(14) ramidus

Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia

Tim D. White[*], **Gen Suwa**[†] **& Berhane Asfaw**[‡]

Laboratory for Human Evolutionary Studies, University of California, Berkeley, California 94720, USA
† Department of Anthropology, University of Tokyo, Bunkyo-Ku, Hongo, Tokyo 113, Japan
‡ Ethiopian Ministry of Culture and Sports Affairs, Paleoanthropology Laboratory, PO Box 5717, Addis Ababa, Ethiopia

Seventeen hominoid fossils recovered from Pliocene strata at Aramis, Middle Awash, Ethiopia make up a series comprising dental, cranial and postcranial specimens dated to around 4.4 million years ago. When compared with *Australopithecus afarensis* and with modern and fossil apes the Aramis fossil hominids are recognized as a new species of *Australopithecus*—*A. ramidus* sp. nov. The antiquity and primitive morphology of *A. ramidus* suggests that it represents a long-sought potential root species for the Hominidae.

WORK in southern Africa established *Australopithecus* as a human ancestor and revealed specific diversity within that genus. Subsequent work in eastern Africa extended the known geographical and temporal distribution of the genus. Until now, the earliest hominid species known was *Australopithecus afarensis*, dated to between 3 and 4 Myr. *A. afarensis* narrowed the temporal and morphological gap between Miocene hominoids and other early hominids[1]. Its primitive craniodental anatomy offered some support for molecular work[2] which had suggested a late Miocene or early Pliocene age for the common ancestor of hominids and African apes. Because details of the ape and human divergence are poorly understood[3-9], taxonomically diagnostic hominoid fossil evidence antedating the existing record of *A. afarensis* has been eagerly anticipated.

Description of *A. ramidus*

Order Primates Linnaeus 1758
Suborder Anthropoidea Mivart 1864
Superfamily Hominoidea Gray 1825

Australopithecus DART 1925

Australopithecus ramidus sp. nov.

Etymology. In recognition of the Afar people who occupy the Middle Awash study area and contribute to fieldwork there. The name is from the Afar language. 'Ramid' means 'root' and it applies to both people and plants.

Holotype. ARA-VP-6/1 (Fig. 1*a*) is an associated set of teeth from one individual that includes: upper left I^1, C, P^3, P^4, right I^1, C (broken), P^4, M^2; and lower right P_3 and P_4. Found by Gada Hamed on Wednesday, 29 December 1993. Holotype and paratype series housed at the National Museum of Ethiopia, Addis Ababa.

Paratypes. Table 1 lists the holotype and paratype series, all from Aramis. Included are associated postcranial elements, two partial cranial bases, a child's mandible, associated and isolated teeth.

Locality. Aramis localities 1–7 are in the headwaters of the Aramis and Adgantoli drainages, west of the Awash river in the Middle Awash palaeoanthropological study area, Afar depression, Ethiopia[10]. Aramis VP Locality 6 is at 10° 28.74′ north latitude; 40° 26.26′ east longitude; ~625 m elevation.

Horizon and associations. All hominid specimens were surface finds located in the section within 3 m of the Daam Aatu Basaltic Tuff. The immediately underlying Gàala Vitric Tuff Complex is dated at 4.39±0.03 Myr (ref. 10).

Diagnosis. *A. ramidus* is a species of *Australopithecus* distinguished from other hominid species, including *A. afarensis*, by the following: upper and lower canines larger relative to the postcanine teeth; lower first deciduous molar narrow and obliquely elongate, with large protoconid, small and distally placed metaconid, no anterior fovea, and small, low talonid with minimal cuspule development; temporomandibular joint without definable articular eminence; absolutely and relatively thinner canine and molar enamel; lower third premolar more strongly asymmetrical, with dominant, tall buccal cusp and steep, posterolingually directed transverse crest; upper third premolar more strongly asymmetric, with relatively larger, taller, more dominant buccal cusp.

A. ramidus is distinguished as a hominid from modern great apes and known elements of *Sivapithecus*, *Kenyapithecus*, *Ouranopithecus*, *Lufengpithecus* and *Dryopithecus* by the following: canine morphology more incisiform, crowns less projecting, with relatively higher crown shoulders; cupped distal wear pattern on lower canine; mandibular P_3 with weaker mesiobuccal projection of the crown base and without functional honing facet; modally relatively smaller mandibular P_3; modally relatively broader lower molars; foramen magnum anteriorly placed relative to carotid foramen; hypoglossal canal anteriorly placed relative to internal auditory meatus; carotid foramen placed posteromedial to tympanic angle.

A. ramidus is further distinguished from both *Pan* and *Gorilla* by the following: upper canine not mesiodistally elongate.

A. ramidus is further distinguished from *Pan troglodytes* and *Pan paniscus* by the following: upper central incisors small relative to postcanine teeth; lower third molars elongate and larger relative to other molars; molars not as crenulated, occlusal foveae not as broad.

A ramidus is further distinguished from *Gorilla* by the following: smaller absolute tooth and upper limb size; flatter temporomandibular joint; lack of strong molar cusp relief; less sectorial first deciduous molar, dm_1.

