New hominin fossils from Kanapoi, Kenya, and the mosaic evolution of canine teeth in early hominins

Authors:
Fredrick K. Manthi[1]
J. Michael Plavcan[2]
Carol V. Ward[3]

Affiliations:
[1]Department of Earth Sciences, National Museums of Kenya, Nairobi, Kenya

[2]Department of Anthropology, University of Arkansas, Fayetteville, USA

[3]Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, USA

Correspondence to:
Carol Ward

Email:
wardcv@missouri.edu

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

Dates:
Received: 25 Apr. 2011
Accepted: 15 Sept. 2011
Published: 02 Mar. 2012

How to cite this article:
Manthi FK, Plavcan JM, Ward CV. New hominin fossils from Kanapoi, Kenya, and the mosaic evolution of canine teeth in early hominins. S Afr J Sci. 2012;108(3/4), Art. #724, 9 pages. http://dx.doi.org/10.4102/sajs.v108i3/4.724

Whilst reduced size, altered shape and diminished sexual dimorphism of the canine–premolar complex are diagnostic features of the hominin clade, little is known about the rate and timing of changes in canine size and shape in early hominins. The earliest *Australopithecus, Australopithecus anamensis,* had canine crowns similar in size to those of its descendant *Australopithecus afarensis*, but a single large root alveolus has suggested that this species may have had larger and more dimorphic canines than previously recognised. Here we present three new associated dentitions attributed to *A. anamensis*, recently recovered from the type site of Kanapoi, Kenya, that provide evidence of canine evolution in early *Australopithecus*. These fossils include the largest mandibular canine root in the hominin fossil record. We demonstrate that, although canine crown height did not differ between these species, *A. anamensis* had larger and more dimorphic roots, more like those of extant great apes and *Ardipithecus ramidus*, than those of *A. afarensis.* The canine and premolar occlusal shapes of *A. anamensis* also resemble those of *Ar. ramidus*, and are intermediary between extant great apes and *A. afarensis*. *A. afarensis* achieved *Homo*-like maxillary crown basal proportions without a reduction in crown height. Thus, canine crown size and dimorphism remained stable during the early evolution of *Australopithecus*, but mandibular root dimensions changed only later within the *A. anamensis*–*afarensis* lineage, coincident with morphological changes in the canine–premolar complex. These observations suggest that selection on canine tooth crown height, shape and root dimensions was not coupled in early hominin evolution, and was not part of an integrated adaptive package.

Introduction

One of the earliest derived features of the hominin clade is canine tooth size reduction, with a decrease in sexual dimorphism in canine crown height, and the loss of maxillary canine tooth 'honing' against the lower third premolar that occurs in most primate species. Canine tooth crown reduction was originally thought to have first appeared in *Australopithecus*,[1] but now is known to have characterised even earlier taxa – *Sahelanthropus*,[2] *Orrorin*,[3] *Ardipithecus kadabba*[4,5,6] and *Ardipithecus ramidus*.[7,8,9,10] However, the morphology of the *Australopithecus* canine–premolar complex is derived morphologically relative to these earlier hominins. Furthermore, canine tooth form appears to have changed throughout the early evolution of *Australopithecus*.[9,11,12] The pattern and timing of canine evolution is significant for understanding early hominin evolution because alterations in canine tooth size and dimorphism constitute evidence of social and/or dietary adaptations.[13,14]

The earliest member of the *Australopithecus*–human clade is *Australopithecus anamensis* (4.17 Ma – 3.9 Ma).[9,15,16,17,18] *A. anamensis* appears to represent the initial part of a lineage culminating in the better-known *Australopithecus afarensis* (3.77 Ma – 3.0 Ma).[9,11,19] Compared to *A. afarensis*, *A. anamensis* had larger canine basal crown dimensions relative to postcanine tooth size, more ape-like canine and premolar shapes, and altered topography of the maxilla and mandible in the regions of the canine juga.[11,16,17,18] The canine tooth crowns known for *A. anamensis* appear no more variable in their dimensions than those of either *A. afarensis*,[17,18] or *Ar. ramidus*,[7] which would seem to suggest that absolute canine crown height and breadth remained stable with minimal dimorphism throughout the origin and evolution of early *Australopithecus.*

However, a single large *A. anamensis* mandibular canine alveolus (KNM-KP 29287), and to some extent a large canine root with heavily worn crown from Fejej, Ethiopia (FJ-4-SB-1a),[20] has led to the suggestion that there may have been more canine sexual dimorphism early in this lineage than is represented in the fossil record of preserved canine tooth crowns.[17,18] This suggestion would be surprising, given that data from *Ardipithecus, Orrorin* and *Sahelanthropus* indicate that reduction in canine tooth crown height and breadth, as well as a decrease in dimorphism, are basal hominin traits.

The intermediate temporal position of *A. anamensis,* between the earlier *Ardipithecus, Orrorin* and *Sahelanthropus,* and *A. afarensis,* makes this species of great interest in documenting the rate and timing of changes in the canine–premolar complex. Whilst a gradual, integrated change in the complex[5,9] might suggest a single vector of selective change to integrate canine function with that of the incisors, a mosaic pattern of change[11] implies a pattern of sequential selective pressures and possible unappreciated functional diversity over time.

From 2003 to 2007, several new fossils attributed to *A. anamensis* were recovered from the type site of Kanapoi, Kenya by a team led by one of us (F.K.M.). The new Kanapoi hominin fossils include three partial, associated dentitions, each including a canine tooth (Figure 1; Table 1). All are from the lower fluvial sequence at the site, and are dated to between 4.195 Ma and 4.108 Ma.[21] There are two mandibular dentitions: KNM-KP 47951 is a mandibular canine with associated premolars and KNM-KP 47953 is a mandibular dentition preserving the right canine and premolars, along with the second and third molar. KNM-KP 47952 is a maxillary dentition with two maxillary canines and an incisor.

