Anterior dental evolution in the *Australopithecus anamensis*–*afarensis* lineage

Carol V. Ward^{1,*}, J. Michael Plavcan² and Fredrick K. Manthi^{3,4}

¹Department of Pathology and Anatomical Sciences, University of Missouri, M263 Medical Sciences Building, Columbia, MO 65212, USA

²Department of Anthropology, University of Arkansas, 330 Old Main, Fayetteville, AR 72701, USA

³Department of Earth Sciences, National Museums of Kenya, P.O. Box 40658, Nairobi, Kenya

⁴Turkana Basin Institute, Stony Brook University, Stony Brook, NY 11794, USA

Australopithecus anamensis is the earliest known species of the *Australopithecus*–human clade and is the likely ancestor of *Australopithecus afarensis*. Investigating possible selective pressures underlying these changes is key to understanding the patterns of selection shaping the origins and early evolution of the *Australopithecus*–human clade. During the course of the *Au. anamensis*–*afarensis* lineage, significant changes appear to occur particularly in the anterior dentition, but also in jaw structure and molar form, suggesting selection for altered diet and/or food processing. Specifically, canine tooth crown height does not change, but maxillary canines and P₃s become shorter mesio-distally, canine tooth crowns become more symmetrical in profile and P₃s less unicuspid. Canine roots diminish in size and dimorphism, especially relative to the size of the postcanine teeth. Molar crowns become higher. Tooth rows become more divergent and symphyseal form changes. Dietary change involving anterior dental use is also suggested by less intense anterior tooth wear in *Au. afarensis*. These dental changes signal selection for altered dietary behaviour and explain some differences in craniofacial form between these taxa. These data identify *Au. anamensis* not just as a more primitive version of *Au. afarensis*, but as a dynamic member of an evolving lineage leading to *Au. afarensis*, and raise intriguing questions about what other evolutionary changes occurred during the early evolution of the *Australopithecus*–human clade, and what characterized the origins of the group.

Keywords: *Australopithecus anamensis*; *Australopithecus afarensis*; dental evolution

1. INTRODUCTION

Fossil evidence documenting the first 4 Myr of hominin evolution has grown substantially over the past two decades. While several early taxa have been identified (*Ardipithecus*, *Sahelanthropus* and *Orrorin*), much of our understanding of what the earliest members of the *Australopithecus*–human clade were like still comes from the best-known species of *Australopithecus*, *Australopithecus afarensis*. However, *Au. afarensis* only appears as early as 3.6 Ma and is not well represented in the fossil record until 3.4–3 Ma (review in Kimbel *et al.* 2006, see also White *et al.* 2000). The new fossils from Woranso-Mille, Ethiopia (Haile-Selassie *et al.* 2010), are 3.7–3.8 Ma and probably part of this lineage as well. *Australopithecus anamensis* is the earliest known member in this clade, appearing by 4.17 Ma in Kenya and Ethiopia, and is the likely ancestor of *Au. afarensis*. Unfortunately, *Au. anamensis* is relatively poorly represented in the fossil record, so our understanding about this first 400 000 to about 800 000 years of the evolution of the *Australopithecus*–human

clade is only sketchy at present. Even so, emerging evidence from what few fossils are known is beginning to hint that *Au. anamensis* was a species in transition and may offer important insights into the origins of a number of key hominin traits.

A previous detailed investigation of morphological changes through time in the successive site samples of *Au. anamensis* and *Au. afarensis* (Kimbel *et al.* 2006) documented a series of apomorphies that progressively appear throughout these samples, involving primarily the dentition, but also some aspects of maxillary and mandibular form. The pattern of the appearance of these traits strongly supports the hypotheses of anagenetic evolution of *Au. anamensis* to *Au. afarensis*.

One of the most important apomorphies of the *Australopithecus*–human clade is habitual terrestrial bipedality with loss of significant climbing abilities. Unfortunately, little is known about the postcranial skeleton of *Au. anamensis*. *Australopithecus anamensis* is only known from a femoral shaft, along with some unpublished vertebral fragments, partial metatarsal, eroded distal pedal phalanx and manual phalanx, all from Asa Issie (White *et al.* 2006), a distal humerus, capitate, partial manual phalanx and partial tibia from Kanapoi (Patterson & Howells 1967;

* Author for correspondence (wardcv@missouri.edu).

One contribution of 14 to a Discussion Meeting Issue ‘The first four million years of human evolution’.

Leakey *et al.* 1995, 1998), and a nearly complete radius from Allia Bay (Patterson & Howells 1967; Heinrich *et al.* 1993; Leakey *et al.* 1995, 1998). The tibial diaphysis is oriented orthogonally to the talocrural joint, as is that of all later hominins, indicating a knee placed directly over the ankle during the single-limb support phase of terrestrial bipedal gait (Ward *et al.* 1999b). However, more cannot be said at the present time about the details or extent of its adaptation to terrestrial bipedality. In almost all other major features, the known *Au. anamensis* postcranial elements resemble those attributed to *Au. afarensis*. The exception may be in the capitate, which appears to have separate dorsal and plantar articular facets for MC2 like in extant African apes, and unlike *Australopithecus*, *Homo*, *Ardipithecus*, *Proconsul* (Beard *et al.* 1986; Lovejoy *et al.* 2009) or the unknown 3.5 Ma hominin from South Turkwel, Kenya (Leakey *et al.* 1998; Ward *et al.* 1999a). This small feature may indicate some differences in locomotor or manipulative function, but until more fossils are recovered our ability to infer postcranial variation among species is highly limited, and little more than can be said about whether the same pattern of locomotor or manipulative ability seen in *Au. afarensis* also characterized *Au. anamensis*.

Even less is known about its cranial anatomy. Only a temporal bone and some maxillary fragments are known. *Australopithecus anamensis* appears to have a smaller external auditory foramen than later hominins, and a potentially more obtuse angle of the tympanic plate along with a weakly developed articular eminence (Leakey *et al.* 1995; Ward *et al.* 2001). However, little can be said of the functional or evolutionary significance of this morphology without more cranial fossils.

In contrast to the skeleton and skull, there are several aspects of the jaws and teeth that are preserved for both *Au. anamensis* and *Au. afarensis*, enabling significant comparisons to be made in these elements. Previous research has noted evolutionary changes in relative canine size, canine and premolar morphology, mandibular and maxillary contours and incisor dimensions (Leakey *et al.* 1995; Ward *et al.* 2001; Kimbel *et al.* 2006; White *et al.* 2006). However, the relative paucity of fossils attributable to *Au. anamensis* obscures detailed understanding of the quality, quantity and integration of many features that impact hypotheses about the evolution of adaptations in this lineage.