Dental description

The ARA-VP-1/129 child's mandible retains a first deciduous molar (dm_1). The dm_1 has been crucially important in studies of *Australopithecus* since the discovery of the genus 70 years ago, and has been used frequently as a key character for sorting apes and hominids[11-13]. The Aramis dm_1 is morphologically far closer to that of a chimpanzee than to any known hominid (Fig. 2). It is very small—more than 4 s.d. units below the combined *A. afarensis/africanus* mean. It is at the low end of the common chimpanzee size range ($n=29$) and comparable to the bonobo mean ($n=21$) (Table 2). The apelike Aramis dm_1 lacks the

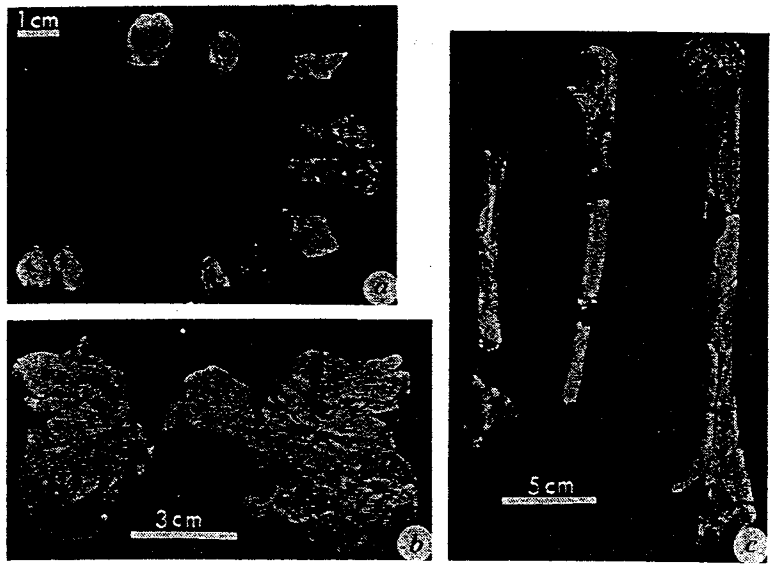

FIG. 1 *a*, Holotype specimen, ARA-VP-6/1 upper and lower dentition from a single individual; *b*, partial adult basicranium, ARA-VP-1/500; *c*, associated adult arm elements, ARA-VP-7/2. All alignments approximate. See text for descriptions.

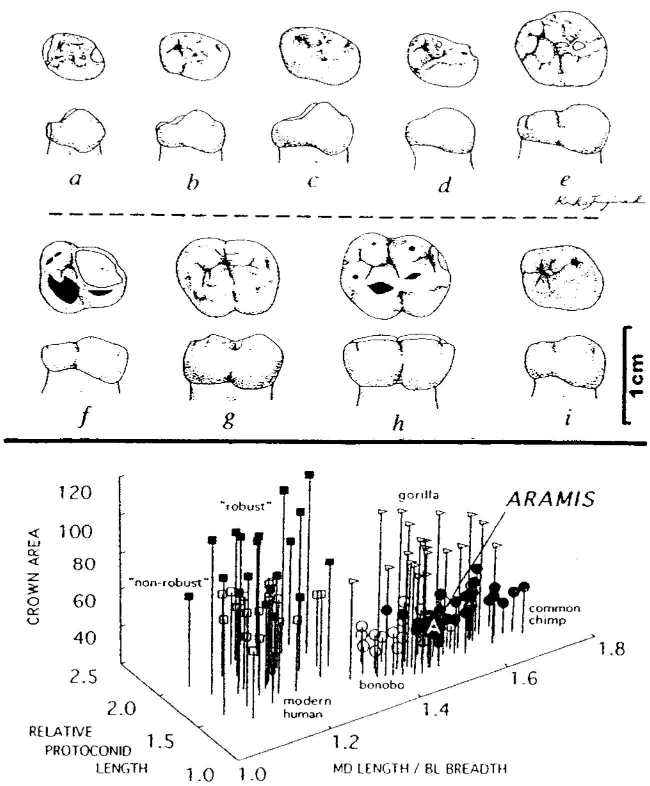

FIG. 2 Deciduous first molar comparisons. Metric and morphological comparisons show a wide separation between the dm_1 of Aramis and those of other early hominid species. *a*, *Dryopithecus* (IPS 42/1784); *b*, *Pan paniscus* (T-26992); *c*, *Pan troglodytes* (PRI 1372); *d*, *Australopithecus ramidus* (ARA-VP-1/129); *e*, *A. afarensis* (A.L. 333-43B); *f*, *A. africanus* (Taung); *g*, *A. robustus* (TM 1601); *h*, *A. boisei* (KNM ER-1477); *i*, *Homo sapiens* (modern). The three-dimensional plot shows dm_1 crown area (buccolingual (BL) multiplied by mesiodistal (MD)) in square mm on the vertical axis. MD length divided by total protoconid length is shown on the left depth axis. The third axis represents a measure of tooth crown narrowness, the MD length divided by the BL breadth. Individual specimens are shown. The 'robust' sample includes *A. robustus*, *A. aethiopicus* (L704) and *A. boisei*. The 'non-robust' sample includes *A. africanus*, *A. afarensis* and early *Homo* (KNM ER-1[illegible] Omo 222). The new species *A. ramidus* is centred in the chimpanzee ranges for these measures. It represents a good ancestral morphotype for all later hominid species.

