologically younger taxa, including *A. anamensis* and *A. afarensis*, exhibit progressively more derived states.

Relaxed selection for maintenance of the ancestral honing function of the C/P₃ complex may have been the basis for the unlinking of previously correlated traits of the canine/premolar complex, opening the way for mosaic change and its refashioning (of the premolars, at least) as part of the postcanine dental battery. It is clear, moreover, that the progressive incorporation of the premolars (and the P₃ in particular) into the postcanine grinding mechanism was a geologically long-term phenomenon that in *Australopithecus* (and probably in some representatives of early *Homo* as well) carried into the early Pleistocene, by which time it had become enmeshed within a highly derived masticatory complex. In the Hadar record of *A. afarensis*, spanning less than 0.4 million years, the evolving P₃ is “captured” at a critical transitional stage, with significant frequencies of both primitive (e.g., no or poorly expressed lingual cusp) and derived (e.g., molarized, with well-developed lingual cusp) occlusal forms (Johanson et al., 1982; Leonard and Hegmon, 1987; Kimbel et al., 2004; Deleuzene, 2004). The fact that all hypothesized sister taxa of *A. afarensis* (*A. africanus*, et seq.) have only the derived P₃ form, and all of the known more basal hominin taxa (*A. anamensis*, *Ardipithecus*) have mainly the primitive form, suggests a progressive shift in frequency distribution over time. The polymorphism exhibited by the Hadar sample is therefore consistent with the idea of anagenetic change in this tooth driven by directional selection.

To what selective conditions were these characters responding? In most explanations of hominin postcanine dental evolution, the molarization of the australopith premolars is thought to track the expansion of open, dry habitats during the Pliocene. However, paleoenvironmental reconstructions of early and middle Pliocene hominin fossil localities imply that a wide range of closed and open woodland, gallery forest, bushland, and wet and dry grassland habitats was available to *A. anamensis* and *A. afarensis* across more than a million years of time and more than 1100 linear km of space (Leakey et al., 1995; Reed, 1997; Wynn, 2000; Kingston and Harrison, 2001; Bonnefille et al., 2004; Campisano and Feibel, in press). These habitats fluctuated across time, locally and regionally (at least in part according to 23–19-thousand-year

⁹ For the Kanapoi and Hadar samples, the temporal bone and hand (capitate) differences may also be adaptively significant, but are beyond the scope of this paper (see Ward et al., 2001).