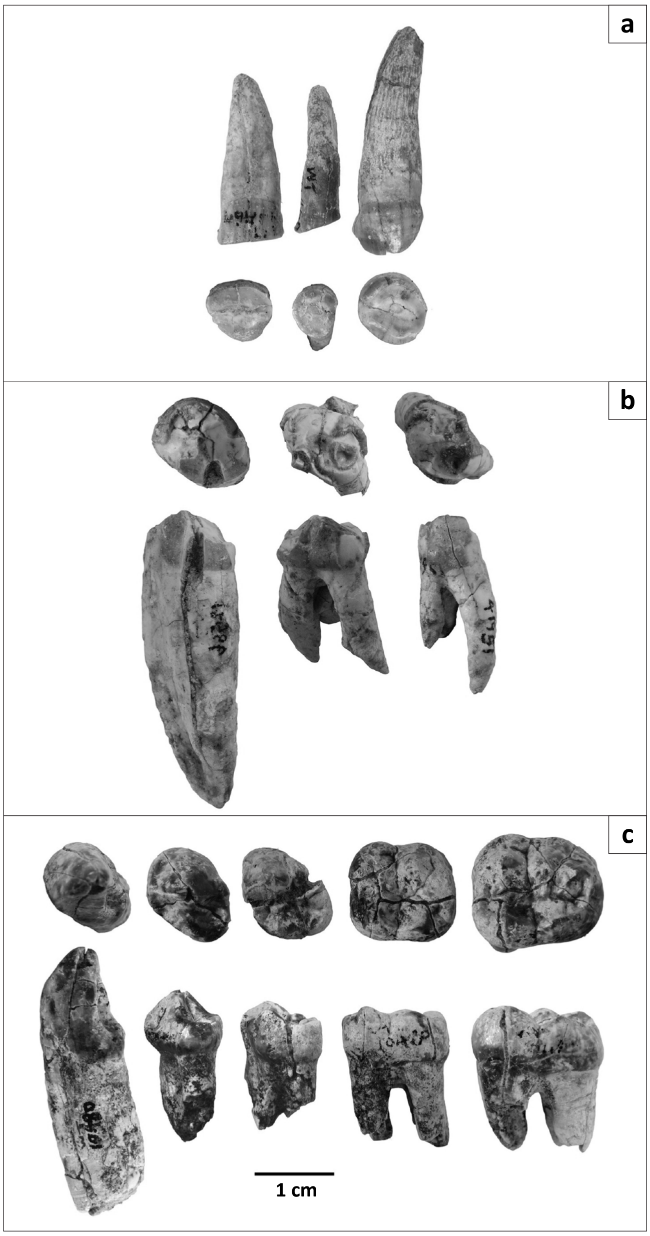
These fossils provide important new evidence of canine evolution in early *Australopithecus*. Here we present these fossils and consider their implications for understanding canine tooth evolution in early hominins.

Materials and methods

The newly discovered *A. anamensis* teeth were compared with those of extant great apes (*Gorilla gorilla n* = 25, *Pongo pygmaeus n* = 7, *Pan troglodytes n* = 15, *Pan paniscus n* = 17 and *Homo sapiens n* = 25) (Table 2), as well as *A. afarensis* (*n* = 11), previously described *A. anamensis* (*n* = 9) and *Ar. ramidus* (*n* = 6) (Table 3).

Linear data from fossils were taken on original Kenyan *A. anamensis* specimens by one of us (C.V.W.). *A. afarensis* data were kindly provided by William Kimbel and checked against measurements from casts taken by CVW to ensure consistency amongst data sets. Data for the Fejej fossils were taken by C.V.W. from casts kindly provided by John Fleagle and checked against the originals by C.V.W. *Ar. ramidus* data were taken from Suwa et al.[7] with supplementary data on crown heights kindly provided by Gen Suwa, Tim White and Berhane Asfaw (2009, personal communication, December 1), with the stipulation that the unpublished numbers are not for reproduction. Data for the Asa Issie *A. anamensis* specimens were taken from White et al.[9] and checked against the originals by C.V.W.

Maxillary canine basal dimensions are measured as 'mesiodistal' and 'buccolingual'. Morphologically, the maximum diameter of the canine embraces, or nearly embraces, the base of the mesial and distal crests of the tooth in most non-human primates. Because the human tooth is mesiodistally compressed relative to its



Scale = 1 cm.

FIGURE 1: New associated dentitions from Kanapoi, Kenya. All are comparable morphologically to other published specimens attributed to *Australopithecus anamensis* from Kanapoi, Asa Issie and Allia Bay. (a) KNM-KP 47952, labial and occlusal views: left I^{1-2} and C^x. (b) KNM-KP 47951, occlusal and lingual views: LC_x, RP_{3-4} shown, canine reversed for comparison. LP_3 and two tooth fragments not figured. These teeth are missing much of their enamel in places, and the canine crown is broken off. Despite the missing enamel, the large centrally placed protoconid of the P_3, the metaconid that existed mainly as a tubercle along a large lingual ridge, a small anterior fovea, and oblique occlusal profile are typical of other Kanapoi P_3s. Similarly, the cusp and basin morphology of the P_4 match those described for *A. anamensis* from Kanapoi. The premolar roots are widely splayed, but splaying is a variable characteristic of *Australopithecus*. The root morphology is typical of that of other early *Australopithecus* premolars with the double fused mesiobuccal root and independent lingual root. (c) KNM-KP 47953, occlusal and lingual views: RC_x-P_4, M_{2-3}. We attribute the molars to second and third because of the broad, centrally placed interstitial facet on the mesial face of the M_2, the distally elongate shape of the third and the matching contact facets. Tooth crowns are complete, but the roots are broken towards their tips. The distal third molar root is just completing formation. Although this specimen is amongst the larger *A. anamensis* fossils, even when it is included, *A. anamensis* mandibular canine crowns are equivalent in height and variation to those of *A. afarensis*. KNM-KP 47953 displays the blade-like morphology of the mandibular canine crown characteristic of *A. anamensis*, and indeed is among the most extreme specimens yet known in this regard. Similarly, its P_3 has the most centrally placed paraconid and the most ovoid crown outline of any discovered so far.

TABLE 1a: Dimensions (mm) of the newly discovered Kanapoi hominin maxillary dentition.

Dentition	Side	Incisor^1		Incisor^2		Canine		Molar^2	
		Mesiodistal	Buccolingual	Mesiodistal	Buccolingual	Mesiodistal	Buccolingual	Mesiodistal	Buccolingual
KNM-KP 47952	Left	9.1	8.5	6.3†	7.5	9.9	10.2	12.4	13.5

†, denotes the specimen measured had existing interstitial wear.

TABLE 1b: Dimensions (mm) of the newly discovered Kanapoi hominin mandibular dentitions.

Dentition	Side	Canine		Premolar$_3$		Premolar$_4$		Molar$_2$		Molar$_3$	
		Maximum	Minimum	Maximum	Minimum	Mesiodistal	Buccolingual	Mesiodistal	Buccolingual	Mesiodistal	Buccolingual
KNM-KP 47951	Right	-	-	13.1‡	10.1	9.3‡	13.2‡	-	-	-	-
KNM-KP 47951	Left	13.9	10.7	13.7‡	9.8‡	-	-	-	-	-	-
KNM-KP 47953	Right	12.0	10.1	12.8	9.4	9.4‡	12.8‡	13.8	12	16.8	15.1
KNM-KP 47953	Left	-	-	-	-	-	-	-	-	16.7‡	15.2‡

‡, reflects an estimated value of original tooth size.

buccolingual diameter, the maximum diameter of the tooth is not homologous to its mesiodistal dimensions, as in other species. However, mandibular canine basal dimensions are presented using 'maximum' and 'minimum' (being the greatest dimension perpendicular to the maximum) diameters, because, in hominins, the relative position of the tubercles are not located at the mesial and distal margins of the tooth. The same definitions apply to the mandibular canine measurements for non-human primates. Similarly, because the P_3 is normally oriented obliquely relative to the tooth row, basal dimensions of the P_3 are also measured as maximum and minimum in all human and non-human primates.