apparently derived hominid features of buccolingual crown expansion, mesiolingually prominent metaconid, well-defined anterior fovea, and large talonid with well differentiated cusps. The only probable hominid derived feature shared with *A. afarensis* is an occlusally and mesiobuccally reduced protoconid, possibly associated with a loss of deciduous canine honing. The relative size of the talonid, whether judged by relative protoconid length or actual area ratios, lies at the chimpanzee means. The Aramis tooth stands farther in this feature from *A. afarensis* than *A. afarensis* is separated from robust *Australopithecus* homologues. The crown length to breadth ratio (1.49) shows a very narrow dm_1, surpassed in mean values only by the common chimpanzee (mean = 1.58) among fossil hominids and modern hominoids. The ratio between labiolingual breadth of the deciduous canine root and the square root of the computed dm_1 area shows a relatively large Aramis canine, nearly matching the *Pan paniscus* ratio mean and exceeding the *P. troglodytes* average and the *G. gorilla* range ($n = 20$). The only measurable *A. afarensis* specimen (L.H.-2) lies closer to the most extreme *A. boisei* condition (KNM-ER 1477) than it does to Aramis in this ratio.

The *A. ramidus* permanent dentition is represented at most positions (Fig. 3; Table 3). Upper and lower incisors do not exhibit the large size typical of extant *Pan*. Upper and lower central incisor size relative to postcanine teeth is comparable to Miocene hominoids and gorillas. Of the five individuals for whom canine size is determinable, all five have crowns at or larger than the *A. afarensis* mean. Upper and lower canines are also large relative to postcanine teeth. ARA-VP-1/128 is over 5 s.d. units above the *A. afarensis* mean in measures of relative canine size within known individuals ($C \div P_4$; $C \div M_1$; and $C \div M_3$ ratios of maximum labiolingual canine crown breadth $\div$ square root of computed molar or premolar crown area). In ARA-VP-6/1 relative canine crown area is comparable to the female great ape condition. Morphology of the known Aramis canines, however, diverges from that of known apes (Fig. 3).The upper canines are slightly less incisiform than homologues of *A. afarensis* but more incisiform than any ape counterpart, with occlusally placed terminations of the mesial and distal apical crests (Fig. 3*g*). The visual result of apically placed crown shoulders is a low, blunt canine tooth relative to more projecting ape canines, a morphological condition which may have important evolutionary implications. The Aramis upper canine is large buccolingually, forming a further contrast with mesiodistally elongate African ape canines. Wear pattern also differs significantly from the ape condition. Mandibular canine wear does not show the pattern typical of great apes. Some worn female *Pan* canines are superficially similar, but still lack the distal crown cupping seen on Aramis. Instead, they feature planar wear surfaces from contact with the upper canine, even on individuals with rounding (not honing) of the buccal P_3 face.

The broken canines and lower P_3 in ARA-VP-1/128 and -6/1 exhibit thin enamel distinct from previously known hominid conditions. Canine enamel thickness approximates the chimpanzee condition, with a lack of apical thickening we observe in other hominids. The 1.0 mm buccal enamel thickness of the ARA-VP-6/1 broken upper right canine slightly exceeds the 0.9 mm maximum recorded in our small sample of broken female *P. troglodytes* upper canines ($n = 6$) and is approximately 2.4 s.d. units above our combined-sex chimpanzee mean of 0.65 mm ($n = 14$). The broadly constant enamel thickness of the Aramis maxillary canine above the midcrown height level contrasts with the *A. afarensis* condition in which buccal enamel thickens towards the apex, commonly reaching ~1.5 mm. The significance of maxillary canine enamel thickness can be evaluated in the light of proposed wear mechanics of the $\underline{C}/P_3$ complex[14]. The relatively thin enamel and large size of the Aramis canine, together with its primitive P_3 morphology, suggest a $\underline{C}/P_3$ complex morphologically and functionally only slightly removed from the presumed ancestral ape condition.

The ARA-VP-6/1 P_3 is markedly more apelike than any *A. afarensis* homologue in its high protoconid with extensive buccal face and steep, distolingually directed transverse crest (Fig. 3*g*). In these features it is indistinguishable from ape homologues. The strong mesiobuccal protrusion of its crown base is also outside the known *A. afarensis* range. The Aramis P_3 deviates toward the *A. afarensis* condition in some details. These include a more occlusal termination of the mesial protoconid crest, weaker mesiobuccal protrusion of the crown base (especially ARA-VP-1/128), and a smaller size relative to P_4–M_3 although rare individual *Pan* specimens do approximate the Aramis condition in