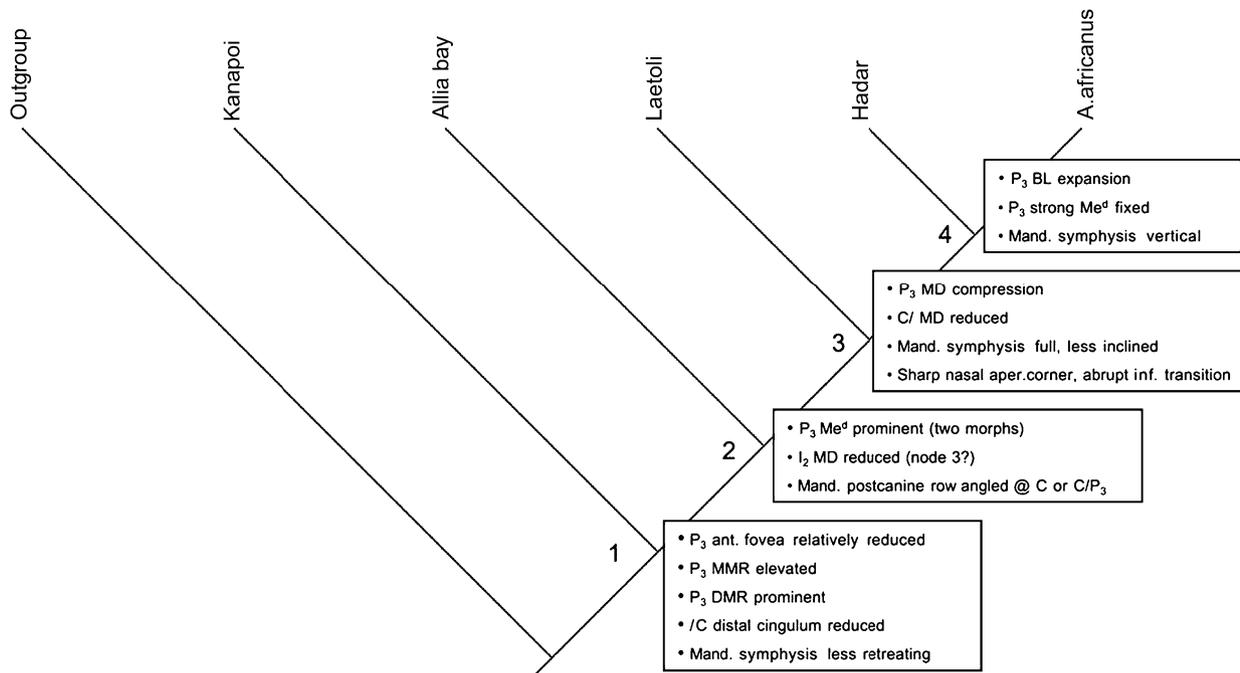


Fig. 10. Summary cladogram showing the character-state changes supporting the most parsimonious arrangement of the four OTUs and *A. africanus*.

precessional climatic cycles), but did not shift to a directional trend towards more xeric conditions until after ca. 3.0 Ma (Demenocal, 2004). The lack of directional environmental change within this mosaic across the preceding interval in which the *A. anamensis*–*A. afarensis* lineage flourished suggests that the anagenetically evolving C/P₃ characters were not an adaptive response to stepwise increases in the prevalence of dry, open habitats. Perhaps, instead, under fluctuating seasonal conditions across the range of locally available habitats (Reed and Fish, in press), it was periodically advantageous to incorporate lower-quality foods efficiently into the diet (Teaford and Ungar, 2000; Ungar, 2004). That maintenance of dental function in mature lactating primate females plays an important role in infant survivorship, especially in the face of fluctuating environmental conditions, has been argued by King et al. (2005). Thus, selection may have placed a premium on the amount of occlusal area available for postcanine food processing, as reflected in the changing form of the P₃.

In sum, the changes in the *A. anamensis* and *A. afarensis* C/P₃ complex appear to have occurred in the absence of the fragmentation of habitat that can stimulate adaptive differentiation of local populations, niche divergence, and, ultimately, speciation, as evinced in the post-3.0-Ma record of hominin lineage diversity. Of such characters, Futuyma (1987: 468) has remarked, “for character changes that are adaptive throughout the range of a species, in all the habitats that its various populations may occupy, simple phyletic transformation (via directional selection) of the entire species may be expected.” Support for an anagenetic trend, with its basis in directional selection, does not necessarily mean constant selective regimes or continuous change. As the samples analyzed here capture only thin slices of a long period of time, they cannot yield detailed information about the tempo of evolution, which may have been either a

series of abrupt shifts or a more gradual process of change. In either case, however, anagenesis is supported as a mechanism responsible for trans-specific magnitudes of change.

Conclusions

Currently available character-state and stratigraphic data are consistent with the hypothesis that early Pliocene *A. anamensis* was ancestral to middle Pliocene *A. afarensis*, and further suggest that these taxa constituted an anagenetically evolving lineage. Despite the evidence that the Kanapoi, Allia Bay, Laetoli, and Hadar site-samples represent morphologically differentiated populations, in the case of these two “species,” the shape of the hominin phylogenetic tree is likely to have been less, rather than more, bushy.