Overall, while the Kanapoi and Allia Bay fossils are distinguishable from those at Laetoli and Hadar, *Au. anamensis* is generally considered to be just an early member of the *Au. afarensis* lineage, with a few isolated morphological plesiomorphies. However, there is general consensus that *Au. afarensis* demonstrates evidence of a greater emphasis on the ability to masticate tougher or more abrasive food items, possibly associated with shifts in habitat or resource exploitation (Teaford & Ungar 2000; Ward *et al.* 2001; White *et al.* 2006) and/or broadening potential ecological niches. New fossil evidence provides even more evidence for shifting adaptations throughout this lineage.

The purpose of this paper is to review and summarize the morphology of the jaws and teeth of

Au. anamensis and *Au. afarensis* based on previously published fossils, integrate data from some newly discovered specimens from Kanapoi (Manthi *et al.* in preparation) which provide new insights and consider the suite of differences seen between these taxa in an adaptive and evolutionary context. We note that most change occurs in the anterior portion of the face and jaws, with the most dramatic alterations occurring at or near the canine–premolar complex, but that patterns of change within teeth in proportions and shape often are uncorrelated. We propose that these changes signal possible dietary change and/or altered use of the anterior dentition in food processing in the early evolution of the *Australopithecus*–human clade, in conjunction with shifts in masticatory adaptations.

2. CANINE TOOTH SIZE, DIMORPHISM AND THE CANINE/P₃ COMPLEX

The evolution of the canine teeth and mandibular honing premolar in hominins has received a great deal of attention ever since Darwin (1871). Canine tooth size reduction is one of the few defining features of the hominin clade (Wolpoff 1980; Greenfield 1992; Haile-Selassie 2001, 2004; White *et al.* 2006, 2009; Suwa *et al.* 2009) and is recognized as a signal of important behavioural and adaptive changes (Plavcan & Van Schaik 1997). For example, recent discussion of *Ardipithecus ramidus* places great emphasis on the importance of the canine/premolar complex for inferring changes in behaviour and diet—an assessment with a long tradition in anthropology (e.g. Darwin 1871; Brace 1971; Leutenegger & Kelly 1977; Wolpoff 1978, 1979, 1980; Lovejoy 1981, 2009).

At this point, two major features in hominin canine evolution are widely accepted. First, male canine teeth reduced in size relative to a likely ape ancestral condition, with a concomitant reduction of canine sexual dimorphism, early in the hominin lineage (Brace 1963; Jungers 1978; Wolpoff 1980; Greenfield 1992; Suwa *et al.* 2009). Second, by *Au. afarensis*, the canine honing complex is reduced or lost (Greenfield 1992; Haile-Selassie 2001, 2004; Kimbel *et al.* 2006; White *et al.* 2006). It is widely assumed that the loss of the hone is associated with selection for use of the tooth in diet, probably in food acquisition. The most explicit functional statement is that the mandibular canine changes to a more diamond-shaped profile so that the mesial crest can occlude with the lateral maxillary incisor (Greenfield 1992; Haile-Selassie 2004). This observation is used to support the hypothesis that canine reduction and changes in morphology are a consequence of selection for incorporation of the tooth into a functional incisal battery (Greenfield 1992).

While it may seem that canine crown reduction is a necessary precursor to alterations in canine form for other, presumably dietary, functions, an alternative hypothesis has been proposed. It is possible that canine tooth crown shape change is integrally linked to selection for the use of the canine in food processing and so would have occurred concomitantly with size reduction, not after it (Greenfield 1992). Such reduction could be linked in two ways—first would

be a general selective pressure for the use of canines in food processing that results in crown size reduction following relaxation of selection for the use of the tooth as a weapon. Second would be that selection for canine crown reduction would only be linked with changes in tooth form associated with dietary use of the tooth following an initial canine crown reduction and loss of dimorphism through a separate, unspecified mechanism. In other words, one model posits that canine tooth size in all primates, including hominins, reflects a balance between conflicting selection pressures for large canines as weapons and small canines for food acquisition (Greenfield 1992), and the other posits that selection for dietary functions only occurred after canine dimorphism was lost, with a secondary crown reduction associated with the development of occlusal features that transform the canine into a tool for food processing and/or acquisition.

The large sample of *Ar. ramidus* fossils from 4.4 Ma strongly suggests that substantial reduction in male canine crown size and loss of significant dimorphism probably occurred near the origin of hominins and may not be apomorphic for the *Australopithecus*–human clade (White *et al.* 1994, 1995; Suwa *et al.* 2009). Indeed, *Au. anamensis* canine crowns appear to be approximately the same overall size as those of *Ar. ramidus*. Comparisons of associated dentitions demonstrate *Au. anamensis* had slightly larger basal dimensions of its canines relative to postcanine tooth size than did *Au. afarensis* (Ward *et al.* 2001). Overall, individual tooth sizes do not differ between the species, with the exception of the maxillary canine mesiodistal dimension and some dimensions of P₃ and P₄. The few preserved canine crowns in *Au. anamensis* appear no more variable, or presumably dimorphic, than those of *Au. afarensis* so there appears to be no evidence of evolution of dimorphism during this time period, either.

However, a single large *Au. anamensis* mandibular canine alveolus (KNM-KP 29287; Ward *et al.* 2001), and to some extent a canine root with heavily worn crown from Fejej, Ethiopia (FJ-4-SB-1a; Fleagle *et al.* 1991), suggested potentially greater canine crown size sexual dimorphism early in this lineage than previously appreciated, with the implication that canine dimorphism decreased at some point in the *Au. anamensis*–*afarensis* lineage. If so, this would be evidence of social and/or dietary evolution.

Three new associated dentitions from Kanapoi have clarified details of canine size and proportions of *Au. anamensis* (Manthi *et al.* in preparation), provided new data on canine proportions and morphology, and suggested that *Au. anamensis* is a key taxon for understanding the adaptive significance of changes in canine form.

