

New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya

Meave G. Leakey^{*}, Craig S. Feibel[†], Ian McDougall[‡] & Alan Walker[§]

^{*} National Museums of Kenya, PO Box 40658, Nairobi, Kenya

[†] Department of Anthropology, Rutgers University, New Brunswick, New Jersey 08903-0270, USA

[‡] Research School of Earth Sciences, The Australian National University, Canberra, ACT 0200, Australia

[§] Departments of Anthropology and Biology, The Pennsylvania State University, University Park, Pennsylvania 16802, USA

Nine hominid dental, cranial and postcranial specimens from Kanapoi, Kenya, and 12 specimens from Allia Bay, Kenya, are described here as a new species of *Australopithecus* dating from between about 3.9 million and 4.2 million years ago. The mosaic of primitive and derived features shows this species to be a possible ancestor to *Australopithecus afarensis* and suggests that *Ardipithecus ramidus* is a sister species to this and all later hominids. A tibia establishes that hominids were bipedal at least half a million years before the previous earliest evidence showed.

THE recently described early hominid *Ardipithecus ramidus*, from Aramis, Ethiopia, extends the temporal distribution of known fossil hominids to 4.4 Myr^{1, 3}. The relationship between *A. ramidus* and *Australopithecus afarensis* from Hadar, Ethiopia, and Laetoli, Tanzania, (3.0–3.6 Myr) remains speculative, and so the recent recovery of hominid specimens from Kanapoi, Kenya, more than 4 Myr old, helps to test the hypotheses that *A. ramidus* represents a potential root species for the Hominidae¹ and that there was prolonged stasis within *A. afarensis* between 3.9 and 3.0 Myr⁴.

Description of *Australopithecus anamensis*

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

Australopithecus DART 1925

Australopithecus anamensis sp. nov.

Etymology. The name 'anam' means 'lake' in the Turkana language. All specimens found so far are from near present Lake Turkana and were found in sediments associated with the ancient precursor lake, Lake Lonyumun.

Types. The holotype is KNM-KP 29281 (Fig. 1), a mandible with all teeth, but lacking rami, found by Peter Nzube in 1994. A partial left temporal is probably from the same individual. The paratypes are listed in Table 1. The repository is the National Museums of Kenya, Nairobi.

Localities. Kanapoi localities are situated about 36°04' E and 2°19' N between the Kalabata and Kakurio rivers in Turkana District, northern Kenya (Fig. 2). Specimens from East Lake Turkana come from Site 261-1 and a nearby locality 1 km to the northeast in Area 261. Locations of individual fossils are marked on aerial photographs housed in the National Museums of Kenya.

Horizon. The type is from Pliocene strata at Kanapoi, between the lower and upper pumiceous tephra (about 4.1 Myr). Paratypes from Kanapoi come from this level or slightly higher in the section while those from Allia Bay lie below or within the Moiti Tuff (about 3.9 Myr) in the Koobi Fora Formation.

Diagnosis. A species of *Australopithecus* distinguished from all others by the following features: a small external acoustic meatus presenting a narrow ellipse in outline; long axes of mandibular bodies and tooth rows nearly parallel and close together; mental region of mandible not strongly convex; long axis of symphysis slopes markedly posteroinferiorly; canines with very long robust

roots; trigons of upper molars much wider than talons; distal humerus with thick cortex enclosing small medullary cavity. It can be distinguished from *A. afarensis* by the following: upper canine root and associated facial skeleton less posteriorly inclined; lower molars tend to have more sloping buccal sides and upper molars more sloping lingual sides; tympanic plate very horizontal without defining grooves. It can be distinguished from *Ardipithecus* by the following features: absolutely and relatively thicker tooth enamel; upper canine buccal enamel thickened apically; molars more buccolingually expanded; first and second lower molars not markedly different in size; tympanic tube extends only to the medial edge of the postglenoid process, rather than to the lateral edge or beyond it; lateral trochlear ridge of humerus weak.