The concordant support of both data sources for a hypothesis of macroevolutionary change (i.e., of trans-specific magnitude; see Levinton, 1988) by anagenesis is rare in the early hominin fossil record. Another proposed example, that of the east African “robust” *Australopithecus* species *A. aethiopicus* and *A. boisei*, is consistent with stratophenetic data from the postcanine dental remains in the Pliocene Omo Group succession (Suwa et al., 1996) but is inconsistent with the results of most phylogenetic analyses of anatomically more global character-state data, which demonstrate that *A. aethiopicus* is the plesiomorphic sister taxon to an *A. robustus* + *A. boisei* clade (e.g., Strait et al., 1997; Strait and Grine, 2004; Kimbel et al., 2004). The younger part of the Hadar fossil record of *A. afarensis* itself appears to demonstrate anagenetic change (in the 3.18–3.00 Ma time range), but this transformation, apparently involving size-related characters of the skull or possibly body size itself (Lockwood et al., 2000), does not appear to have been trans-specific, as the later Hadar crania

and jaws share the same fundamental set of diagnostic characters with earlier Hadar specimens (Kimbel et al., 2004). In the case of *A. anamensis* and *A. afarensis*, in contrast, the morphological changes across site-samples bridge character-state differences generally considered to diagnose hominin species.

To test the hypothesis of anagenetic evolution of the *A. anamensis*–*A. afarensis* lineage using other anatomical regions, a more densely sampled eastern African fossil record is necessary. The time period between ca. 3.9 Ma (Allia Bay) and ca. 3.5 Ma (Laetoli) is the one in which evidentiary support for the hypothesis is weakest. Future discoveries from this interval, as well as further study of other postulated hominin taxa between 3.0 Ma and 4.0 Ma (Leakey et al., 2001; Partridge et al., 2003), may show whether the lineage identified here is real or is instead a poorly resolved record of speciation events.

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Appendix. Characters and states used in cladistic analysis

Character 1. Angle of mandibular symphysis

- 0 strongly inclined
- 1 moderately–weakly inclined
- 2 weakly inclined

Character 2. Location of posteriormost point on mandibular symphysis

- 0 inferior
- 1 intermediate (variable)
- 2 elevated

Character 3. Horizontality of postincisive planum of mandible

- 0 strong
- 1 intermediate (variable)
- 2 moderate

These three symphyseal characters are treated separately because they vary independently of one another in the Hadar sample. Character 2 relates to the degree to which the external plate of the symphyseal region is retreating or “cut away,” as described in the text.

Character 4. Mandibular lateral contour in occlusal view

- 0 angled at canine
- 1 angled at C/P₃
- 2 angled at P₃

Kanapoi, 0; Allia Bay, 0; Laetoli, 1; Hadar, 2; *A. africanus*, 2.

Character 5. Mandibular dental arch shape

- 0 parallel-sided
- 1 intermediate
- 2 divergent posteriorly

Kanapoi, 1; Allia Bay, ?; Laetoli, 2; Hadar, 2; *A. africanus*, 2.

Character 6. Nasal aperture corner

- 0 rounded
- 1 sharp
- 2 anterior pillar present

Kanapoi, 0; Allia Bay, ?; Laetoli, 0; Hadar, 1; *A. africanus*, 2

Gorilla has state 1, but this is most likely not the primitive state for hominoids (state 0 = rounded is present in *Pan* and *Pongo*); state 1 in Hadar would therefore be a homoplasy. The morphology in *Gorilla* is related to a pronounced eversion of the lateral nasal margins that is not present in other hominoids (see text).

Character 7. Inferior nasal margin (transition at entrance to nasal cavity)

- 0 smooth
- 1 abrupt

Kanapoi, 0; Allia Bay, ?; Laetoli, 0; Hadar, 1; *A. africanus*, 1

Character 8. Position of I² root in relation to nasal aperture

- 0 lateral
- 1 medial

Kanapoi, 0; Allia Bay, ?; Laetoli, 1; Hadar, 0; *A. africanus*, 1

Gorilla has state 1, but this is most likely an autapomorphy (state 0 is present in *Pan* and *Pongo*) possibly related to the condition underlying the morphology of character 6.

Character 9. Mandibular lateral incisor shape (index: MD/LL)

- 0 mesiodistally expanded
- 1 mesiodistally compressed

Kanapoi ($n = 3$): 0.98 (0.87–1.12)
Allia Bay: n/a

Laetoli ($n = 1$): 0.75
 Hadar + Maka ($n = 6$): 0.85 ± 0.14 (0.57–0.93);
 Maka value is 0.90
 Sterkfontein ($n = 9$): 0.94 ± 0.09 (0.82–1.08)

Ward et al. (2001) noted that *A. anamensis* lower lateral incisors are longer mesiodistally than those of *A. afarensis*. This is true, though Kanapoi shares this plesiomorphy with the Sterkfontein sample. The Hadar sample mean is autapomorphic, although its range overlaps that of both of the other samples. Given the observed variation and an n of 1, we code Laetoli as “?”, although it falls only within the Hadar range.