KNM-KP 47951 has the largest mandibular root of any known hominin (figure 1). Comparison of mandibular root size in *Au. anamensis* with those *Au. afarensis*, extant great apes and *Homo* reveals that root size variation in *Au. anamensis* was very strong, most like *Pongo* in magnitude (figure 1, table 1), implying strong dimorphism. This stands in stark contrast to *Au. afarensis*, which shows much less variation in root dimensions, and is intermediate to extant *Homo* and *Pan* in mean size. Unlike the roots, mandibular

canine crowns are similar in all dimensions in *Au. anamensis* and *Au. afarensis*, and both have slightly larger and more dimorphic crowns than do modern humans, as also reported for *Ar. ramidus* (Suwa *et al.* 2009) but less so than in extant apes. Therefore, not only was there a clear dissociation between crown size and root size in *Au. anamensis*, such that size and dimorphism in the crowns were lost while size and dimorphism in the roots were retained, but the loss of root size dimorphism occurred sometime during the evolution of *Au. anamensis* into *Au. afarensis*. Interestingly, not only does KNM-KP 47951 demonstrate that the large alveolus of KNM-KP 29287 did not imply unusual crown size dimorphism, it also demonstrates that the canine root of KNM-KP 29287 would not have been unusually large, and may in fact have been a small male. It would not, however, have supported a larger crown than those preserved for *Au. anamensis* (Plavcan *et al.* 2009).

Even with the new data, no dimensions of the mandibular canine crowns (length, breadth or height) differ between species (figure 1, table 2). However, there are dimensional differences in the maxillary canines (see also Ward *et al.* 2001; White *et al.* 2006) (figure 2, table 2). *Australopithecus anamensis* and *Au. afarensis* are equivalent in maxillary canine crown height and buccolingual breadth, but *Au. anamensis* maxillary canines are mesiodistally longer than are those of *Au. afarensis* (figure 3a, tables 2 and 3). Proportionately, *Au. anamensis* canines are almost exactly intermediate in basal crown shape (measured as mesiodistal length relative to buccolingual breadth) between extant great apes and *Au. afarensis* (figure 3a). Furthermore, *Au. afarensis* canine basal shape proportions are identical to those of extant *Homo*, after accounting for their size difference. The apparent progressive decrease in relative canine size from *Au. ramidus* to *Au. afarensis*, through *Au. anamensis* (White *et al.* 2006), tracks mesiodistal length only, but not overall size of the tooth.

The change in canine basal proportions reflects change in canine–P₃ function. It has long been noted that the *Au. afarensis* canine/premolar complex loses its ‘honing’ function, in the sense that the distal edge of the maxillary canine no longer exclusively wears against the labial surface of the mandibular P₃ as in other primates (Wolpoff 1979; Greenfield 1992; Haile-Selassie 2004). Metrically, it is only the maxillary canine and mandibular premolar—the honing teeth—that change basal shape (figure 3b) to become less elongate in outline. Mandibular canines and maxillary P₃s do not. This implies no overall selection to reduce the teeth, but only selection to alter contact between the honing pair. So, while there may have been a loss of honing with early hominins (Haile-Selassie 2001, 2004; Brunet *et al.* 2002), canine–P₃ occlusal relationships continue to evolve.

In addition to basal outlines, the canines and P₃ change other aspects of their crown shape significantly from *Au. anamensis* to *Au. afarensis*, strongly suggesting that selection favoured an altered function of these teeth. Both mandibular and maxillary canines become more symmetrical in lingual profile. Maxillary canines have higher shoulders and shorter mesial crests, and mandibular canines have lower mesial

Figure 1. Dental dimensions for mandibular canine crowns and roots for extant great apes, humans, *Au. anamensis* and *Au. afarensis*. Arrows indicate new specimen KNM-KP 47951. Data in table 1. (a) Crown height, (b) root length, (c) crown mesiodistal, (d) root mesiodistal, (e) crown buccolingual and (f) root buccolingual.

shoulders and a less narrow, blade-like outline (figure 3c). Lower premolars develop a larger metaconid, and the protoconid shifts buccally. Marginal ridges become proportionately more distinctive, and the anterior fovea opens in a more occlusal direction (Leakey *et al.* 1995, 1998; Ward *et al.* 2001; Haile-Selassie 2004; Suwa *et al.* 2009; White *et al.* 2006). These shape changes increase transverse contact area between maxillary and mandibular teeth, most logically owing to increased use of the canine in food acquisition or preparation, and perhaps the premolar in mastication as well.

The fossils demonstrate that canine shape changed significantly along with a shift in canine– P_3 occlusal relationships in the *Au. anamensis*–*afarensis* lineage, while canine size remained approximately the same. It is also notable that *Au. afarensis* canine crowns show the same basal proportions as in *Homo*

(figure 3a), demonstrating that the major proportional changes in canine dimensions in hominin evolution happened between 3.9 and 3.4 Ma.

The dissociation between crown size and shape changes demonstrates that selection impacting crown shape was independent of that causing crown height reduction. This in turn bears on hypotheses that purport to explain the adaptive significance of canine crown size reduction in hominins (Brace 1963; Bailit & Friedlaender 1966; Wolpoff 1969, 1980; Calcagno & Gibson 1988). Crown height was reduced prior to the appearance of *Au. anamensis*, if *Ar. ramidus* indeed reflects the ancestral hominin condition (Suwa *et al.* 2009), and certainly by the origins of the *Australopithecus*–human clade. Data now suggest that crown height did not reduce in order to provide room for expanding postcanine dentitions (Jungers 1978), because basal dimensions and root size did

Table 1. Descriptive statistics for mandibular canine dimensions of extant combined-sex and fossil samples. All data are in millimetres. Data for *Gorilla*, *Pongo*, *Pan troglodytes* and *Homo* were collected for this project. Data for *Pan pansiscus* were taken from [Plavcan \(1990\)](#) and do not include values for root dimensions. Height, crown height; BL, buccolingual; MD, mesiodistal; RBL, root buccolingual; RMD, root mesiodistal; RL, root length.