TABLE 1 Aramis fossil hominid specimens

Specimen number	Collection year	Element	Discoverer	Dental dimensions
ARA-VP-1/1	1992	RM^3	G. Suwa	RM^3: 10.2MD, 12.3BL
ARA-VP-1/2	1992	RI^1	A. Asfaw	RI^1: 8.2LL
ARA-VP-1/3	1992	L_C frag.	G. Suwa	
ARA-VP-1/4	1992	Right humerus, full shaft	S. Simpson	
ARA-VP-1/125	1992	Left temporal	S. Simpson	
ARA-VP-1/127	1992	L^C, RM^1, worn roots of incisors, canine and premolar	T. White	
ARA-VP-1/128	1992	Associated teeth	T. Assebework	L_C: 11.0LL; RP_3: 7.5Mn, (9.8)Mx; LP_3: 7.5 Mn, (9.9)Mx; RP_4: 7.3 (7.5)MD, 9.5BL; LP_4: 7.3 (7.5)MD; RM_1: 10.9 (11.2)MD, (10.3)BL; LM_1: 10.6 (11.0)MD, (10.1)BL; LM_2: 12.8 (13.0)MD, 11.9BL; RM_3: 12.7(MD), 11.0(BL)
ARA-VP-1/129	1992	Right mandible (I_1, dm_1)	A. Asfaw	RI_1: 6.0MD; Rdm_1: 7.3MD, 4.9BL
ARA-VP-1/182	1992	RM3 fragment	Group	
ARA-VP-1/183	1992	UC fragment	Group	
ARA-VP-1/200	1993	LM_1	A. Ademassu	LM_1: 11.0MD, 10.3BL
ARA-VP-1/300	1993	R^C	Y. Haile-Selassie	R^C: (11.2)MD, 11.1LL, 14.3CH
ARA-VP-1/400	1993	LM^2	Y. Beyene	LM^2: (11.3–12.3)MD, (15.0)BL
ARA-VP-1/401	1993	LM_3 fragment	M. Feseha	
ARA-VP-1/500	1993	R. + L. temp. + occ.	T. White	
ARA-VP-6/1	1993	Associated teeth	G. Hamed	LI^1: 9.6 (10.0)MD, 7.5LL, 12.5swCH; R^C: 11.6LL, 14.5CH; L^C: 11.7LL, 14.6CH, 11.5MD; LP^3: 7.7MD, 8.4MxMD; 12.5BL; RP^4: 8.4MD, (11.3)BL; RM^2: 11.8MD, (14.1)BL; RP_3: (8.2)MnMD; (11.5)MxBL; RP_4: 8.9MD, 9.7BL
ARA-VP-7/2	1993	Left humerus, radius, ulna	A. Asfaw	

Fossil hominid specimens recovered from Aramis between December 1992 and December 1993. Dental dimensions are standard, estimates for breakage or interproximal attrition are shown in parentheses. BL, Buccolingual; LL, labiolingual; MD, mesiodistal; CH, distance from buccal enamel line to apex (canine height); Mn, minimum diameter; Mx, maximum diameter; sw, slightly worn. All measurements were taken on original specimens by the authors.

these features. The worn ARA-VP-1/128 P_3 lacks a honing facet but exhibits steep mesial and distal wear slopes not matched in *A. afarensis*.

The P^3 is distinctly primitive in its tall and mesiodistally elongate paracone. Both P^3 and P^4 exhibit a prominent anterior transverse crest. In the P^3 this crest defines an anteriorly facing triangular portion of the occlusal surface, as in apes. The lower P_4 exhibits a prominent transverse crest and minimal talonid development. The P4s from two known individuals are both single rooted.

Molar morphology resembles the *A. afarensis* condition, but lacks the extreme buccolingual breadth relative to mesiodistal length common in that species (Fig. 3*a–e*). The 'serrate' root pattern and deep dentine wear on the buccal cusps described in *A. afarensis*, Tabarin, and Lothagam[15-17] also occur in Aramis specimens. All molars lack the extensive crenulation and broad occlusal foveae characteristic of modern chimpanzees, or the high cusp topography of gorillas. The Aramis lower third molar is rounded distally, like *A. afarensis* and Miocene hominoids. A great size discrepancy between M_1 and M_2 is seen in ARA-VP-1/128.

A distinct difference from known hominids occurs in molar enamel thickness. Maximum radial enamel thickness of crown faces can be measured in three fractured Aramis specimens and it ranges from 1.1 to 1.2 mm buccally, at or near the unworn cusp apex, perpendicular to the enamel-dentine junction. These values are comparable to the uppermost range of our homologous enamel thickness values measured on broken *P. troglodytes* molars ($n=22$; M_1 through to M_3). Equivalent measures in *A. afarensis* range from 1.4 to 2.0 mm ($n=5$). In one case (the