Dental and cranial descriptions

The sample shows some size variation in teeth and mandible that can probably be attributed to sexual dimorphism (Table 1). The type mandible, which lacks the rami, has a relatively small body, but the fragment, KNM-ER 20432, and some pieces associated with the lower teeth, KNM-KP 29286, are both larger, particularly in depth, in the anterior part of the body. The canine in the type mandible is smaller than those in the other two. The type mandible is remarkable in that the long axis of the symphysis is very posteriorly inclined, so that the mental surface extends as far posteriorly as the first molar and curves only slightly between the incisor alveolae and the inferior torus. There is a very long postincisive planum together with a moderately developed superior torus and a well-developed inferior torus. The body becomes everted posteriorly and X-rays reveal a serrate root-pattern⁵, as seen in other early hominids. This specimen is slightly distorted by the forward displacement of the left second incisor and canine roots from their alveoli. *A. anamensis* teeth are similar to those of *A. afarensis*, especially those from Laetoli, with the following major differences. Among the lower teeth: the *A. anamensis* canine is larger in size and usually more asymmetrical with a long robust root; the third premolar is very asymmetrical with a blunt centrally positioned main cusp and with clearly separated mesial and distal roots; the third and fourth premolars have extensive sloping buccal surfaces, and the molars tend to have more sloping buccal sides. Among the upper teeth: the molars of *A. anamensis* have trigons much wider than talons; the canines have long robust roots and crowns with apically thickening enamel which is ~1.3 mm closer to the apex, and similar to *A. afarensis*, but greater than that of *A. ramidus* (>0.9 mm)¹. Naturally cracked upper and lower molars have