We measured all available crown heights for *A. anamensis* and *A. afarensis* (Table 4). For many primates, wear is a normal and necessary part of canine function, and in some species the apex of the tooth is worn before the tooth is finished erupting. Canine crown height data from Plavcan[23] for 89 extant primates demonstrate that 'moderately worn' (teeth showing some blunting of the apex) and unworn canines do not significantly differ in crown height.[24] Given that the criteria used for excluding worn canines for this study were more stringent than for the Plavcan[23] data set, apical wear had no significant impact on our results. Here, we did not correct for wear, but have noted those teeth that clearly show apical blunting. Whilst including worn specimens slightly depresses the mean canine height for the hominin sample, and increases the variance, the overall change in variation and the range of crown height is small by comparison to interspecific differences in canine size. Even adding several millimeters to canine dimensions for worn teeth will not affect the results of this study. Given that the canine crowns of *A. anamensis* and *A. afarensis* were measured by us in the same way, the interspecific differences in canine size are robust, and our conclusions would not be altered by attempting to estimate the unworn size of the canine teeth.

Canine data for *Ar. ramidus* were, as reported to us, 'corrected' for wear and damage. Having not studied the original specimens, we cannot quantify whether the measurements are exactly comparable to ours or not. Nevertheless, restricting crown height comparisons to only unworn teeth does not alter any of our results and conclusions. Here we report only the results for the entire sample. Therefore, conclusions drawn from comparisons between the *Ardipithecus* and *Australopithecus* canine crown heights appear to be robust.

Standard parametric and non-parametric statistical tests were used for most comparisons, as noted where appropriate. To compare the range of variation in root length between hominins and extant apes and *Homo*, a bootstrap analysis was carried out using a program written in Matlab.[25] For each fossil taxon comparison, 1000 random samples from each extant taxon were selected with replacement, and without regard to sex, selecting the same number of specimens as available for the fossil sample. The number of samples with a range equal to or exceeding that of the fossil sample was tabulated.

To evaluate basal canine shape proportions, we used the SMATR[26] software package to test for differences in both slope and elevation of reduced major axis lines fit through ln-transformed mesiodistal and buccolingual canine tooth dimensions amongst all extant ape species, *A. anamensis* and *A. afarensis*, using 1000 iterations (following Wharton et al.[27]). To confirm these results, we also performed a least-squares regression through ln-transformed canine mesiodistal versus buccolingual dimensions of apes only. We calculated the analysis of variance of residuals for extant hominoids, *A. anamensis* and *A. afarensis* derived from this least-squares regression, using Tukey's honestly significantly different two-tailed tests for post-hoc contrasts between groups at an alpha level of 0.05. In no case did the results differ from the SMATR results, so only results from the latter analysis are reported here as they are statistically most appropriate.[27]

Results

KNM-KP 47951 has a strikingly large and robust mandibular canine root that is the largest known for any early hominin, in length, cervical dimensions and volume (Figure 2). The KNM-KP 47951 canine root is substantially larger than the alveolus for KNM-KP 29287, which was sufficiently large to suggest greater canine size and variation in *A. anamensis* compared with all later hominins.[17,18] KNM-KP 47951 demonstrates that neither KNM-KP 29287 nor FJ-4-SB-1a have unusually large canines, nor would KNM-KP 29287 even have belonged to a particularly large male individual. The large root of KNM-KP 47951 increases the observed range of variation in length and occlusal dimensions in *A. anamensis* canine teeth, and so

TABLE 2a: Descriptive statistics for extant ape and human maxillary canine teeth used in this analysis.

Species	Quantity	Male specimens						Female specimens					
		UCH	UCMD	UCBL	UCRMD	UCRBL	UCRL	UCH	UCMD	UCBL	UCRMD	UCRBL	UCRL
Gorilla gorilla	*N*	25	25	25	25	25	25	25	25	25	25	25	25
	Mean	28.3	20.1	16.3	19.2	16.3	45.9	15.9	14.3	11.5	12.5	10.8	34.9
	Minimum	17.7	17.1	13.6	14.8	13.4	34.3	12.1	12.5	10.3	10.8	9.8	25.4
	Maximum	41.6	23.2	22.1	22.9	20.0	54.9	19.1	16.3	13.8	15.7	13.2	41.3
	Range	23.9	6.1	8.5	8.0	6.6	20.6	7.0	3.8	3.5	4.9	3.4	15.9
	Standard deviation	5.45	1.72	1.69	1.92	1.49	5.23	1.61	1.08	0.95	1.09	0.89	3.69
Pongo pygmaeus	*N*	7	7	7	7	7	6	11	11	11	11	11	10
	Mean	27.1	17.9	14.2	17.7	14.1	35.0	15.7	12.8	10.3	11.0	9.8	24.9
	Minimum	22.1	16.3	13.1	16.1	13.2	25.9	12.7	11.1	8.1	10.2	8.0	16.9
	Maximum	30.5	18.6	15.4	18.9	15.4	38.5	20.6	15.4	12.5	13.3	11.9	28.7
	Range	8.3	2.3	2.4	2.79	2.2	12.6	7.9	4.3	4.4	3.2	3.9	11.8
	Standard deviation	2.75	0.86	0.85	1.03	0.89	4.90	1.98	1.08	1.10	0.88	1.00	4.37
Pan troglodytes	*N*	15	15	15	15	15	15	15	15	15	15	15	15
	Mean	21.1	14.6	11.9	14.1	11.8	37.8	15.0	11.0	9.2	9.8	8.9	27.5
	Minimum	17.2	12.5	10.3	12.7	10.1	29.8	11.9	9.6	8.1	7.6	7.5	18.8
	Maximum	27.3	19.3	14.3	17.3	14.6	46.4	22.2	14.4	12.6	13.5	12.4	33.3
	Range	10.1	6.8	4.0	4.6	4.5	16.6	10.4	4.8	4.5	5.9	4.9	14.5
	Standard deviation	2.64	1.62	1.2	1.44	1.28	3.83	2.53	1.12	1.10	1.32	1.30	3.58
Pan paniscus	*N*	12	17	17	-	-	-	12	13	13	-	-	-
	Mean	15.6	11.4	8.8	-	-	-	11.2	9.4	6.9	-	-	-
	Minimum	10.4	9.1	7.1	-	-	-	8.6	8.6	6.1	-	-	-
	Maximum	20.4	14.4	11.1	-	-	-	14.8	10.3	7.9	-	-	-
	Range	10.0	5.3	4.0	-	-	-	6.1	1.6	1.8	-	-	-
	Standard deviation	3.48	1.49	1.33	-	-	-	1.71	0.55	0.49	-	-	-
Homo sapiens	*N*	25	25	25	25	25	25	25	25	25	25	25	25
	Mean	9.5	7.7	8.6	6.1	8.3	18.8	9.1	7.3	7.9	5.4	7.4	17.6
	Minimum	6.6	6.4	7.1	4.8	6.9	14.8	6.5	6.0	6.6	4.3	6.4	14.2
	Maximum	12.3	8.5	9.8	6.6	9.5	24.9	11.0	8.2	9.2	6.0	8.4	20.7
	Range	5.7	2.1	2.7	1.8	2.6	10.0	4.5	2.2	2.7	1.7	2.0	6.5
	Standard deviation	1.34	0.51	0.61	0.46	0.60	2.36	1.09	0.57	0.61	0.40	0.58	1.84