	height	BL	MD	RBL	RMD	RL
<i>Gorilla gorilla</i>						
<i>n</i>	50	50	50	50	50	50
min.	12.65	9.18	11.53	8.65	11.12	22.02
max.	31.25	16.26	21.66	16.03	21.4	45.27
mean	20.89	12.44	15.55	11.89	15.17	33.18
standard deviation	5.47	2.32	2.82	2.41	3.03	4.13
CV	26.2	18.6	18.1	20.3	20.0	12.4
<i>Pongo pygmaeus</i>						
<i>n</i>	16	17	17	17	17	16
min.	13.58	7.97	11.08	7.4	10.2	20.35
max.	26.82	14.53	17.8	14.17	17.52	41.04
mean	19.52	10.49	13.83	10.12	13.39	27.56
standard deviation	4.18	2.51	2.13	2.48	2.31	6.09
CV	21.4	23.9	15.4	24.5	17.25	22.1
<i>Pan troglodytes</i>						
<i>n</i>	30	30	30	30	30	30
min.	12.51	7.98	10.1	7.6	8.19	19.99
max.	25.5	15.22	17.17	14.92	16.9	38.0
mean	17.63	10.93	12.8	10.43	12.18	28.59
standard deviation	3.52	1.77	1.92	1.76	2.26	5.03
CV	20.0	16.2	15.0	16.9	18.6	17.6
<i>Pan paniscus</i>						
<i>n</i>	29	30	30	—	—	—
min.	9.5	5.88	7.88			
max.	16.13	9.13	11.88			
mean	12.27	7.13	9.66			
standard deviation	2.02	0.88	1.16			
CV	16.5	12.3	12.0			
<i>Homo sapiens</i>						
<i>n</i>	36	36	36	36	36	36
min.	7.67	5.45	5.94	3.7	5.82	10.94
max.	12.65	7.9	9.13	6.58	8.99	20.2
mean	9.99	6.72	7.67	5.36	7.49	15.96
standard deviation	1.23	0.64	0.71	0.61	0.68	2.18
CV	12.3	9.5	9.3	11.4	9.1	13.6
<i>Australopithecus afarensis</i>						
<i>n</i>	6	10	11	9	9	3
min.	10.9	6.9	9.3	6.4	8.8	20.91
max.	17	10.6	13.9	9.5	13.1	24.29
mean	13.12	8.48	10.88	7.82	10.54	22.77
standard deviation	2.22	1.25	1.38	1.08	1.31	1.72
CV	16.9	14.7	12.7	13.8	12.4	7.5
<i>Australopithecus anamensis</i>						
<i>n</i>	3	7	7	9	8	3
min.	10	6.6	9	5.9	8.2	20.2
max.	15.71	10.40	13.90	10.3	13.81	31.79
mean	13.27	8.81	11.04	7.99	10.44	26.86
standard deviation	2.94	1.32	1.66	1.43	1.72	5.99
CV	22.2	15.0	15.0	17.9	16.5	22.3

not reduce concomitantly with crowns. Crown height also did not reduce in order to enhance an incisal or biting function ([Szalay 1975](#); [Wolpoff 1980](#); [Greenfield 1992](#)) because shape change in the crown did not accompany crown height reduction. Following a loss of function of the canine teeth as weapons (for behavioural reasons, or following masticatory changes precluding the use of projecting

canines), male canine size—especially crown height—reduced to the size of those of female extant apes, as has occurred in other primates ([Plavcan *et al.* 1995](#)). However, canine shape becomes altered simultaneously with mandibular lateral incisor breadth ([Ward *et al.* 2001](#)) and premolar form only with the appearance of *Au. afarensis* in the absence of further crown height reduction.

Figure 2. Dental dimensions for maxillary canine crowns for extant great apes, humans, *Au. anamensis* and *Au. afarensis*. Data in table 3. (a) Crown height, (b) crown mesiodistal, and (c) crown buccolingual.

It could be possible that smaller canine roots in *Au. afarensis* could be related to decreased loading of the canines in puncturing or crushing (Spencer 2003), but microwear studies in *Au. afarensis* imply that, in fact, use of the canine for these activities probably was greater in *Au. afarensis* than in apes (Ryan & Johanson 1989). Comparisons with *Au. anamensis* microwear will be necessary to explore this possibility further.

To date, the fossil record is insufficient to evaluate whether these events in canine and premolar evolution were indeed simultaneous, but they are so within the current resolution available in the fossil record. In

Table 2. Probabilities from *t*-tests for significant differences between *Au. anamensis* and *Au. afarensis* canine crown areas and linear dimensions using ln-transformed data. Numbers are for two-tailed probabilities. Area is calculated as the length times the breadth of the crown dimensions. Abbreviations as in table 1; mand, mandibular; max, maxillary.

	area	MD	BL	RMD	RBL	height
max	0.546	0.007	0.226	0.009	0.625	0.211
mand	0.482	0.208	0.98	0.831	0.843	0.971

any event, it is now clear that crowns and roots did not change shape and size as part of a unimodal selection pressure that drove the canines to the modern human form. Rather, the patterns of morphological change suggest to us that the selective pressure shaping canine form during the evolution of *Au. anamensis* and early *Au. afarensis* was distinct from that of the earliest hominins, and of later *Homo*. This function almost certainly related to food acquisition or processing, but in a manner distinctive to early *Australopithecus*.

3. MANDIBULAR AND MAXILLARY MORPHOLOGY

Other morphologies distinguishing *Au. anamensis* and *Au. afarensis* also are related to the change in canine tooth size, and in morphology of the canine/premolar complex. In particular, canine tooth root size affects the occlusal outline of the anterolateral corner of the mandible. The mandible of *Au. anamensis* is distinct from that of *Au. afarensis* in having an inflated alveolar profile along the roots, so that the canines are set anteriorly to the postcanine tooth rows (figure 4) (Ward *et al.* 2001). In the male mandible, the effect of a large root is particularly notable. In contrast, in *Au. afarensis*, the broadest region across the anterior mandible is found adjacent to P₃, and the canines are set medial to the premolars. There also is less variation in this contour among mandibles, presumably related to less canine root size dimorphism than in *Au. anamensis*. Certainly, canine size is correlated with mandibular form in primates (Plavcan & Daegling 2006). Another factor influencing the relatively broad anterior portion of the mandible in *Au. anamensis* is that the lower lateral incisors are relatively broader than in *Au. afarensis* (Ward *et al.* 2001). Both canine root breadths and incisor breadth would affect anterior mandibular size and shape.

The maxilla of *Au. anamensis*, and early *Au. afarensis* from Laetoli (Garusi 1; Puech 1986; Puech *et al.* 1986), appears to have narrowly spaced, relatively straight maxillary tooth rows, also seen in the Woranso-Mille sample (Haile-Selassie *et al.* 2010). They also have rounded margins of the lateral nasal aperture. Both of these features are plausibly related to reduction in canine tooth root size. Canine root length may not be related to maxillary shape (Cobb & Willis 2008; Plavcan *et al.* 2009), but root basal area would certainly affect maxillary breadth in this region and thus the supporting bone.