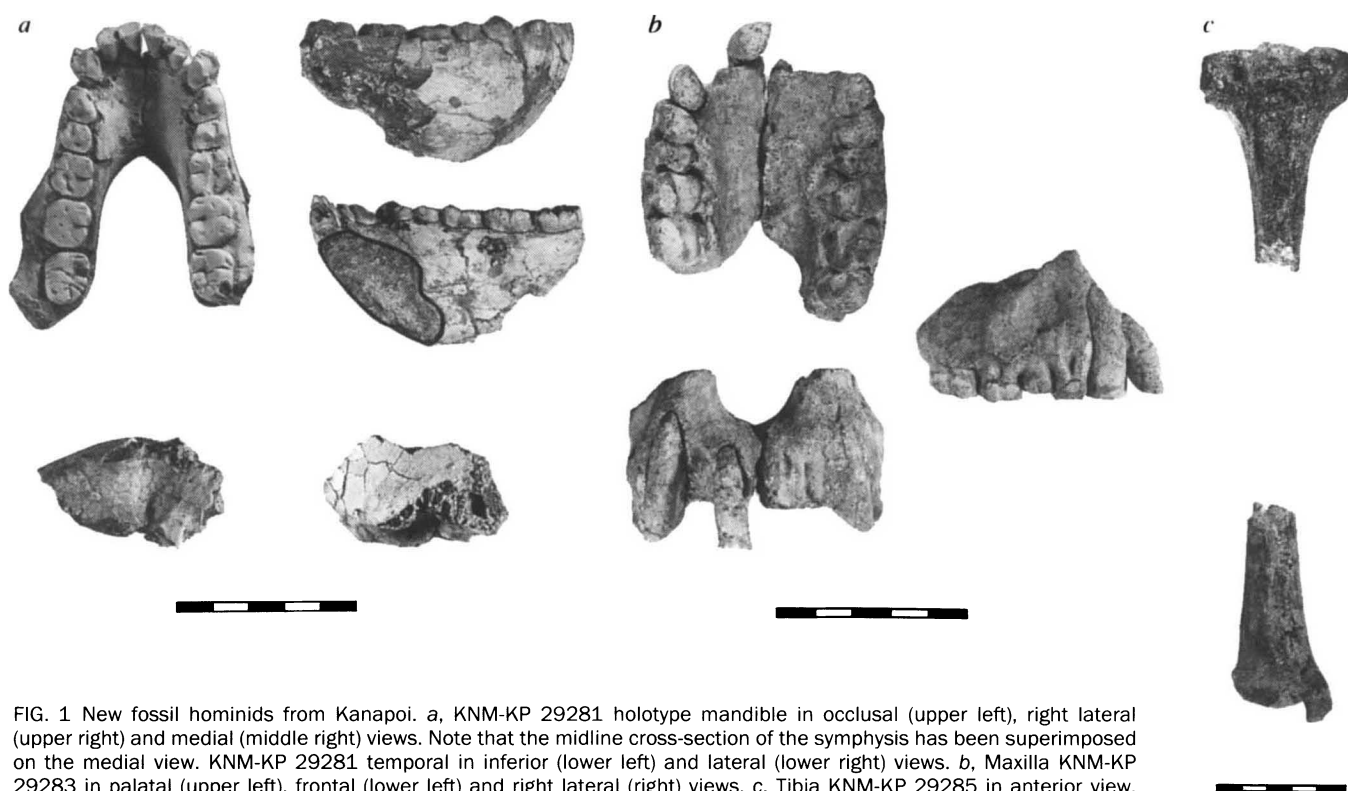


FIG. 1 New fossil hominids from Kanapoi. a, KNM-KP 29281 holotype mandible in occlusal (upper left), right lateral (upper right) and medial (middle right) views. Note that the midline cross-section of the symphysis has been superimposed on the medial view. KNM-KP 29281 temporal in inferior (lower left) and lateral (lower right) views. b, Maxilla KNM-KP 29283 in palatal (upper left), frontal (lower left) and right lateral (right) views. c, Tibia KNM-KP 29285 in anterior view. Scale bars are in cm.

enamel as thick as that reported for *A. afarensis*, and thicker than that of *A. ramidus*; enamel thickness near cusp apices can be measured between 1.5 and 2.0 mm ($n=9$), almost exactly matching the range reported from similar measurements at uncontrolled locations in *A. afarensis*, and about twice that reported for *A. ramidus*.

Part of a left temporal bone is probably associated with the type mandible. It consists of the lower part of the squamous portion, the tympanic and most of the mandibular fossa. The tympanic is flat inferiorly and set at a very high angle to the roof of the mandibular fossa. The entoglenoid process is incomplete, but clearly small, and the articular eminence very slight. The squama and the root of the zygomatic process are pneumatized. The external acoustic meatus is small (8.9 mm vertically by 5.7 mm anteroposteriorly with an area of 50.7 mm²) and its shape in outline, a vertically oriented ellipse, is most often found in chimpanzees. African apes have small meatuses (areas for *Pan troglodytes*, $\bar{x}=43.7$ mm², s.d. 10.5, $n=21$; for *Gorilla gorilla*, $\bar{x}=53.9$ mm², s.d. 18.5, $n=21$) whereas humans and *A. afarensis* have large meatuses (areas for *Homo sapiens*, $\bar{x}=115.1$ mm², s.d. 17.3, $n=22$; for *A. afarensis*, $\bar{x}=97.9$, $n=5$ (W. H. Kimbel, personal communication)). It must be noted, however, that the sample from Hadar is extremely variable, ranging from 44 to 139.2 mm². Two *A. ramidus* specimens have small meatuses (T. D. White, personal communication). The tympanic of the Kanapoi specimen also lacks the deep furrows bounding it anteriorly and posteriorly that are described for *A. ramidus*¹. The maxilla, KNM-KP 29283, together with KNM-ER 30200, which has relatively unworn molars, shows several differences from later *A. afarensis*. The canine root in *A. anamensis* is placed more vertically, and because of this the lower lateral margins of the piriform aperture appear to be more vertical. Note that the Garusi specimen, a small maxillary fragment from Laetoli⁶, is very similar in this respect to KNM-KP 29283. It also preserves a small part of the midline suture⁷, showing that the palate was very shallow and narrow, as is also the case in KNM-ER 30200. The upper molars in *A. anamensis* have more lingual flare and are

wider mesially than distally, which gives them a posteriorly wedged outline, whereas they are more square in *A. afarensis*.

Postcranial description

The tibia, KNM-KP 29283, is larger than the largest from Hadar (A.L. 333-42). The middle of the shaft was not recovered. We estimate that between a third and a half of the total length of the bone is missing. Using regression equations based on humans⁸, the estimated body weight of this individual is 55 kg (based on the upper epiphysis) and 47 kg (based on the distal epiphysis). This is somewhat higher than the mean body weight recently estimated for the males of *Australopithecus afarensis*, and 1.7 times higher than that computed for presumed females⁸. The most important features of this bone are those that indicate bipedalism^{9,10}. These include: rectangular proximal surface with anterior/posterior lengthening of the articular surfaces, condyles both concave and of roughly equal area, expanded metaphyseal bone, probably small fibular articulation, very straight shaft in those parts preserved, and a distal articular surface that faces directly inferiorly. Although the proximal fibular facet is broken away, the small size of the missing area shows that the articulation must also have been small, as in humans. We conclude that bipedal locomotion had evolved at least half a million years before the previous earliest evidence (the footprints at Laetoli) suggests. There are a few primitive features of this bone. These include a projecting attachment for the fascia lata, a less swollen superior metaphysis, and a strongly marked gracilis insertion next to the anterior border of the shaft. In these respects the specimen resembles African apes and *A. afarensis*. The distal humerus, KNM-KP 271, was originally seen to be human-like^{11,14}, and it does show many derived hominid features, including a marked median anterior capsular ligament tubercle (I. Herskovitz, personal communication).