Sources: All data were collected by the authors, except data for *Pan paniscus*, which were taken from Plavcan[23].

All measurements are in millimetres.

U, maxillary (upper); C, canine; H, crown height; MD, crown mesiodistal diameter; BL, crown buccolingual diameter; RMD, root mesiodistal diameter; RBL, root buccolingual diameter; RL, root length.

TABLE 2b: Descriptive statistics for extant ape and human mandibular canine teeth used in this analysis.

Species	Quantity	Male specimens						Female specimens					
		LCH	LCmax	LCmin	LCRmax	LCRmin	LCRL	LCH	LCmax	LCmin	LCRmax	LCRmin	LCRL
Gorilla gorilla	*N*	25	25	25	25	25	25	25	25	25	25	25	25
	Mean	25.7	18.0	14.5	17.9	14.1	35.7	16.1	13.1	10.4	12.5	9.7	30.7
	Minimum	19.3	14.8	11.7	14.5	11.9	30.9	12.7	11.5	9.2	11.1	8.7	22.0
	Maximum	31.3	21.7	16.3	21.4	16.0	45.3	19.9	14.7	12.8	13.9	12.3	35.7
	Range	12.0	6.9	4.6	6.9	4.2	14.4	7.2	3.2	3.6	2.7	3.6	13.6
	Standard deviation	3.18	1.67	1.13	1.76	1.05	3.59	1.57	0.88	0.83	0.74	0.81	2.94
Pongo pygmaeus	*N*	7	7	7	7	7	6	9	10	10	10	10	10
	Mean	23.6	15.8	13.3	15.6	12.9	33.5	16.3	12.4	8.5	11.8	8.2	24.0
	Minimum	21.5	12.8	12.0	12.3	11.6	28.7	13.6	11.1	8.0	10.2	7.4	20.3
	Maximum	26.8	17.8	14.5	17.5	14.2	41.0	20.3	14.7	9.8	13.6	9.8	30.6
	Range	5.3	5.0	2.5	5.2	2.6	12.3	6.8	3.7	1.8	3.4	2.4	10.3
	Standard deviation	1.81	1.57	0.98	1.63	0.87	4.81	1.99	1.07	0.55	1.01	0.71	3.42
Pan troglodytes	*N*	15	15	15	15	15	15	15	15	15	15	15	15
	Mean	20.2	14.1	12.0	13.9	11.6	32.5	15.1	11.5	9.9	10.5	9.3	24.7
	Minimum	16.3	12.3	9.8	12.1	10.2	27.6	12.5	10.1	8.0	8.2	7.6	20.0
	Maximum	25.5	17.2	15.2	16.9	14.9	38.0	21.3	14.5	12.8	13.9	12.2	31.0
	Range	9.2	4.9	5.4	4.8	4.7	10.4	8.8	4.4	4.8	5.7	4.6	11.0
	Standard deviation	2.34	1.36	1.50	1.40	1.29	3.56	2.56	1.44	1.40	1.60	1.40	2.63
Pan paniscus	*N*	15	16	16	-	-	-	14	14	14	-	-	-
	Mean	13.5	10.4	7.7	-	-	-	10.9	8.9	6.5	-	-	-
	Minimum	10.5	8.9	6.5	-	-	-	9.5	7.9	5.9	-	-	-
	Maximum	16.1	11.9	9.1	-	-	-	13.6	10.0	7.3	-	-	-
	Range	5.6	3.0	2.6	-	-	-	4.1	2.1	1.4	-	-	-
	Standard deviation	1.86	1.05	0.76	-	-	-	1.12	0.62	0.48	-	-	-
Homo sapiens	*N*	18	18	18	18	18	18	18	18	18	18	18	18
	Mean	10.5	8.1	7.0	7.9	5.7	16.9	9.5	7.2	6.5	7.0	5.0	15.0
	Minimum	7.9	7.1	5.6	7.0	5.0	13.0	7.7	5.9	5.5	5.8	3.7	10.9
	Maximum	12.7	9.1	7.9	9.0	6.6	20.2	11.2	8.3	7.3	7.7	5.7	17.3
	Range	4.7	2.0	2.3	2.0	1.6	7.2	3.5	2.3	1.8	1.9	2.0	6.3
	Standard deviation	1.28	0.57	0.61	0.59	0.58	2.11	0.96	0.56	0.56	0.42	0.43	1.81

Sources: All data were collected by the authors, except data for *Pan paniscus*, which were taken from Plavcan[23].

All measurements are in millimetres.

L, mandibular (lower); C, canine; H, crown height; max, maximum crown diameter; min, minimum crown diameter; RL, root length.

TABLE 3: Descriptive statistics for fossil hominin canine teeth used in this analysis.