TABLE 2 Lower first deciduous molar (dm_1) measurements

	Mesiodistal (MD) length	Buccolingual (BL) breadth	MD × BL area	Protoconid length	MD Length + protoconid length
Aramis ($n=1$)	7.3	4.9	35.8	5.2	1.4
A. afarensis					
n	4	4	4	4	4
min	8.5	7.6	68.0	4.3	1.7
max	9.6	8.4	80.6	5.6	2.0
mean	**9.2**	**7.9**	**72.5**	**5.1**	**1.8**
s.d.	0.5	0.4	5.7	0.6	0.1
A. africanus					
n	7	5	5	3	3
min	8.4	7.1	59.6	5.2	1.6
max	9.1	8.1	73.7	5.3	1.7
mean	**8.8**	**7.6**	**66.6**	**5.2**	**1.7**
s.d.	0.2	0.4	5.5	0.1	0.1
A. robustus					
n	8	8	8	8	8
min	9.0	7.7	71.0	4.3	1.8
max	10.8	9.7	101.9	5.8	2.3
mean	**10.1**	**8.3**	**83.7**	**4.9**	**2.1**
s.d.	0.5	0.6	9.5	0.5	0.1
P. paniscus					
n	21	21	21	20	20
min	6.3	4.4	27.7	4.3	1.3
max	8.8	5.5	48.4	6.0	1.6
mean	**7.4**	**5.1**	**37.6**	**5.0**	**1.5**
s.d.	0.6	0.31	4.7	0.5	0.1
P. troglodytes					
n	29	29	29	29	29
min	7.0	4.6	32.9	5.0	1.3
max	9.4	5.8	54.5	6.7	1.6
mean	**8.1**	**5.2**	**42.2**	**5.8**	**1.4**
s.d.	0.6	0.4	5.2	0.5	0.1
G. gorilla					
n	20	20	20	20	20
min	9.8	6.7	71.4	6.7	1.3
max	12.2	8.9	108.6	9.0	1.6
mean	**11.0**	**7.5**	**82.3**	**7.8**	**1.4**
s.d.	0.7	0.6	10.7	0.6	0.1
P. pygmaeus					
n	6	6	6	6	6
min	8.4	6.4	53.8	5.8	1.3
max	10.2	8.1	82.6	8.1	1.5
mean	**9.2**	**7.1**	**66.2**	**6.7**	**1.4**
s.d.	0.7	0.6	10.3	0.8	0.1
H. sapiens					
n	21	21	21	21	21
min	7.4	6.4	47.4	4.0	1.4
max	9.2	8.1	69.9	5.7	2.1
mean	**8.4**	**7.2**	**60.4**	**4.9**	**1.7**
s.d.	0.5	0.4	6.1	0.5	0.2

Comparative metrics on deciduous lower first molars (dm_1) of various hominoid taxa. Abbreviations and conventions as in Table 1.

ARA-VP-1/128 third molar) Aramis radial enamel thickness at the buccal protoconid face can be evaluated relative to cervical breadth. A comparison of this ratio of enamel thickness suggests that *A. ramidus* may be characterized as intermediate between the chimpanzee and the *A. afarensis/africanus*/early *Homo* conditions.

In postcanine size, the range of the available Aramis sample includes specimens smaller than known *A. afarensis* homologues (the two known M_1 teeth are both more than 3 s.d. units below the mean). Of the seven Aramis individuals for whom postcanine tooth size is determinable, all have crown sizes smaller than the *A. afarensis* mean. We interpret the limited morphology and metrical data available as indicating a single species with a postcanine dentition significantly smaller than in *A. afarensis*.

The postcanine mandibular row can be reconstructed for ARA-VP-1/128 by juxtaposing interproximal facets (Fig. 3*a*–*c*). This shows that the C to M_2 dental row is weakly concave buccally, as in modern and fossil apes and some *A. afarensis* specimens. The P_3 axis is less oblique than in most apes. The canine is positioned directly in line with the mesiodistal axis of the postcanine tooth row rather than being set mesiolingually to the postcanine axis as in the case for most *A. afarensis*. This is a more primitive arrangement shared with modern and Miocene great apes, and may suggest that the mesial part of the lower canine was not functionally incorporated into the incisal row as seen in *A. afarensis*[17].

Cranial description

The ARA-VP-1/125 and -1/500 specimens represent adult temporal and occipital regions (Fig. 1*b*). Both are smaller than their *A. afarensis* counterparts, but no female temporal is known for that species. The Aramis cranial fossils evince a strikingly chimpanzee-like morphology that includes marked pneumatization of the temporal squama which even invades the root of the zygoma. The occipital condyle is small, measuring 16 × 7.5 mm. The anterior border of the foramen magnum (basion) is intersected by a bicarotid chord connecting the centres of right and

TABLE 3 Comparative dental metrics for permanent dentition

a, Upper dentition

	Mesiodistal					Labio/buccolingual					Crown area (MD × BL)				
	n	Min	Max	Mean	s.d.	*n*	Min	Max	Mean	s.d.	*n*	Min	Max	Mean	s.d.
I^1															
A. afarensis	3	10.8	11.8	11.2	0.6	5	7.1	8.6	8.20	0.6	3	90.5	99.1	94.2	4.5
Aramis	1	—	—	(10.0)	—	2	7.5	8.2	—	—	1	—	—	(75.0)	—
C															
A. afarensis	9	8.9	11.6	10.0	0.8	10	9.3	12.5	10.9	1.1	9	82.8	145.0	109.9	18.9
Aramis	2	(11.2)	11.5	—	—	2	11.1	11.7	—	—	2	(124.3)	134.5	—	—
P^3															
A. afarensis	9	7.5	9.3	8.7	0.5	8	11.3	13.4	12.4	0.6	8	84.7	120.9	108.0	11.0
Aramis	1	—	—	7.7	—	1	—	—	12.5	—	1	—	—	96.3	—
P^4															
A. afarensis	10	7.6	9.7	9.0	0.6	6	11.1	12.6	12.1	0.6	6	84.4	119.7	106.8	12.6
Aramis	1	—	—	8.4	—	1	—	—	(11.3)	—	1	—	—	(94.9)	—
M^2															
A. afarensis	5	12.1	13.5	12.8	0.5	6	13.4	15.1	14.7	0.6	5	162.1	199.8	187.5	14.6
Aramis	2	(11.8)	11.8	—	—	2	(14.1)	(15.0)	—	—	2	(166.4)	(177.0)	—	—
M^3															
A. afarensis	8	10.5	14.3	11.9	1.4	8	13.0	15.5	13.8	1.0	8	136.5	215.9	165.1	30.9
Aramis	1	—	—	10.2	—	1	—	—	12.3	—	1	—	—	125.5	—