Thus, the selective force that shaped canine root size reduction is plausibly linked to pressures that

Figure 3. Illustrations of canine shape differences between *Au. anamensis* and *Au. afarensis*. (a) Scatterplot of ln-transformed maxillary canine mesiodistal length compared with buccolingual breadth. Open squares: *Gorilla gorilla*, *Pan paniscus*, *P. troglodytes*, *Pongo pygmaeus*; open triangles: *Homo sapiens*; grey diamonds: *Au. afarensis*; black circles: *Au. anamensis*. *Australopithecus anamensis* retains relatively long canines mesiodistally and are most similar in proportions to extant apes. *Australopithecus afarensis* canines are similar buccolingually but are mesiodistally shorter than those of *Au. anamensis*. Humans have the same proportions as seen in *Au. afarensis*, but are smaller overall. (b) Basal proportion differences are seen only in the maxillary canine and mandibular premolar, the teeth that hone, but not mandibular canine or maxillary premolar, illustrating that observed shape changes are associated with a further reduction in honing and a shift in occlusal relationships in this complex. (c) Morphologic differences in canines and P₃. *Australopithecus anamensis* has a lower mesial crown shoulder and longer mesial crest in the maxillary canine, a narrower, more blade-like mandibular crown with pronounced distal tubercle and a more unicuspid P₃ with centrally placed paraconid compared with *Au. afarensis*. Data in tables 1 and 3. Scale bar, 1 cm.

altered mandibular and possibly maxillary geometry. Teaford & Ungar (2000) noted that mandibular corpus robusticity is intermediate in *Au. anamensis* between that of great apes and later hominins, suggesting an increase in adaptation to resist heavier masticatory stresses with *Au. afarensis*. That *Au. afarensis* was adapted to greater masticatory stresses is also suggested by the increased height of its molar crowns (Leakey *et al.* 1995; Ward *et al.* 1999b, 2001). *Australopithecus afarensis* mandibles also tend to have more posteriorly divergent tooth rows than does *Au. anamensis*, whose tooth rows are narrower and more parallel, more like those of extant apes (Ward *et al.* 2001). Narrow tooth rows increase symphyseal stresses owing to wishboning and torsion of the mandible during mastication

(Hylander 1984, 1985; Ravosa 2000). *Australopithecus anamensis* had a correspondingly large post-incisive planum and strongly developed mandibular tori, probably related to this overall geometry. A wider geometry in *Au. afarensis* would reduce forces from wishboning owing to pull of the external masticatory muscles and bone (Hylander 1985). More divergent tooth rows also decrease symphyseal torsional stresses. It is notable, therefore, that despite altered mandibular geometry, symphyseal robusticity still tends to be relatively greater in *Au. afarensis* than *Au. anamensis*.

Given the effects of mandibular geometry on symphyseal stresses, it may be that selection for more divergent tooth rows influenced the reduction of lateral incisor breadth and canine root size in order to reduce

Table 3. Descriptive statistics for maxillary canine crown dimensions of extant combined-sex and fossil samples. Abbreviations as in table 1.

	height	BL	MD
<i>Gorilla gorilla</i>			
<i>n</i>	50	50	50
min.	12.14	10.26	12.54
max.	41.56	22.12	23.23
mean	22.08	13.88	17.17
standard deviation	7.44	2.78	3.24
CV	33.7	20.0	18.9
<i>Pongo pygmaeus</i>			
<i>n</i>	18	18	18
min.	12.74	8.09	11.11
max.	30.45	15.43	18.56
mean	20.15	11.80	14.76
standard deviation	6.15	2.19	2.72
CV	30.5	18.6	18.4
<i>Pan troglodytes</i>			
<i>n</i>	30	30	30
min.	11.86	8.09	9.63
max.	27.27	14.25	19.31
mean	18.05	10.56	12.82
standard deviation	4.03	1.79	2.31
CV	22.3	17.0	18.0
<i>Pan paniscus</i>			
<i>n</i>	24	30	30
min.	8.63	6.13	8.63
max.	20.38	11.13	14.38
mean	13.40	8.01	10.54
standard deviation	3.48	1.44	1.56
CV	26.0	18.0	14.8
<i>Homo sapiens</i>			
<i>n</i>	50	50	50
min.	6.48	6.56	5.96
max.	12.26	9.82	8.49
mean	9.28	8.24	7.45
standard deviation	1.23	0.71	0.57
CV	13.3	8.6	7.7
<i>Australopithecus afarensis</i>			
<i>n</i>	8	8	8
min.	9.2	9.3	8.9
max.	15.4	12.5	11.6
mean	12.35	10.7	9.81
standard deviation	2.18	1.00	0.84
CV	17.7	9.3	8.6
<i>Australopithecus anamensis</i>			
<i>n</i>	3	7	8
min.	12	8.8	9.91
max.	16	11.2	12.4
mean	14.4	10.20	11.10
standard deviation	2.12	0.75	0.82
CV	14.7	7.4	7.4

the breadth of the anterior mandible in *Au. afarensis*. This may have co-occurred with widening of the posterior part of the mandible, too. In order to maintain appropriate occlusal relationships, this could also have led to concomitant reduction in maxillary canine root dimensions, and corresponding reduction in maxillary inflation along the canine juga and lateral nasal aperture.

Thus, the mandibular morphology of *Au. afarensis* implies selection for the ability to process harder-to-chew foods, possibly opening up new niches. However, it is not only the masticatory system that has changed; reduction in lateral incisor breadth and reshaping of the canine crowns and the canine–premolar complex also suggest that selection for altered function of the anterior dentition in food processing occurred in the transition from *Au. anamensis* to *Au. afarensis*.

4. TOOTH WEAR

One feature not previously appreciated from published fossils is that for those specimens showing substantial tooth wear, there appears to be differentially heavy anterior tooth wear in *Au. anamensis* compared with *Au. afarensis*. Quantitative comparisons of gross wear patterns are difficult owing to the fragmentary preservation of the dentitions, but qualitative comparisons can be made. Overall, *Au. anamensis* appear to have higher frequencies of heavier tooth wear than seen in *Au. afarensis*.

Three out of four known *Au. anamensis* maxillae that preserve molars and anterior teeth all have heavy anterior wear relative to that of the molars (figure 5). KNM-KP 29283 has dentine exposure crossing both lingual cusps of M¹ and M². Its incisors and canines preserve only a narrow band of enamel labially, but were wearing onto the roots lingually. The new specimen, KNM-KP 47952 (Manthi *et al.* in preparation), also has unusually high anterior tooth wear, with only 1–2 mm of enamel remaining along the lingual surfaces of its incisors and canines. In apparent contrast, dentine is only exposed on M² as a tiny pit on the paracone. Even if this molar is not associated, which it almost certainly is, there is an unusually heavy amount of anterior wear. Another Kanapoi fossil, KNM-KP 30498, has M² preserved, but on M¹ has a small area of dentine exposed only on the paracone. Its I¹ is worn all the way up to the basal tubercle, probably about halfway through the original length of the tooth. The canine of this same specimen is worn almost up to its mesial or distal tubercles. In fact, no unworn incisors are known from *Au. anamensis* at all, except those of young individuals whose teeth are either not yet or barely in occlusion, and/or who exhibit little or no molar wear. The only relatively unworn maxilla with canine is ASI-VP-2/344 from Aramis, which has no dentine exposure on M² but still exhibits apical wear on its canine (White *et al.* 2006). This specimen appears comparable in wear to teeth in the *Au. afarensis* maxilla AL 200-1.