Species	Quantity	Maxillary canines						Mandibular canines					
		UCH	UCMD	UCBL	UCRMD	UCRBL	UCRL	LCH	LCmax	LCmin	LCRmax	LCRmin	LCRL
Australopithecus afarensis	*N*	8	13	13	7	7	7	6	11	7	9	10	3
	Mean	12.4	10.8	9.8	9.6	7.1	22.8	13.1	10.8	8.4	10.1	7.4	22.8
	Minimum	9.2	9.3	8.8	7.2	6.2	18.8	10.9	9.0	6.9	8.8	5.8	21.0
	Maximum	15.4	12.5	11.6	10.9	8.2	28.1	17.0	13.9	10.6	11.5	9.5	24.3
	Range	6.2	3.2	2.8	3.7	2.0	9.3	6.1	4.9	3.7	2.7	3.7	3.3
	Standard deviation	2.18	0.91	0.83	1.38	0.63	3.71	2.22	1.41	1.42	0.95	1.02	1.67
Australopithecus anamensis	*N*	3	7	8	4	4	3	3	7	7	8	9	3
	Mean	14.4	10.2	11.1	10.0	8.7	25.6	13.3	11.0	8.8	10.4	8.0	26.7
	Minimum	12.0	8.8	9.9	9.0	7.9	23.3	10.0	9.0	6.6	8.2	5.9	20.3
	Maximum	16.0	11.2	12.4	10.9	10.0	28.4	15.7	13.9	10.4	13.8	10.3	31.8
	Range	4.0	2.4	2.5	1.9	2.1	5.1	5.7	4.9	3.8	5.6	4.4	11.6
	Standard deviation	2.12	0.75	0.82	1.04	0.95	2.60	2.94	1.66	1.32	1.72	1.43	5.99
Ardipithecus ramidus	*N*	4	8	9	9	8	6	2	4	5	6	6	4
	Mean	u.p.	u.p.	11.3	8.5	11.0	28.7	u.p.	u.p.	11.2	10.8	8.2	26.9
	Minimum	u.p.	u.p.	9.9	7.4	9.8	24.5	u.p.	u.p.	10.3	9.8	7.2	25.0
	Maximum	u.p.	u.p.	12.2	9.3	12.2	34.9	u.p.	u.p.	12.1	12.2	9.5	31.4
	Range	u.p.	u.p.	2.3	1.9	2.4	10.4	u.p.	u.p.	1.8	2.4	2.3	6.4
	Standard deviation	u.p.	u.p.	0.65	0.73	0.71	3.89	u.p.	u.p.	0.77	0.94	0.88	3.03

Sources: Data include published and new fossils. *Ardipithecus* measurements are provided for published specimens from Suwa et al.[7] and from Suwa, White and Asfaw, who kindly provided unpublished data on crown heights and buccolingual dimensions. Unpublished data (u.p.) were loaned with the stipulation that they not be published here, but they are included in the figures and analyses.

All measurements are in millimetres.

U, maxillary (upper); L, mandibular (lower); C, canine; H, crown height; MD, crown mesiodistal diameter; BL, crown buccolingual diameter; RMD, root mesiodistal diameter; RBL, root buccolingual diameter; RL, root length; max, maximum crown diameter; min, minimum crown diameter.

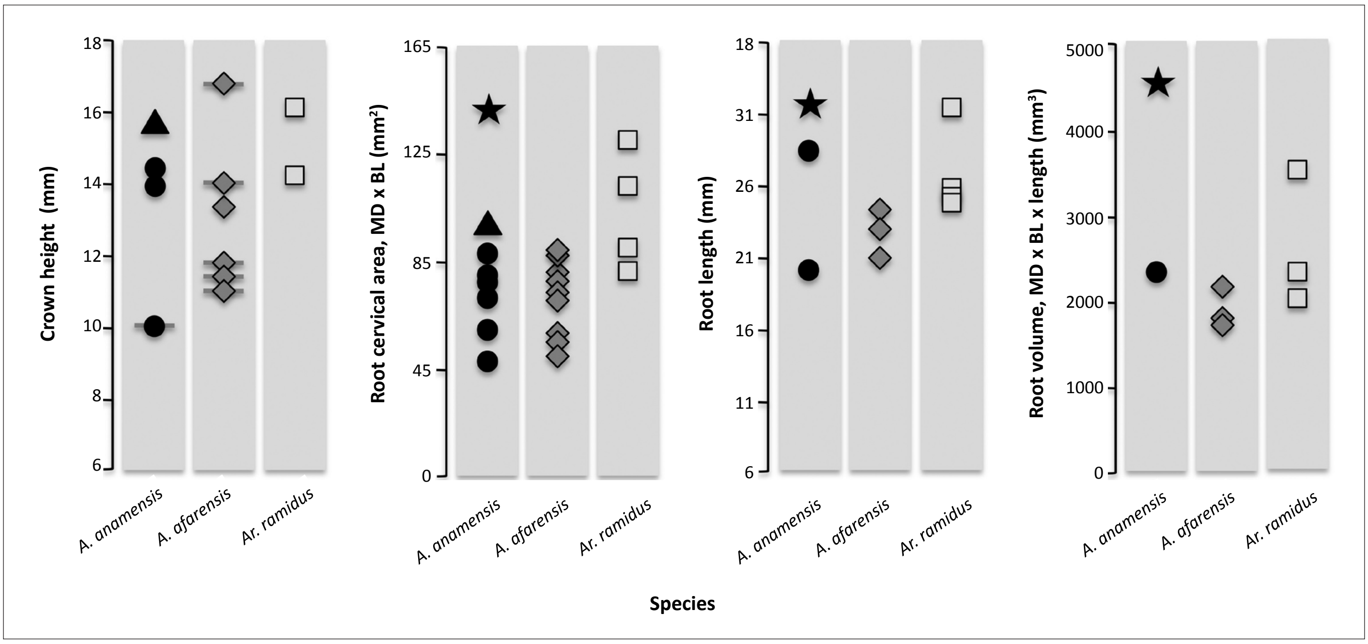
TABLE 4: Listing of canine crown heights for specimens used in this analysis, with an assessment of wear.

Dentition type	Species	Dentition	Crown height (mm)	Apical wear
Maxillary	*Australopithecus afarensis*	A.L. 199-1	9.2	Worn, strong blunting wear
		A.L. 200-1a	12.7	Worn, moderate blunting wear, not as strong as LH 5
		A.L. 333-2	10.2	Worn, strong blunting wear
		A.L. 333X-3	15.4	Slight blunting, tip sharp from convergent facets
		A.L. 400-1b	12.5	Worn, moderate blunting, dentine exposed
		LH 3	14.2	Unworn
		LH 5	10.6	Worn, moderate blunting wear
		LH 6	14.0	Very slight apical wear
	Australopithecus anamensis	KNM-KP 35839	15.2	Unworn
Mandibular	*Australopithecus afarensis*	A.L. 198-1	10.9	Worn, moderate blunting, dentine exposed
		A.L. 333-90	11.5	Worn, strong blunting wear
		A.L. 333w-58	17.0	Worn, strong blunting wear, crown fractured
		A.L. 400-1a	12.0	Worn, moderate blunting
		LH 3	13.3	Unworn
		BMNH 18773	14.0	Worn, moderate wear, hard to assess because of chipped enamel
	Australopithecus anamensis	KNM-ER 30731	10.0	Worn, strong blunting wear
		KNM-KP 29284	14.1	Unworn, crown nearly complete, no root
		KNM-KP 29286	14.5	Slight apical wear
		KNM-KP 47953	15.7	Slight apical wear

also in overall size (Figure 2). It is far greater in length and size than any *A. afarensis* specimen. Long, large mandibular canine roots also are seen in *Ar. ramidus* (9) and extant great apes, suggesting that this is a primitive trait for the hominin clade (Figure 2).