b, Lower dentition

	Mesiodistal					Labio/buccolingual					Crown area (MD × BL)				
	n	Min	Max	Mean	s.d.	*n*	Min	Max	Mean	s.d.	*n*	Min	Max	Mean	s.d.
I_1															
A. afarensis	2	6.2	8.0	—	—	—	—	—	—	—	—	—	—	—	—
Aramis	1	—	—	6.0	—	—	—	—	—	—	—	—	—	—	—
C															
A. afarenis						13	8.8	12.4	10.4	1.1	—	—	—	—	—
Aramis	—	—	—	—	—	1	—	—	11.0	—	—	—	—	—	—
P_3 (min/max)															
A. afarensis	19	6.5	9.8	8.6	1.1	19	9.7	13.3	11.6	1.1	19	63.1	127.7	99.7	20.4
Aramis	2	7.5	(8.2)	—	—	2	(9.9)	(11.5)	—	—	2	(74.2)	(94.3)	—	—
P_4															
A. afarensis	15	7.7	11.1	9.7	1.0	14	9.8	12.8	10.9	0.8	14	77.0	129.7	106.5	16.8
Aramis	2	7.5	8.9	—	—	2	9.5	9.7	—	—	2	71.2	86.3	—	—
M_1															
A. afarensis	17	11.2	14.0	13.0	0.6	16	11.0	13.9	12.6	0.8	16	124.3	194.6	164.9	17.1
Aramis	2	11.0	11.1	—	—	2	(10.2)	10.3	—	—	2	(113.2)	113.3	—	—
M_2															
A. afarensis	23	12.4	16.2	14.3	1.0	22	12.1	15.2	13.5	0.9	22	152.5	234.1	193.3	24.3
Aramis	1	—	—	(13.0)	—	1	—	—	11.9	—	1	—	—	(154.7)	—
M_3															
A. afarensis	14	13.7	16.3	14.8	0.8	14	12.1	14.9	13.3	0.8	13	172.0	231.5	195.7	17.7
Aramis	1	—	—	12.7	—	1	—	—	11.0	—	1	—	—	139.7	—

Comparative metrics for the permanent teeth of *A. afarensis* (comprises the Hadar pre-1990 sample and the full Laetoli and Maka samples) and *A. ramidus* (from Table 1). Data are shown only for tooth positions represented in both species. Measurements are standard and were taken by the authors on original specimens with conventions and abbreviations as in Table 1. There is considerable overlap between the known species ranges, as there is among other species in the genus. As documented in the text and illustrations, however, proportional differences within individual dentitions combine with other morphological considerations to warrant the recognition of *A. ramidus* as a species distinct from *A. afarensis*.