In contrast, no comparably heavy differential wear is found in the associated maxillary dentitions of *Au. afarensis* at Hadar or Laetoli, and none is as heavily worn as any of the three Kanapoi specimens. The M²s of AL 444 (Kimbél *et al.* 2004) are more worn than those of KNM-KP 47952, but less than those of KNM-KP 29283, but most of the incisor and canine crowns are intact in AL 444. AL 199-1 and AL 200-1 have less wear on their molars than any *Au. anamensis* maxilla, and while they have some wear on the incisors and canines, it is not heavy. The

Figure 4. Top row photos: occlusal views of all three Kanapoi mandibles, from left to right KNM-KP 29281, KNM-KP 29287, KNM-KP 31713. Bottom row line drawings: several mandibles of *Au. afarensis*, from left to right: LH 4, AL 123-23, AL 333w-60, AL 266-1, AL 400-1a, AL 277-1 and AL 198-1. Arrows denote anterolateral inflection of occlusal outline. Note the canine roots set medial to that of P_3 in the *Au. afarensis*, and in contrast that the canines are set anterior to the P_3 in the *Au. anamensis* fossils so that the anterolateral corner of the occlusal profile is formed by the canine juga in this earlier species. Scalar bar, 0–4 cm.

Figure 5. Lingual views (top) of anterior teeth of KNM-KP 30498 and KNM-KP 47952 and occlusal views (bottom) of these anterior teeth and their associated molars. KNM-KP 29283 shown in lingual (top) and occlusal (bottom) views for comparison. KNM-KP 30498 preserves I^1 , C, P^3 , M^1 and M^3 crowns, relevant teeth reversed to show all as if they were from the left side. KNM-KP 47952 preserves I^1 , I^2 , C and M^2 . All three specimens show relatively heavy anterior wear relative to molar wear. See text for discussion. Scalar bar, 0–4 cm.

most worn published *Au. afarensis* incisor is AL 198-17a (Johanson *et al.* 1982) which is comparable to that of KNM-KP 30498. Unfortunately it is not associated with any postcanine teeth, so further comparison cannot be made.

Mandibular tooth wear is not directly comparable to maxillary wear, but even in sufficiently preserved mandibular dentitions, anterior tooth wear is at least as great or greater on the teeth relative to the molars in *Au. anamensis* when compared with *Au. afarensis*. The *Au. afarensis* mandible with the most heavily worn molars, AL 198-1, has dentine exposed across the occlusal face of M₁ and buccal cusps of M₂, but still has most of its canine crown preserved. It is only slightly less worn anteriorly than the *Au. anamensis* type mandible KNM-KP 29281. The most heavily worn mandibular dentition of all is the *Au. anamensis* specimen FJ-4-SB-1a from Fejej, Ethiopia (Fleagle *et al.* 1991), which has a similar level of molar wear to AL 198-1, yet it has dentine exposure over almost the entire P₃ cusp and the associated canine is almost completely worn to the root, preserving only a narrow band of enamel.

In summary, no anterior teeth are known from Hadar in which the entire crown is missing, yet many specimens attributed to *Au. anamensis* are very heavily worn. All individuals with sufficiently heavy molar wear to expose dentine on M₂ have very heavily worn anterior teeth in *Au. anamensis*, whereas this is not the case for *Au. afarensis*. Only expanding sample sizes will provide an adequate test of how typical this distinction is, but current fossils are suggestive.

There could be three possible explanations for this, which are not mutually exclusive, and all hint at selection for altered involvement of the anterior dentition. The first possibility is that the anterior permanent dentition erupts earlier relative to the molars in *Au. anamensis* than *Au. afarensis*, and that there was a shift to delay eruption of the incisors and canines in *Au. afarensis* relative to molar development. The second would be ingesting or biting foods with higher levels of tannins, which might increase intra-oral friction and cause higher tooth wear (Prinz & Lucas 2000). The third possibility is that there is a difference between these samples in patterns of food processing involving the anterior dentition in which the teeth are suffering greater mechanical abrasion (Teaford & Ungar 2000). Under any of these scenarios, anterior tooth use or dietary properties probably would have differed between *Au. afarensis* and *Au. anamensis*.

We suggest that the chemical hypothesis does not provide the most satisfactory explanation because relative anterior wear appears to decrease in concert with shape changes in incisor breadth, canine length and crown shape, as well as premolar proportions and crown morphology. The combination of changes in both wear gradient and dental morphology hints at a mechanical factor. Detailed study of anterior tooth microwear and dental growth patterns are needed to help test the various hypotheses of altered tooth wear between these species. Regardless, no matter what the explanation, the pattern suggests a shift in diet or anterior tooth use of some sort.

5. SUMMARY AND CONCLUSIONS

The discovery of new fossils, even though representing only a small portion of the anatomy of *Au. anamensis*, dictates a more careful, circumspect view of the role of this taxon in hominin evolution, and thereby the pattern of the origin of the adaptive suite of behaviours and characters shaping the early evolution of the *Australopithecus*–human clade. *Australopithecus anamensis* documents a morphology in the anterior face and dentition that is clearly transitional between a more primitive hominin form, and that seen in *Au. afarensis*.

Given that the fossil record consists of mainly teeth and jaws, it should come as no surprise that the evidence suggests that any adaptive shift from *Au. anamensis*–*afarensis* lineage was related to diet. The data from the new Kanapoi fossils, in combination with previously published data, demonstrate that adaptively significant differences exist between *Au. anamensis* and *Au. afarensis*. These morphologies are not isolated, but seem to reflect an adaptive shift to a diet involving heavier mastication and at the same time altered use of the anterior dentition in food processing.

Taken together, the greatest known differences between *Au. anamensis* and *Au. afarensis* are associated with evolutionary changes within the canine/P₃ complex, and with adaptations for coping with increasing masticatory loads on the postcanine dentition. It has long been supposed that reduction in canine crown height accompanied selection for an increased ability to masticate tougher or harder foods, as well as with origins of habitual terrestrial bipedality. *Ardipithecus ramidus* demonstrates that crown height reduction is not linked to increased ability to masticate tougher or harder foods (White *et al.* 1994; Suwa *et al.* 2009), and *Au. anamensis* demonstrates that shape change altering occlusal relationships between the canine and premolar, and reduction in canine crowns and roots were dissociated. Even though the canine/P₃ complex changed form in the *Au. anamensis*/*Au. afarensis* lineage, canine crown size itself remained stable, while the dentition and mandible showed progressive changes that suggest adaptation to heavy loads.