Even though sample sizes of complete root lengths are small, *A. anamensis* has greater variation than minimally dimorphic *Homo* (Figure 2; Table 5). *A. afarensis* and *Ar. ramidus* root length variation, by contrast, is minimal, although too few specimens are preserved with which to assess degrees of variation in either species. Mandibular root size in both *A. anamensis* and *Ar. ramidus* is similar, and both are substantially greater than *A. afarensis*. There is no overlap in mandibular root volume between *A. anamensis* and *A. afarensis* (Figure 2). In combination, the data suggest a decline in mandibular root size from the primitive size in *A. anamensis* to a derived condition in *A. afarensis*.

The canine crown of the other new mandibular dentition, KNM-KP 47953, supports the observation that although canine crowns were not absolutely taller or broader in *A. anamensis* than in *A. afarensis* (11, 16, 17, 18), *A. anamensis* canines have larger basal dimensions relative to the size of their postcanine teeth (Figure 3). This shift in relative size ratios apparently continues a general trend seen when comparing *Ar. ramidus* to *Australopithecus*, and at least partly reflects increasing postcanine tooth size.[7,9,13]



Sources: Data for *Ardipithecus ramidus* crown heights provided by Gen Suwa, Tim White and Berhane Asfaw. Data for *Ar. ramidus* roots from White et al.[9]
MD, mesiodistal; BL, buccolingual.

FIGURE 2: Crown height, root cervical area (calculated as maximum x minimum diameters), root length and an estimate of root volume (calculated as root cervical area x length) for mandibular canines. Black symbols represent *Australopithecus anamensis*, circles represent previously known specimens, stars represent KNM-KP 47951 and triangles represent KNM-KP 47953. Grey diamonds represent *Australopithecus afarensis* specimens (bars through points indicate moderately worn to worn crowns). Squares represent *Ardipithecus ramidus* specimens. Crown height is similar in both *Australopithecus* species, but root length is smaller and less variable in *A. afarensis*.

TABLE 5: Results from a bootstrap analysis of mandibular root length variation tabulating how often a randomly drawn sample from an extant species shows a range matching or exceeding that of each fossil hominin sample.

First species	Second species	*N* exceeding fossil sample	Percentage (of 1000)
Australopithecus anamensis	*Homo sapiens*	49	4.9
	Pongo pygmaeus	179	17.9
	Pan troglodytes	140	14.0
	Gorilla gorilla	37	3.7
Australopithecus afarensis	*Homo sapiens*	706	70.6
	Pongo pygmaeus	869	86.9
	Pan troglodytes	823	82.3
	Gorilla gorilla	619	61.9
Ardipithecus ramidus	*Homo sapiens*	623	62.3
	Pongo pygmaeus	836	83.6
	Pan troglodytes	827	82.7
	Gorilla gorilla	581	58.1

N, the number of random samples from 1000 iterations, each drawing a sample the same size as that for the fossils (*A. afarensis n* = 3, *A. anamensis n* = 3, *Ar. ramidus n* = 4) from mixed-sex samples of each extant species that matched or exceeded the range for the fossil taxon.

Together, KNM-KP 47951 and KNM-KP 47953, along with previously known specimens, suggest that mandibular canine crown height, breadth and root size variation were not coupled in early *Australopithecus*. Specifically, the new specimens suggest that whilst canine crowns appear to have reduced in height and dimorphism prior to the appearance of the genus *Australopithecus*,[5,7] root size and variation decreased within the *A. anamensis–afarensis* lineage independently of crown dimensions. Thus, the apparently large alveolus of KNM-KP 29287 reflects the relatively large roots in the earlier species, and not greater canine crown size as previously hypothesised.[17,18]

Preserved *A. anamensis* and *A. afarensis* fossils do not differ in relative maxillary canine basal crown and root size, but all four *A. afarensis* specimens are small, suggesting that they may be female individuals, thereby obscuring comparisons. Maxillary canine crown shape does differ as part of an overall shift in morphology of the C–P_3 complex during the evolution of *A. anamensis* into *A. afarensis*.[5,7,8,9,11,19] KNM-KP 47952 demonstrates the previously documented *A. anamensis* condition of having mesiodistally longer maxillary crowns and roots than does *A. afarensis* (Figure 4a; Table 6) (see also Leakey et al.[15] and Ward et al.[18]). Notably, *A. anamensis* is nearly identical to *Ar. ramidus* in the absolute size and occlusal proportions of the maxillary canines, but both differ from *A. afarensis*, which has a shape equivalent to that of the more diminutive human canines (Figure 4a; Tables 2 and 3). Thus, *A. anamensis* retained the primitive condition, and shape change occurred during the evolution of *A. afarensis*.

Accompanying this shift in maxillary canine crown proportions, mesial crest length reduced as a function of the mesial shoulder of the tooth shifting apically[5,7,9,11]

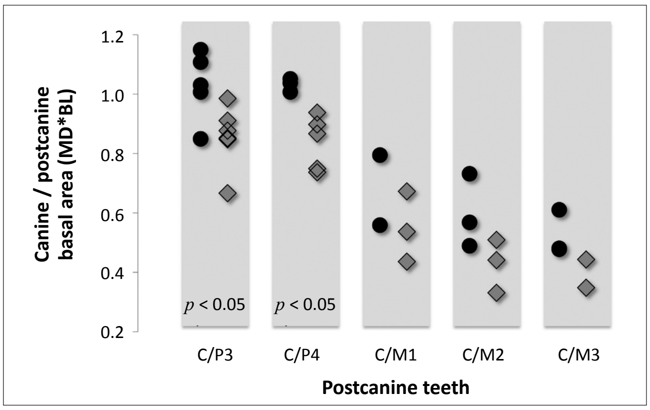


FIGURE 3: Mandibular canine crown basal area (computed as maximum x minimum diameters) divided by basal area for each postcanine tooth (maximum x minimum for P_3, mesiodistal (MD) x buccolingual (BL) for P_4–M_3). Black circles represent *Australopithecus anamensis* and grey diamonds represent *A. afarensis*. Canines tend to be larger relative to the postcanine dentition in *A. anamensis* than in *A. afarensis*; the differences are only statistically significant for the canine compared to the premolars ($p < 0.05$, two-tailed Kruskal Wallis test for both comparisons: C–P_3, $n = 10$, $p = 0.045$: C–P_4, $n = 8$, $p = 0.025$), but the trend is the same for all teeth.