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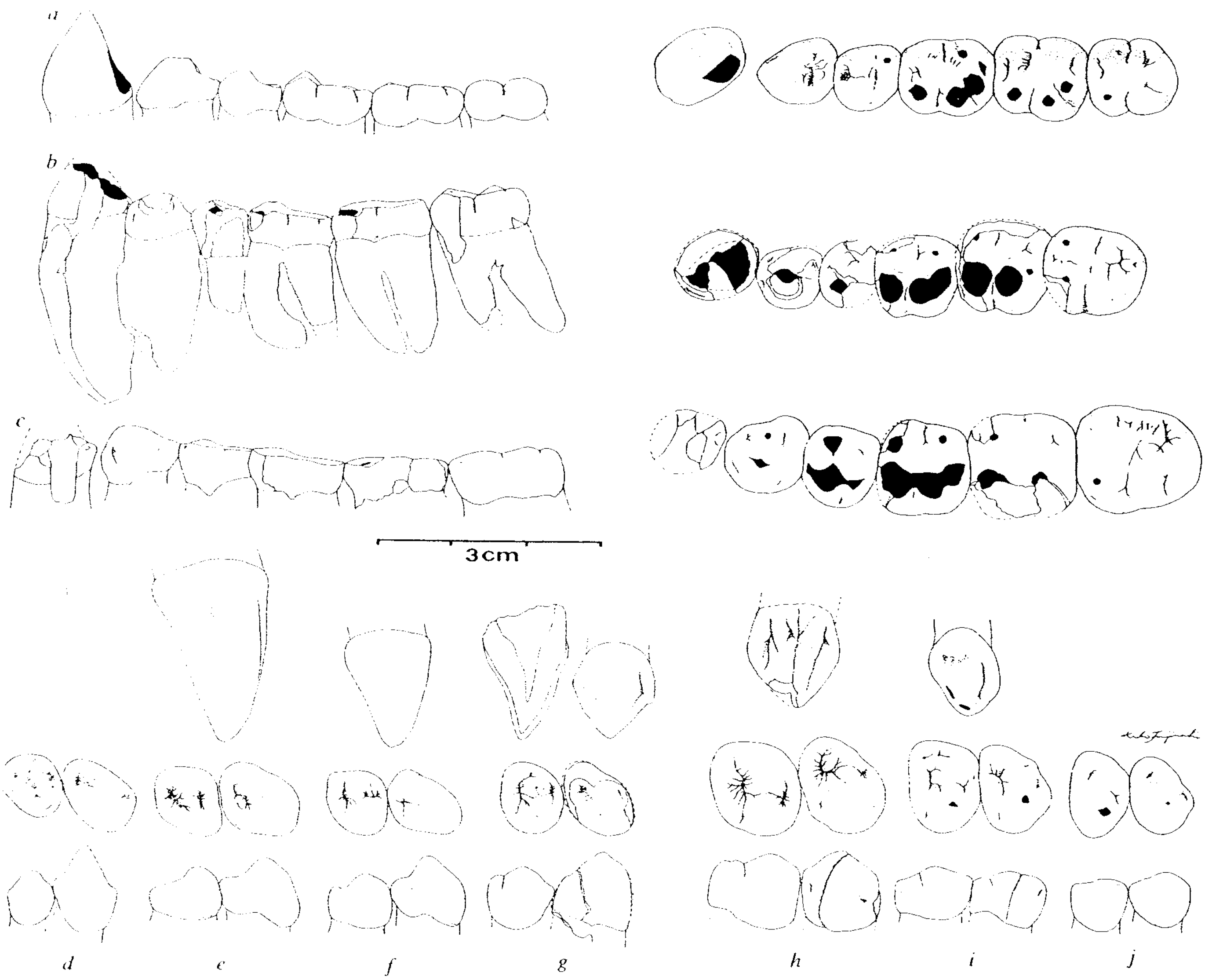

FIG. 3 Comparisons of upper canine/lower premolar complexes and tooth rows. Top three rows, Occlusal and lateral views of the lower tooth rows of: *a*, *Pan troglodytes* female (CMNH B1770); *b*, *A. ramidus* (ARA-VP-1/128); *c*, *A. afarensis* holotype (Laetoli Hominid 4). Bottom three rows, Lingual views of upper canines and occlusal and buccal views of lower third and fourth premolars of: *d*, *Dryopithecus* (MNHNP); *e*, *Pan troglodytes* male (CMNH B1882); *f*, *P. troglodytes* female (CMNH B1721); *g*, *A. ramidus* holotype (ARA-VP-6/1; split right canine on the left); *h*, *A. afarensis* (LH-3); *i*, *A. afarensis* (A.L. 400); *j*, *A. afarensis* (A.L. 288-1, 'Lucy'). *a*, *c* and *h* reversed for comparison.

carotid foramina, and the endocranial opening of the hypoglossal canal is placed more anteriorly relative to the internal auditory meatus than in great apes. This condition, as in other fossil hominid taxa, reflects a shortened basioccipital component of the cranial base relative to modern African ape crania. The temporomandibular joint is very flat, with virtually no articular eminence and weak inferior projection of the entoglenoid process. The tympanic is tubular, bounded anteriorly and posteriorly by deep furrows, and the tube extends to the lateral edge of the postglenoid process in one individual and beyond it in the second. The mastoid process is a blunt eminence rather than the inflated, inflected pyramidal structure diagnostic of the chimpanzee. The digastric groove is distinctly deeper than in the chimpanzee.

Postcranial description

The ARA-VP-7/2 specimen (Fig. 1*c*) is a rare association of all three bones from the left arm of a single individual. In size the specimen indicates a hominid larger than the A.L. 288-1 *A. afarensis* from Hadar and smaller than other individuals of this species. Fracture of the specimen currently precludes length estimates for the three elements, but the humeral head is approximately 30% larger than the smallest (A.L. 288-1) *A. afarensis* specimen (breadth: Aramis = 34.6, A.L. 288-1 = 27.0; height: Aramis = 36.5, A.L. 288-1 = 28.1). The arm displays a mosaic of characters usually attributed to hominids and/or great apes. From proximal to distal, probable derived characters shared with other hominids include an elliptical humeral head; a blunt, proximally extended ulnar olecranon process surmounting a straight dorsal upper shaft profile; an anteriorly oriented trochlear notch; and, an anteriorly facing ulnar brachialis insertion. The specimen also shows a host of characters usually associated with modern apes, including a strong angulation of the distal radial articular surface due to a large styloid process, a strong lateral trochlear ridge on the distal humerus (also seen in some *A. afarensis*), and an elongate, superoposteriorly extended lateral humeral epicondyle. The Aramis arm diverges from the African ape condition in other features. The proximal humerus lacks the deep, tunnel-like bicipital groove often seen on African apes. Further studies will unravel the functional and phylogenetic significance (polarities) of these and other postcranial characters.