Character 10. Mandibular canine distal cingulum development

- 0 strong
- 1 weak

Kanapoi, 0; Allia Bay, 1; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character 11. Maxillary canine crown shape (index: MD/LL)

- 0 mesiodistally elongate
- 1 intermediate elongation
- 2 mesiodistally compressed

Kanapoi ($n = 2$): 1.04 ($\times 2$)
 Allia Bay: n/a
 Laetoli ($n = 3$): 0.97 (0.93–1.01)
 Hadar ($n = 12$): 0.89 ± 0.05 (0.81–0.96)
A. africanus ($n = 13$): 0.95 ± 0.06 (0.84–1.08)

Small Kanapoi and Laetoli sample sizes and observed variation hamper categorical definition of states. We opt for three states here, with Laetoli and *A. africanus* intermediate between Kanapoi and Hadar, while recognizing the potential for greater overlap with larger samples.

Character 12. Maxillary canine lingual profile

- 0 symmetric
- 1 asymmetric

Kanapoi, 0; Allia Bay, ?; Laetoli, 0; Hadar, 1; *A. africanus*, 0

Character 13. Maxillary canine crown shoulder height

- 0 high (cervical)
- 1 low

Kanapoi, 0; Allia Bay, ?; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character 14. Maxillary canine cingulum

- 0 present
- 1 absent

Kanapoi, 0; Allia Bay, ?; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character 15. Mandibular P3 crown length (index: MD/BL)

- 0 long
- 1 short

Kanapoi ($n = 4$): 0.96 (0.82–1.15)
 Allia Bay ($n = 1$): 0.82
 Laetoli ($n = 5$): 1.00 ± 0.12 (0.87–1.19)
 Hadar ($n = 21$): 0.89 ± 0.09 (0.71–1.14)
A. africanus ($n = 15$): 0.83 ± 0.06 (0.75–1.01).

The outgroup state (0) is an index of ≥ 1.0 . We code Kanapoi and Laetoli as plesiomorphic and Hadar and *A. africanus* as apomorphic (1). Given the observed variation and $n = 1$, we code Allia Bay as “?”.

Character 16. Mandibular P3 anterior:posterior fovea size

- 0 anterior > posterior
- 1 posterior > anterior

Kanapoi, 0; Allia Bay, 1; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character 17. Mandibular P3 anterior fovea depth

- 0 open to cervix
- 1 high notch or closed

Kanapoi, 0; Allia Bay, 1; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character 18. Mandibular P3 metaconid frequency

- 0 absent
- 1 variable
- 2 fixed

Kanapoi, 0; Allia Bay, 0; Laetoli, 1; Hadar, 1; *A. africanus*, 2

Character 19. Mandibular P3 orientation

- 0 oblique to tooththrow
- 1 intermediate
- 2 perpendicular to tooththrow

Kanapoi, 0; Allia Bay, 0; Laetoli, 1; Hadar, 1; *A. africanus*, 2

Character 20. Mandibular P3 distal marginal ridge

- 0 thin crest
- 1 wide, elevated shelf

Kanapoi, 0; Allia Bay, 1; Laetoli, 1; Hadar, 1; *A. africanus*, 1

Character Matrix

OTU/Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Chimpanzee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gorilla	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Kanapoi	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allia Bay	?	?	?	0	?	?	?	?	?	1	?	?	?	?	?	1	1	0	0	1
Laetoli	1	2	2	1	2	0	0	1	?	1	1	0	1	1	0	1	1	1	1	1
Hadar	1	2	2	2	1	1	0	1	1	2	1	1	1	1	1	1	1	1	1	1
<i>A. africanus</i>	2	2	2	2	2	1	1	0	1	1	0	1	1	1	1	1	1	2	2	1

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