(Figure 4b). This change mirrors the broadening of the mandibular canine, which also experienced morphological alterations through time, becoming less blade-like. Additionally, the mandibular premolar transformed, with the protoconid shifting buccally, affecting the fovea form, and the metaconid expanded in size.[11,17,19]

Metric changes in basal shape from *A. anamensis* to *A. afarensis* occurred in the maxillary canine and mandibular premolar, the honing pair, but not in the mandibular canine or maxillary premolar (Figure 4c). This shape change reflects change in C–P_3 function, increasing transverse contact area between maxillary and mandibular teeth, most logically due to increased use of the canine in food acquisition or preparation. This shape change suggests that any associated change in function occurred between *A. anamensis* and *A. afarensis*, and not with the origin of *Australopithecus*. Also, it is now clear that shape changes in the canine–premolar complex did not accompany selection for reduced canine crown height, which was already diminished in earlier hominins (*Ardipithecus*, *Orrorin* and *Sahelanthropus*).[2,4,6,9]

Discussion

Canine crown reduction is one of the hallmarks of hominin evolution and so plays an important role in identifying potential adaptive changes at the origins of the clade. Multiple hypotheses have been put forward to explain canine reduction amongst hominins in general, including the loss of canine teeth as weapons, dental crowding and selection altering the canines for food ingestion and/or processing.[13,22,28,29,30,31,32,33] Hypotheses concerning the co-option of the canine for food processing or gathering either implicitly or explicitly link canine reduction directly to selection for a change in dietary function. Furthermore, whilst large canine roots have been noted in early hominins, the relationship between root and crown reduction (and dimorphism) has not been evaluated.

These new *A. anamensis* fossils help demonstrate that whilst canine tooth size reduction probably occurred basally in

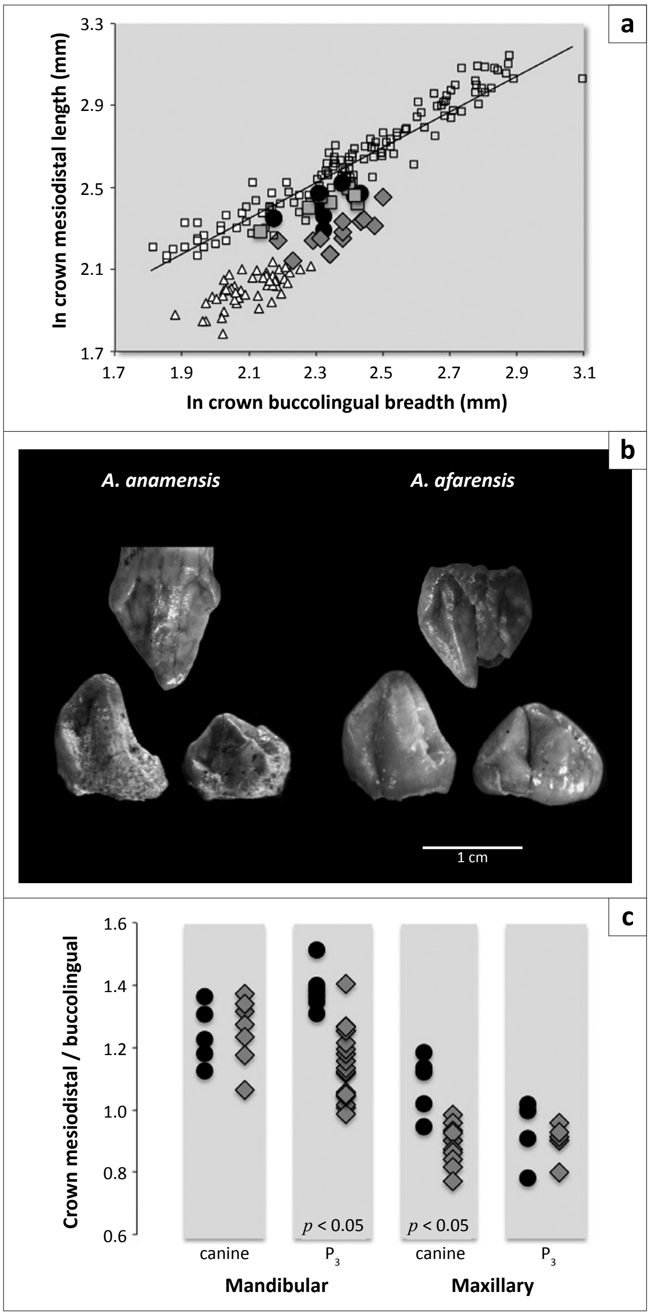


FIGURE 4: (a) Scatter plot of ln-transformed maxillary canine mesiodistal length compared to buccolingual breadth in extant and fossil samples. White squares represent extant great apes *(Pan troglodytes, Pan paniscus, Gorilla gorilla* and *Pongo pygmaeus*); white triangles represent *Homo sapiens;* black circles represent *Australopithecus anamensis*; grey diamonds represent *A. afarensis* and grey squares represent *Ardipithecus ramidus*. *A. afarensis* canines are similar in buccolingual size to *A. anamensis*, but are clearly mesiodistally shorter than those of *A. anamensis*. *A. afarensis* canines are proportionally identical to humans but humans are smaller overall, with almost no overlap in size with *A. afarensis*. (b) Morphological differences in canines and third premolars (5, 9, 11, 17, 18). The maxillary canines of *A. anamensis* have a lower mesial shoulder and are more symmetrical than those of *A. afarensis* (*A. afarensis* maxillary canine reversed for comparison). In the mandibular teeth, *A. anamensis* has a lower mesial crown shoulder and longer mesial crest, a narrower, more blade-like mandibular crown with pronounced distal tubercle and a more unicuspid P_3 with centrally placed paraconid compared with *A. afarensis.* (c) Crown basal proportions measured as mesiodistal ÷ buccolingual diameters for maxillary canine and P^3, maximum ÷ minimum breadths for mandibular canine and P_3. Black circles represent *A. anamensis* and grey diamonds represent *A. afarensis*. Interspecific differences are seen only in the maxillary canine ($p = 0.001$, two-tailed Kruskal Wallis test, $n = 19$) and mandibular premolar ($p < 0.001$, two-tailed Kruskal Wallis test, $n = 26$), that is, in the teeth that hone, but not in the mandibular canine ($p = 0.529$, two-tailed Kruskal Wallis test, $n = 16$) or maxillary premolar ($p = 0.44$, two-tailed Kruskal Wallis test, $n = 13$), illustrating that observed shape changes are associated with a shift in occlusal relationships in this complex.

TABLE 6a: Results for tests in elevation for reduced major axis regressions of all apes and hominins comparing maxillary canine mesiodistal (dependent) versus maxillary canine buccolingual (independent) dimensions: Post-hoc multiple comparisons for pair-wise differences in elevation between groups.