Discussion

This new species of *Australopithecus* has a mixture of features that are both primitive and derived for the Hominidae. Of par-

TABLE 1 Fossil hominids from Kanapoi and Allia Bay

(a)				
Specimen number	Date	Site	Body part	Discoverer
KNM-KP 271	1965	Kanapoi	Distal left humerus	B. Patterson
KNM-KP 29281	1994	Kanapoi	Holotype mandible with left and right I ₁ -M ₃ and probably associated partial left temporal bone	P. Nzube
KNM-KP 29282	1994	Kanapoi	M ₂	P. Nzube
KNM-KP 29283	1994	Kanapoi	Maxilla with right I ¹ , C-M ² and left C-M ³ , with associated left I ₂	W. Mangao
KNM-KP 29284	1994	Kanapoi	Associated lower right C and P ₃ germs	Sieving team
KNM-KP 29285	1994	Kanapoi	Right tibia lacking middle half-third of shaft	K. Kimeu
KNM-KP 29286	1994	Kanapoi	Associated lower dentition, lacking right I ₁ with fragments of mandibular body	P. Nzube
KNM-KP 29287	1994	Kanapoi	Right and left mandible fragments with molar roots	S. Ngui
KNM-KP 29288	1994	Kanapoi	Tooth fragments and partial upper C	Sieving team
KNM-ER 7727	1982	Allia Bay 261-1	left M ²	J. Kithumbi
KNM-ER 20419	1988	Allia Bay 251	left radius	M. Kyeve
KNM-ER 20420	1988	Allia Bay 261-1	left M ²	J. Kimengich
KNM-ER 20421	1988	Allia Bay 261-1	right M ³	Sieving team
KNM-ER 20422	1988	Allia Bay 261-1	left M ₁	Sieving team
KNM-ER 20423	1988	Allia Bay 261-1	left M ₂	Sieving team
KNM-ER 20427	1988	Allia Bay 261-1	left M ¹	Sieving team
KNM-ER 20428	1988	Allia Bay 261-1	left M ₃	Sieving team
KNM-ER 20432	1988	Allia Bay 261-1	left mandible fragment with canine root and P ₃₋₄	Sieving team
KNM-ER 22683	1988	Allia Bay 261-1	left P ₄	Sieving team
KNM-ER 24148	1988	Allia Bay 261-1	left dm ²	Sieving team
KNM-ER 30202	1995	Allia Bay 261-1	right I ¹	A. Walker
KNM-ER 30200	1995	Allia Bay 261	left maxilla with M ¹⁻³	K. Kimeu
(b)				
Specimen number	Side	Tooth	Mesiodistal diameter (mm)	Buccolingual diameter (mm)
KNM-KP 29281	L	I ₁	6.0	7.5
	R	I ₁	6.1	7.5
	L	I ₂	6.4	8.7
	R	I ₂	6.7	8.7
	L	C	(9.0)	9.6
	R	C	9.6	10.9
	L	P ₃	10.6	9.6
	R	P ₃	9.8	10.9
	L	P ₄	8.4	10.0
	R	P ₄	8.2	10.6
	L	M ₁	12.0	11.9
	R	M ₁	12.1	12.0
	L	M ₂	13.0	12.7
	R	M ₂	13.2	12.5
	L	M ₃	14.5	12.4
	R	M ₃	14.8	12.3
KNM-KP 29283	R	I ¹	8.4	8.6
	R	C	11.7	9.2
	L	P ³	9.0	12.6
	R	P ³	8.9	11.6
	L	P ⁴	7.7	11.7
	L	M ¹	(11.0)	(13.0)
	L	M ²	13.5	
	R	M ²	13.5	14.8
KNM-KP 29284	L	M ³	12.7	13.8
KNM-KP 29284	R	C	13.0	9.1
	R	P ₃	10.9	9.6
KNM-KP 29286	L	I ₁	6.6	
	L	I ₂		7.8
	R	I ₂		7.7
	R	C	9.2	11.7
	L	P ₃	9.9	12.4
	R	P ₃	9.6	12.0
	L	P ₄	9.7	11.7
	R	P ₄	9.6	11.6
	L	M ₁	12.3	12.0
	R	M ₁	12.3	12.2
	L	M ₂	14.6	13.7
	R	M ₂	14.6	13.6
	L	M ₃	14.4	12.8
	R	M ₃	13.8	12.3
KNM-ER 30200	L	M ¹	10.2	11.9
	L	M ²	11.5	13.2
	L	M ³	(11.0)	(12.0)
KNM-ER 30202	R	I ¹	10.5	9.0