The dissociation between changes in root and crown size is distinctive in the evolution in *Au. anamensis*–*afarensis*. Given that *Ardipithecus* also has large roots relative to its crowns (Suwa *et al.* 2009), the *Au. anamensis* condition appears primitive for hominins. A reduction in root size is achieved with the appearance of *Au. afarensis*, a species in which the premolars are more molariform, lower lateral incisors less broad and maxillary canine crowns are mesiodistally shorter with concomitant shorter mesial crests, mandibular canines less blade-like and more symmetrical in profile. Tooth rows are less parallel and anterolateral mandibular and maxillary contours less inflated, probably related to the presence of smaller canine roots. An association between root size reduction and a shift to a more functionally advantageous jaw morphology is worth investigating.

Furthermore, the new Kanapoi fossils highlight the nature of *Au. anamensis* as a truly transitional species between a more primitive condition to what is seen in *Au. afarensis*, and to some extent later hominins.

Australopithecus anamensis was not just a primitive version of *Au. afarensis*, it was the species at the root of the *Australopithecus*–human clade in which some key aspects of *Australopithecus* morphology were developing (see also Haile-Selassie *et al.* 2010). At the same time, not all of the characteristics seen in *Au. afarensis* were present at the origin of the *Australopithecus*–human clade, so not all distinguish members of this clade from its sister taxa.

Whether apparent dietary evolution co-occurred with shifts in locomotor or manipulative adaptations, body size, dimorphism, cranial morphology or brain size during the early evolution of the *Australopithecus*–human clade can only be elucidated with more fossils from the time of first occurrence of *Australopithecus* (4.17 Ma) and *Au. afarensis* from Hadar (3.4–3.0 Ma). We hypothesize that *Au. anamensis* is best viewed as not simply a primitive precursor to *Au. afarensis*, but rather part of a dynamic morphological transition from a primitive, ape-like morphology to the unique set of morphological adaptations and behaviours that characterized the australopithecine bauplan and the early evolution of the *Australopithecus*–human clade.

We thank the National Museums of Kenya, Emma Mbua, Robert Moru, the Royal Museum of Central Africa, Cleveland Museum of Natural History and United States National Museum for access to specimens. We thank Chris Dean, Bill Kimbel, Meave Leakey, Faydre Paulus, Matt Ravosa, Peter Ungar and Bernard Wood for assistance, advice and helpful discussions. We thank Alan Walker and Chris Stringer for generously inviting us to participate in this symposium. We thank the Wenner Gren Foundation, Leakey Foundation, Turkana Basin Institute and National Science Foundation for support in various aspects of this project.

REFERENCES

- Bailit, H. & Friedlaender, J. 1966 Tooth size reduction: a hominid trend. *Am. Anthropol.* **68**, 665–672. (doi:10.1525/aa.1966.68.3.02a00030)
- Beard, K. C., Teaford, M. F. & Walker, A. 1986 New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. *Folia Primatol.* **47**, 97–118. (doi:10.1159/000156268)
- Brace, C. 1963 Structural reduction in evolution. *Am. Nat.* **97**, 39–49. (doi:10.1086/282252)
- Brace, C. L. 1971 Sexual dimorphism in human evolution. *Nature* **228**, 31–49.
- Brunet, M. *et al.* 2002 A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**, 145–151. (doi:10.1038/nature00879)
- Calcagno, J. & Gibson, K. 1988 Human dental reduction: natural selection or probable mutation effect? *Am. J. Phys. Anthropol.* **77**, 505–517. (doi:10.1002/ajpa.1330770411)
- Cobb, S. & Willis, A. 2008 Is premaxilla morphology determined by the spatial requirements of the developing incisor dentition? *Am. J. Phys. Anthropol.* **135**, 79–80.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
- Fleagle, J. G., Rasmussen, D. T., Yirga, S., Bown, T. M. & Grine, F. E. 1991 New hominid fossils from Fejej, Southern Ethiopia. *J. Hum. Evol.* **21**, 145–152. (doi:10.1016/0047-2484(91)90005-G)
- Greenfield, L. O. 1992 Origin of the human canine: a new solution to an old enigma. *Yrbk Phys. Anthropol.* **35**, 153–185. (doi:10.1002/ajpa.1330350607)
- Haile-Selassie, Y. 2001 Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* **412**, 187–191. (doi:10.1038/35084063)
- Haile-Selassie, Y. 2004 Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* **303**, 1503–1505. (doi:10.1126/science.1092978)
- Haile-Selassie, Y. 2010 Phylogeny of early *Australopithecus*: new fossil evidence from the Woranso-Mille (central Afar, Ethiopia). *Phil. Trans. R. Soc. B* **365**, 3323–3331. (doi:10.1098/rstb.2010.0064)
- Haile-Selassie, Y., Saylor, B. Z., Deino, A., Alene, M. & Latimer, B. M. 2010 New hominid fossils from Woranso-Mille (Central Afar, Ethiopia) and taxonomy of early *Australopithecus*. *Am. J. Phys. Anthropol.* **141**, 406–417. (doi:10.1002/ajpa.21159)
- Heinrich, R. E., Rose, M. D., Leakey, R. E. & Walker, A. C. 1993 Hominid radius from the middle Pliocene of Lake Turkana, Kenya. *Am. J. Phys. Anthropol.* **92**, 139–148. (doi:10.1002/ajpa.1330920203)
- Hylander, W. L. 1984 Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. *Am. J. Phys. Anthropol.* **64**, 1–46. (doi:10.1002/ajpa.1330640102)
- Hylander, W. L. 1985 Mandibular function and biomechanical stress and scaling. *Am. Zool.* **25**, 315–330. (doi:10.1093/icb/25.2.315)
- Johanson, D., White, T. & Coppens, Y. 1982 Dental remains from the Hadar Formation, Ethiopia: 1974–1977 collections. *Am. J. Phys. Anthropol.* **57**, 545–604. (doi:10.1002/ajpa.1330570406)
- Jungers, W. 1978 On canine reduction in early hominids. *Curr. Anthropol.* **51**, 155–156.
- Kimbel, W. H., Rak, Y. & Johanson, D. 2004 *The skull of Australopithecus afarensis*. New York, NY: Oxford University Press.
- Kimbel, W., Lockwood, C., Ward, C. V., Leakey, M., Rak, Y. & Johanson, D. 2006 Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *J. Hum. Evol.* **51**, 134–152. (doi:10.1016/j.jhevol.2006.02.003)
- Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. 1995 New four-million-year-old hominid species from Kanapoi and Alia Bay, Kenya. *Nature* **376**, 565–571. (doi:10.1038/376565a0)
- Leakey, M. G., Feibel, C. S., MacDougall, I., Ward, C. V. & Walker, A. 1998 New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* **363**, 62–66.
- Leutenegger, W. & Kelly, J. T. 1977 Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* **18**, 117–136. (doi:10.1007/BF02382954)
- Lovejoy, C. O. 1981 The origin of man. *Science* **211**, 341–350. (doi:10.1126/science.211.4480.341)
- Lovejoy, C. 2009 Reexamining human origins in light of *Ardipithecus ramidus*. *Science* **326**, 74e1–74e8. (doi:10.1126/science.1175834)
- Lovejoy, C., Simpson, S., White, T., Asfaw, B. & Suwa, G. 2009 Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* **326**, 70e1–70e8. (doi:10.1126/science.1175827)
- Manthi, F., Plavcan, J. & Ward, C. V. In preparation. New fossils attributed to *Australopithecus anamensis* from Kanapoi, Kenya.
- Patterson, B. & Howells, W. W. 1967 Hominid humeral fragment from early Pleistocene of Northwestern Kenya. *Science* **156**, 64–66. (doi:10.1126/science.156.3771.64)
- Plavcan, J. M. 1990 Sexual dimorphism in the dentition of extant anthropoid primates. PhD dissertation, Duke University. University Microfilms: Ann Arbor, MI.