Species	*Gorilla gorilla*	*Pongo pygmaeus*	*Pan troglodytes*	*Pan paniscus*	*Homo*	*Australopithecus afarensis*	*Australopithecus anamensis*
Gorilla gorilla	1	-	-	-	-	-	-
Pongo pygmaeus	948	1	-	-	-	-	-
Pan troglodytes	0.068	0.031	1	-	-	-	-
Pan paniscus	0.21	0.159	0.001	1	-	-	-
Homo	< 0.001	< 0.001	< 0.001	< 0.001	1	-	-
Australopithecus afarensis	< 0.001	< 0.001	< 0.001	< 0.001	0.424	1	-
Australopithecus anamensis	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	1
Ardipithecus ramidus	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.704

TABLE 6b: Results for tests in slope for reduced major axis regressions of all apes and hominins comparing maxillary canine mesiodistal (dependent) versus maxillary canine buccolingual (independent) dimensions: Post-hoc tests for shift along the common slope.

Species	*Gorilla gorilla*	*Pongo pygmaeus*	*Pan troglodytes*	*Pan paniscus*	*Homo*	*Australopithecus afarensis*	*Australopithecus anamensis*
Gorilla gorilla	1	-	-	-	-	-	-
Pongo pygmaeus	0.003	1	-	-	-	-	-
Pan troglodytes	< 0.001	0.022	1	-	-	-	-
Pan paniscus	< 0.001	< 0.001	< 0.001	1	-	-	-
Homo	< 0.001	< 0.001	< 0.001	< 0.001	1	-	-
Australopithecus afarensis	< 0.001	< 0.001	0.002	0.002	< 0.001	1	-
Australopithecus anamensis	< 0.001	< 0.001	0.067	< 0.001	< 0.001	0.264	1
Ardipithecus ramidus	< 0.001	< 0.001	0.128	< 0.001	< 0.001	0.13	0.742

Analyses were carried out using SMATR,[26] using 1000 iterations, ln-transformed data.
There were no significant differences amongst slopes ($p = 0.394$, $t = 7.20$, two-tailed test).

hominin evolution prior to the evolution of *Australopithecus*, changes in canine shape, in both crowns and roots, occurred in a mosaic fashion throughout the *A. anamensis–afarensis* lineage. Whatever selective pressure led to canine tooth crown size reduction in human evolution did not occur at the same time as that leading to tooth crown shape change. This finding suggests, in turn, that multiple independent factors altered the complex over time. These phenomena, therefore, appear to have been a result of different pressures. These pressures, in turn, suggest at least the possibility that the canines of australopithecines may have served a different function from those of either their ancestors or their descendants.

Canine crown size and dimorphism were already reduced in all earlier hominins (*Ardipithecus*, *Sahelanthropus* and *Orrorin*) prior to the appearance of *Australopithecus*,[7,8] suggesting that the ancestor of *Australopithecus* probably had reduced crown size and dimorphism as well. However, substantial shape change did not accompany this crown height reduction. This observation stands in contrast to the hypothesis that shape changed in association with crown height reduction and incorporation of the tooth into an incisal functional field.[13] The short canine crowns imply that canines no longer played a role as weapons for intrasexual or intraspecific aggression early in hominin evolution. It follows that changes in canine shape almost certainly do not signal changes in social behaviour in later hominins.

Therefore, further alterations in canine shape within early *Australopithecus* by default probably reflect changes in food processing. Shorter canine crowns also did not accompany a shift towards thicker tooth enamel and enhanced mastication with the origins of *Australopithecus*. Rather, canine crown reduction in earlier hominins likely exapted the canines to serve a unique, derived function in *Australopithecus*, probably in food acquisition and/or processing. The development of the mesial cristid, which contacts the lateral maxillary incisor, and the elevation of the shoulders of the maxillary canine accompanies the shift in canine occlusal shape in *Australopithecus*, strongly suggesting a dietary function of the canines.[13] However, the lack of simultaneous canine size reduction suggests that this change did not reflect a gradual integration of the canine into an integrated anterior incisal mechanism. Rather, it suggests a dietary function unique to *Australopithecus*, and not simply human-like. Unfortunately, little is known about anterior tooth use and function in early hominins. Recent work suggesting similar overall diets in *A. anamensis* and *A. afarensis* is based on molar morphology and microwear.[34] These data demonstrate that the diets of both species involved heavy mastication of tough food items with similar material properties, but do not address possible variation in incision or ingestion behaviours, nor do they provide evidence of canine use, which may have differed. To date, evidence of canine use in early hominin canines, such as with microwear, has not been evaluated.

The addition of the new fossils of *A. anamensis* presented here reveals a dissociation of canine root morphology that appears to have accompanied morphological shifts in the C–P$_3$ complex, but not canine crown height reduction. Canine tooth root size likely accounts, at least in part, for the inflated anterolateral margins of the mandible seen in *A. anamensis* as compared with *A. afarensis*, in which the canines are set directly anterior to the postcanine tooth rows in *A. anamensis*, but more medially in *A. afarensis*. Relatively large canine roots may also contribute to the inflated canine jugal area and rounded lateral nasal aperture seen in *A. anamensis* and possibly the earliest *A. afarensis* (Garusi 1).[17] These changes in facial and mandibular form, which may in turn affect masticatory biomechanics, may be spatially linked to the reduction in canine root size and dimorphism. Unfortunately, little is known about the functional significance of variation in canine root size or morphology. At the least, these results suggest that crown and root size are not tightly integrated functionally.

The new Kanapoi fossils underscore the complex, mosaic nature of evolution in the hominin canine honing complex during early hominin evolution, and highlight new questions about hominin dentognathic adaptations. Identifying the order and timing of these morphological and proportional changes provides a basis for developing accurate hypotheses to explain the selective factors acting on crown height, crown shape and root dimensions in *Australopithecus* that will play a key role in understanding the adaptive transition from *A. anamensis* to *A. afarensis*.

Acknowledgements

We thank the curators and staff of the National Museums of Kenya, National Museum of Ethiopia, Turkana Basin Institute, Cleveland Museum of Natural History, National Museum of Natural History and Royal Museum of Central Africa for access to collections in their care and assistance. We would also like to thank Gen Suwa, Tim White, Berhane Asfaw and William Kimbel for data and access to original fossils; John Fleagle and William Kimbel for casts; and William Kimbel, Milford Wolpoff, Alan Walker, Bernard Wood, Luke Delazene, Yohannes Haile-Selassie, Scott Simpson, John Fleagle and anonymous reviewers for helpful comments and discussion. This project was supported by the Leakey Foundation, PAST (South Africa), Turkana Basin Institute and the Wenner Gren Foundation for Anthropological Research.

Competing interests

We declare that we have no financial or personal relationships which may have inappropriately influenced us in writing this article.

Authors’ contributions

F.K.M. led the team that recovered the fossils; J.M.P. conducted the statistical analyses; C.V.W. described the fossils; and all authors contributed to writing the manuscript.

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