(a) List of fossil hominids from Kanapoi and Allia Bay. The Allia Bay hominids, with the exception of KNM-ER 30200 and ER 30202, have been described by Coffing *et al.*¹⁷. (b) Tooth measurements of new Kanapoi and Allia Bay hominids. Measurements for other Allia Bay teeth are given in Coffing *et al.*¹⁷.

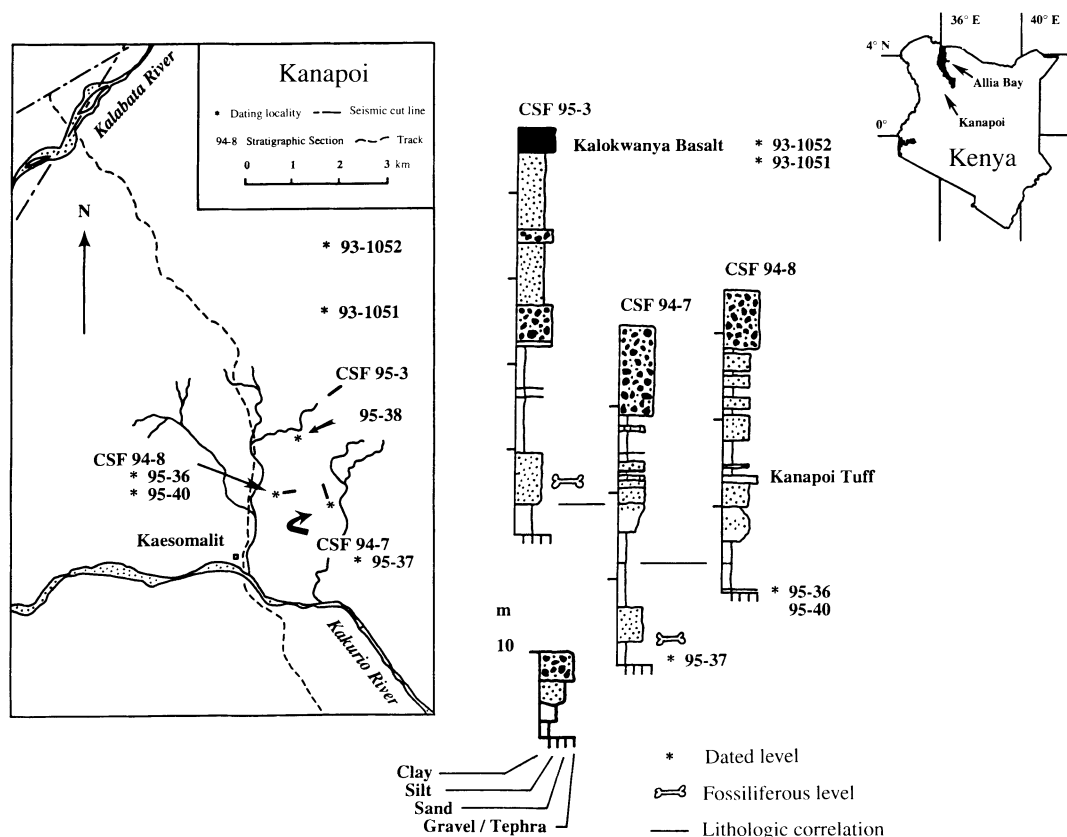


FIG. 2 Location maps and stratigraphic sections of the Kanapoi area. Geographic context of stratigraphic sections and dating samples, and lithostratigraphic sections showing relationship of fossiliferous units and dating samples. In the basal claystone unit of section CSF 94-8, small altered clasts (probably former pumices) were found to contain relatively fresh alkali feldspar crystals up to 1 mm in size. Samples from this level were used to prepare feldspar concentrates 95-36 (=K94-5401),