Comparisons and remarks

The pre-5 Myr record of hominid evolution is sparse. Although the Lothagam fragment has been attributed to *A.* cf. *afarensis*[18-20] this assignment was made mostly on the basis of primitive characters and in the absence of associated cranial, anterior dental or postcranial remains. Hominid remains from the period between 4 and 5 Myr are also few and poor, comprising a proximal humerus and jaw fragment from Baringo[16,19-22], and a distal humerus from Kanapoi of more uncertain age. These and the slightly younger Kubi Algi[23,24] and Fejej[25] specimens have all been attributed to *A. afarensis*.

To our knowledge, no fossils predating 4 Myr have been identified as representing taxa other than *Australopithecus afarensis* and *Australopithecus africanus*[16,19,20,23-26]. Assignment of the limited available >4 Myr sample to *A. afarensis* was warranted for the comparatively undiagnostic Lothagam, Baringo, Kanapoi and Tabarin specimens from Kenya[16]. The discovery of more complete, more diagnostic specimens at Aramis allows a recognition of characters which distinguish them at (minimally) the species level from Hadar, Maka and Laetoli hominid fossils. The limited preserved morphology in the Lothagam, Tabarin and Baringo specimens broadly matches both the Aramis sample and *A. afarensis*. The discovery of the Aramis hominids demonstrates, however, that some of the suggested differences between Lothagam and *A. afarensis* (for example, enamel thickness[15]) are likely to be substantiated. However, the preserved anatomy of these Kenyan specimens may well reflect primitive character states for the basal hominid (and perhaps ancestral hominoids). Nothing available for these Kenyan specimens validates inclusion in the new Ethiopian taxon before the recovery of more diagnostic body parts.

We note that Ferguson, referring to casts and literature, has invented a plethora of new names for early African hominids (for instance, he divides *A. afarensis* into three species; an alleged dryopithecine ape[27], a diminutive early human[28], and a subspecies of *A. africanus*[29]). His invalid naming of the A.L. 288 specimen as 'Homo antiquus' (in which he includes KNM-ER 1813)[28] was followed by his 1989 placement of the Baringo Tabarin specimen (which he incorrectly identified as 'KNM-ER TI 13150') into a subspecies ('praegens') of that species[30]. Because of these problems, because Ferguson's diagnosis of that specimen did not differentiate it from *A. afarensis*, and because it lacks any characters that differentiate it from the latter species or unequivocally link it to the Aramis species[16], we consider Ferguson's subspecific nomen '*praegens*' to be a *nomen dubium* and propose that it be suppressed even in the event that the Tabarin specimen be shown conspecific with the Aramis series.

The 1992/93 Aramis hominids share a wide array of traits with *A. afarensis* but also depart anatomically from this species in lacking some of the key traits it possesses and which are shared exclusively among all later hominids. Because of relationships indicated by molecular studies, and because terminal Miocene to Pleistocene fossil African apes are unknown, comparison of the Aramis hominids and modern African apes is warranted. The Aramis remains evince significant cranial, dental and postcranial similarities to the chimpanzee condition, but some or all of these features may be primitive retentions. Only further discoveries and comparisons may elucidate which features actually define the chimp–human and/or African ape–human clades. Meanwhile, the modern African apes are distinct in many dental features from both Aramis and middle to late Miocene hominoids, and thus probably do not represent the ancestral condition[8,9]. At the same time, the relatively thin Aramis molar enamel suggests that a simple "hard object feeder" model[7] is likely to be inaccurate for the ancestral African ape/hominid stock.

We have taken a conservative position here regarding placement of the Aramis fossils at the family and genus levels. The major anatomical/behavioural threshold between known great apes and Hominidae is widely recognized to be bipedality and its anatomical correlates. The two derived craniodental characters shared among all hominids are anterior placement of the occipital condyle/foramen magnum and a more incisiform canine with reduced sexual dimorphism. Acquisition of these states at Aramis may correlate with bipedality[31,32] although this remains to be demonstrated. The postcranial evidence available for *A. ramidus* is not definitive on the issue of locomotor pattern.

The anticipated recovery at Aramis of additional postcranial remains, particularly those of the lower limb and hip, may result in reassessment of these fossils at the genus and family level. Meanwhile, characters such as the modified C/P3 complex, an anterior foramen magnum, and proximal ulnar morphology (shared with later *Australopithecus* species) suggest that the Aramis fossils belong to the hominid clade. Similarity to the *A. afarensis* hypodigm warrants the inclusion of the Aramis fossils in the genus *Australopithecus*. At the same time, *A. ramidus* is the most apelike hominid ancestor known, and its remains suggest that modern apes are probably derived in many characters relative to the last common ancestor of apes and humans. More work at Aramis should further elucidate the sexual dimorphism, locomotion, diet and habitat of this species. The fossils already available indicate that a long-sought link in the evolutionary chain of species between humans and their African ape ancestors occupied the Horn of Africa during the early Pliocene. □

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