- Playcan, J. & Daegling, D. 2006 Interspecific and intra-specific relationships between tooth size and jaw size in primates. *J. Hum. Evol.* **51**, 171–184. (doi:10.1016/j.jhevol.2006.02.005)
- Playcan, J. M. & Van Schaik, C. P. 1997 Intrasexual competition and body weight dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* **103**, 37–68. (doi:10.1002/(SICI)1096-8644(199705)103:1<37::AID-AJPA4>3.0.CO;2-A)
- Playcan, J. M., Van Schaik, C. & Kappeler, P. 1995 Competition, coalitions and canine size in primates. *J. Hum. Evol.* **28**, 245–276. (doi:10.1006/jhevol.1995.1019)
- Playcan, J. M., Ward, C. V. & Paulus, F. 2009 Estimating canine tooth crown height in early *Australopithecus*. *J. Hum. Evol.* **57**, 2–10. (doi:10.1016/j.jhevol.2009.04.005)
- Prinz, J. & Lucas, P. 2000 Saliva tannin interactions. *J. Oral Rehabil.* **27**, 991–994. (doi:10.1046/j.1365-2842.2000.00578.x)
- Puech, F. 1986 *Australopithecus afarensis* Garusi 1, diversité et spécialisation des premiers Hominidés d'après les caractères maxillo-dentaires. *C. R. Acad. Sci., Paris* **303**, 1819–1823.
- Puech, P. F., Cianfarani, F. & Roth, H. 1986 Reconstruction of the maxillary dental arcade of Garusi Hominid 1. *J. Hum. Evol.* **15**, 325–332. (doi:10.1016/S0047-2484(86)80015-X)
- Ravosa, M. J. 2000 Size and scaling in the mandible of living and extinct apes. *Folia Primatol.* **71**, 305–322. (doi:10.1159/000021754)
- Ryan, A. & Johanson, D. 1989 Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and nonhuman primates. *J. Hum. Evol.* **18**, 235–268. (doi:10.1016/0047-2484(89)90051-1)
- Spencer, M. A. 2003 Tooth-root form and function in platyrrhine seed-eaters. *Am. J. Phys. Anthropol.* **122**, 325–335. (doi:10.1002/ajpa.10288)
- Suwa, G., Kono, R., Simpson, S., Asfaw, B., Lovejoy, C. & White, T. 2009 Paleobiological implications of the *Ardipithecus ramidus* dentition. *Science* **326**, 94–99. (doi:10.1126/science.1175824)
- Szalay, F. S. 1975 Hunting-scavenging protohominids: a model for hominid origins. *Man* **10**, 420–429. (doi:10.2307/2799811)
- Teaford, M. F. & Ungar, P. S. 2000 Diet and the evolution of the earliest human ancestors. *Proc. Natl Acad. Sci. USA* **97**, 13 506–13 511. (doi:10.1073/pnas.260368897)
- Ward, C. V., Leakey, M. G., Brown, B., Brown, F., Harris, J. & Walker, A. 1999a South Turkwel: a new Pliocene hominid site in Kenya. *J. Hum. Evol.* **36**, 69–95. (doi:10.1006/jhevol.1998.0262)
- Ward, C. V., Walker, A. & Leakey, M. G. 1999b The new hominid species *Australopithecus anamensis*. *Evol. Anthropol.* **7**, 197–205. (doi:10.1002/(SICI)1520-6505(1999)7:6<197::AID-EVAN4>3.0.CO;2-T)
- Ward, C. V., Leakey, M. & Walker, A. 2001 Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* **41**, 255–368. (doi:10.1006/jhevol.2001.0507)
- White, T. D., Suwa, G. & Asfaw, B. 1994 *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371**, 306–312. (doi:10.1038/371306a0)
- White, T. D., Suwa, G. & Asfaw, B. 1995 Corrigendum. *Nature* **375**, 88.
- White, T., Suwa, G., Simpson, S. & Asfaw, B. 2000 Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am. J. Phys. Anthropol.* **111**, 45–68. (doi:10.1002/(SICI)1096-8644(200001)111:1<45::AID-AJPA4>3.0.CO;2-I)
- White, T. *et al.* 2006 Asa Issie, Aramis and the origin of *Australopithecus*. *Nature* **440**, 883–889. (doi:10.1038/nature04629)
- White, T., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C., Suwa, G. & WoldeGabriel, G. 2009 *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* **326**, 75–86. (doi:10.1126/science.1175802)
- Wolpoff, M. 1969 The effect of mutations under conditions of reduced selection. *Soc. Biol.* **16**, 11–23.
- Wolpoff, M. H. 1978 Some aspects of canine size in the australopithecines. *J. Hum. Evol.* **7**, 115–126. (doi:10.1016/S0047-2484(78)80003-7)
- Wolpoff, M. H. 1979 Anterior dental cutting in the Laetolil hominids and the evolution of the bicuspid P3. *Am. J. Phys. Anthropol.* **51**, 233–234. (doi:10.1002/ajpa.1330510210)
- Wolpoff, M. 1980 *Paleoanthropology*. New York, NY: Knopf.