95-40 (=K95-5501). A third sample from the same horizon at another locality produced concentrate 95-38 (=K94-5490). Results of total fusion ^{40}Ar - ^{39}Ar dating of 8 single crystals from each of these samples are given in Table 2. In section CSF 94-7, a basal claystone unit also was found to contain small altered clasts, probably originally pumices. A bulk separate of alkali feldspar from this horizon, 95-37 (=K94-5385), provides supporting age control (Table 2).

ticular note are the *Homo*-like features of the tibia which complement those already noted for the Kanapoi humerus. This latter is quite large, from an individual judged by regressions based on humans to have weighed about 58 kg⁸. *A. anamensis* is seen as a possible ancestor to *A. afarensis*, although it is recognized that 4 Myr ago there may have been a number of newly emergent hominid species with variations based on the novel bipedal adaptation.

It should be noted that the *A. afarensis* hypodigm was collected from two localities, Laetoli and Hadar, which are ~1,500 km apart. *A. anamensis* can be readily distinguished from the younger Hadar sample, but has closer affinities with the older Laetoli specimens. In particular, similarities are seen in the very large size of the canines, the accessory distal cuspules of the lower canines, the exaggerated flare on the molars, the tapering upper molars and the vertically implanted upper canines. It must be noted, however, that the Laetoli sample is small, consisting almost entirely of parts of mandibles and isolated teeth and with no adult postcranial bones. Based on a fragmentary frontal from Belohdelie and a new skull from Hadar, Kimbel *et al.*⁴ suggested a prolonged stasis in *A. afarensis* between 3.9 and 3.0 Myr ago. These additional specimens from the early time period show both similarities to and considerable differences from the later Hadar sample. Given that mosaic evolution appears common in the Hominidae, and that there is no theoretical reason why there should be only one early hominid species at any one time, we feel that the case for overall stasis in the hominid skeleton for a million years might have been overstated. Detailed compari-

sons with *A. ramidus* cannot yet be made, but several features clearly distinguish it from *A. anamensis*. At present we know of no characters that would preclude *A. ramidus* from a position as the sister taxon to all other hominids.

The differences between *A. anamensis* and *A. ramidus* in tooth proportions and enamel thickness, together with temporomandibular joint differences such as postglenoid process position, probably indicate differences in food processing and/or food material properties. The recent discovery of a mandible of *Ardipithecus*² will allow this idea to be tested.

Geological context and dating

The Kanapoi sedimentary sequence (Fig. 2) includes three stratigraphic intervals. A basal sequence, deposited on a dissected volcanic landscape, includes conglomerates, sandstones and claystones indicative of a fluvial depositional environment. These strata are overlain by a lacustrine interval of claystones, molluscan packstones and an upward-coarsening deltaic cap. Succeeding strata indicate a return to fluvial conditions, with sandstones, claystones and several conglomeratic channels. These are capped by the Kalokwanya basalt.

Two tephra-bearing horizons occur within the lowermost interval of the Kanapoi sequence. Both are brown claystones containing light-coloured, altered clasts, probably former pumices, up to about 10 mm across. Vitric components in these altered clasts have been replaced by clay and zeolite minerals, leaving a residual population of alkali feldspar crystals ranging up to about 1 mm in size, suitable for ^{40}Ar - ^{39}Ar age determina-

TABLE 2 Results of single crystal dating

Sample	Mass (mg)	$^{36}\text{Ar}/^{39}\text{Ar}$ $\times 10^{-4}$	$^{37}\text{Ar}/^{39}\text{Ar}$ $\times 10^{-2}$	$^{40}\text{Ar}/^{39}\text{Ar}$	K/Ca	$^{40}\text{Ar}^*/^{39}\text{Ar}_K$ $\pm \text{c.v.}$	$^{40}\text{Ar}^*$ (%) (10 ⁻¹⁴ mol)	Calculated age Myr ± 1 s.d.		
93-1081A (K93-6024); Moiti Tuff pumice, Lokochot Cliff site, aerial photograph 1699/135-132, Koobi Fora; J=0.001182 \pm 0.30%; level 10, ANU4/211										
crystal 1	0.8	7.782	0.866	2.091	60.8	1.837 \pm 0.76%	87.9	1.14	3.912 \pm 0.032	
2	0.8	11.96	0.715	2.187	73.6	1.810 \pm 0.64%	82.7	1.20	3.854 \pm 0.027	
3	0.6	5.935	0.512	2.048	102.8	1.848 \pm 0.65%	90.3	1.04	3.935 \pm 0.028	
4	1.0	5.656	0.635	2.040	82.9	1.849 \pm 0.43%	90.6	1.48	3.938 \pm 0.021	
5	1.1	3.734	0.848	1.974	62.0	1.840 \pm 0.63%	93.2	1.63	3.917 \pm 0.027	
6	1.5	4.030	0.622	2.005	84.6	1.862 \pm 0.36%	92.9	2.05	3.965 \pm 0.018	
7	1.7	3.245	0.697	1.982	75.6	1.862 \pm 0.31%	94.0	2.33	3.964 \pm 0.017	
8	1.2	13.45	0.695	2.269	75.8	1.848 \pm 0.82%	81.4	1.50	3.934 \pm 0.034	
9	0.8	14.44	0.635	2.272	82.9	1.822 \pm 0.65%	80.2	1.10	3.879 \pm 0.027	
					\bar{x}_9	77.9 \pm 12.7			\bar{x}_9	3.922 \pm 0.037
95-36 (K94-5401); upper pumiceous tuff, section CSF 94-8/1, 0027/160-102, Kanapoi; J=0.001176 \pm 0.30%; level 3, ANU4/211										
crystal 1	1.1	2.371	2.082	2.038	25.3	1.940 \pm 0.51%	95.2	1.66	4.112 \pm 0.024	
2	2.0	2.547	2.235	2.046	23.5	1.943 \pm 0.47%	94.9	2.65	4.118 \pm 0.023	
3	1.0	2.800	2.007	2.052	26.2	1.941 \pm 0.46%	94.6	1.72	4.114 \pm 0.022	
5	1.2	3.036	0.476	2.067	110.6	1.947 \pm 0.72%	94.2	1.85	4.127 \pm 0.032	
7	0.8	3.275	2.369	2.070	22.2	1.945 \pm 0.52%	94.0	1.20	4.123 \pm 0.025	
8	1.0	3.008	1.981	2.061	26.6	1.944 \pm 0.79%	94.3	1.01	4.121 \pm 0.035	
9	1.1	9.475	10.04	2.155	5.2	1.944 \pm 0.40%	90.2	1.75	4.120 \pm 0.021	
					\bar{x}_7	34.2 \pm 34.5			\bar{x}_7	4.119 \pm 0.005
4	1.9	1.265	2.019	2.042	26.1	1.976 \pm 0.27%	96.8	3.62	4.189 \pm 0.017	
95-40 (K95-5501); upper pumiceous tuff, section CSF 94-8/1, 0027/160-102, Kanapoi; J=0.001180 \pm 0.30%; level 9, ANU4/211										
crystal 2	0.7	3.131	1.857	2.056	28.3	1.940 \pm 0.65%	94.4	1.01	4.124 \pm 0.030	
3	0.7	2.497	1.098	2.028	47.9	1.930 \pm 0.47%	95.2	1.28	4.103 \pm 0.023	
4	0.6	4.004	1.759	2.065	29.9	1.923 \pm 0.64%	93.1	1.17	4.088 \pm 0.029	
5	1.2	6.152	2.106	2.150	25.0	1.945 \pm 0.57%	90.5	1.75	4.135 \pm 0.027	
6	1.4	1.278	2.061	2.018	25.5	1.957 \pm 0.40%	97.0	1.98	4.161 \pm 0.021	
7	1.5	1.078	2.355	2.002	22.3	1.947 \pm 0.39%	97.3	2.49	4.139 \pm 0.020	
8	1.5	11.83	2.165	2.305	24.3	1.933 \pm 0.91%	83.8	0.94	4.109 \pm 0.039	
					\bar{x}_7	29.1 \pm 8.7			\bar{x}_7	4.123 \pm 0.025
1	0.7	10.40	1.689	2.210	31.2	1.879 \pm 1.00%	85.0	0.88	3.994 \pm 0.042	
95-38 (K95-5490); upper pumiceous tuff, 0027/148-156, Kanapoi; J=0.001177 \pm 0.30%; level 6, ANU4/211										
crystal 1	1.3	1.850	2.480	2.015	21.2	1.935 \pm 0.42%	96.0	2.60	4.105 \pm 0.021	
2	0.8	2.280	4.777	2.032	11.0	1.942 \pm 0.48%	95.6	1.86	4.120 \pm 0.023	
3	1.3	1.672	2.614	2.031	20.1	1.957 \pm 0.38%	96.4	2.37	4.151 \pm 0.020	
4	1.4	52.22	2.485	3.492	21.2	1.923 \pm 0.87%	55.1	2.07	4.079 \pm 0.037	
5	1.3	6.886	2.235	2.163	23.5	1.934 \pm 0.39%	89.4	2.65	4.102 \pm 0.020	
7	1.9	3.194	1.952	2.059	27.0	1.939 \pm 0.38%	94.2	2.65	4.112 \pm 0.020	
8	1.0	3.778	2.142	2.078	24.6	1.941 \pm 0.40%	93.4	1.54	4.117 \pm 0.021	
					\bar{x}_7	21.2 \pm 5.1			\bar{x}_7	4.112 \pm 0.022
6	2.1	1.502	2.342	2.146	22.5	2.076 \pm 0.36%	96.8	3.25	4.404 \pm 0.020	
95-37 (K94-5385); lower pumiceous tuff, section CSF 94-7/1, 0027/127-098, Kanapoi; J=0.001176 \pm 0.30%; level 4, ANU4/211										
crystal 1	0.9	8.215	2.252	2.206	23.4	1.936 \pm 0.49%	87.8	0.81	4.104 \pm 0.024	
2	1.8	1.360	2.246	2.041	23.4	1.974 \pm 0.91%	96.7	3.02	4.183 \pm 0.018	
3	1.5	13.88	3.653	2.404	14.4	1.968 \pm 0.23%	81.9	2.47	4.171 \pm 0.016	
4	1.2	2.279	2.348	2.074	22.4	1.980 \pm 0.38%	95.4	2.23	4.196 \pm 0.020	
5	1.3	1.836	2.305	2.048	22.8	1.966 \pm 0.37%	96.0	1.73	4.167 \pm 0.020	
7	1.2	2.868	0.796	2.066	66.1	1.952 \pm 0.26%	94.5	1.95	4.137 \pm 0.017	
8	1.1	1.740	0.745	2.060	70.7	1.980 \pm 0.30%	96.1	1.85	4.197 \pm 0.018	
9	1.3	2.386	5.549	2.073	9.5	1.979 \pm 0.24%	95.4	2.45	4.194 \pm 0.016	
10	1.2	2.148	2.582	2.042	20.4	1.952 \pm 0.24%	95.6	2.24	4.137 \pm 0.016	
					\bar{x}_9	30.3 \pm 22.1			\bar{x}_9	4.165 \pm 0.033
6	1.8	8.553	0.486	2.308	108.2	2.026 \pm 0.24%	87.8	3.15	4.295 \pm 0.016	

Results of single crystal laser fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating of anorthoclase crystals from a pumice in the Moiti Tuff, east of Allia Bay, and from tuffaceous horizons at Kanapoi, Kenya. The principles of $^{40}\text{Ar}/^{39}\text{Ar}$ dating and the general techniques utilized are given in McDougall and Harrison²². Approximately 20 crystals of feldspar, usually 0.5–1 mm maximum dimension and mass 0.5–2 mg, from each sample were packed in aluminium foil and placed successively in a silica glass tube, interspersed with small packets of sanidine fluence monitor (92-176, separated from the Fish Canyon Tuff, Colorado) of nominal K–Ar age 27.9 Myr^{23,24}. A synthetic potassium silicate glass was placed at either end of the silica glass tube, and the whole package encased in cadmium 0.2 mm thick within an aluminium reactor vessel for irradiation in facility X33 or X34 in HIFAR nuclear reactor, Lucas Heights, New South Wales, for 48 h. The reactor vessel was inverted three times during the irradiation at exactly 6 h intervals, to minimize the effect of neutron flux gradients. Following irradiation, individual alkali feldspar crystals were loaded into wells in a copper sample tray, installed in an ultra high vacuum system and baked overnight at 200 °C. A focused argon-ion laser beam up to 10 W power was used to fuse individual crystals. The gases released from each crystal were purified over SAES getters and then expanded directly into a Fisons VG3600 gas source mass spectrometer operated statically. Argon isotope measurements were made on ^{36}Ar , ^{37}Ar , ^{38}Ar , ^{39}Ar and ^{40}Ar , collecting data through a Daly detector and photomultiplier system. Mass spectrometer control and data acquisition was done using a Macintosh computer and Noble software. Sensitivity of the VG3600 operated at 200 μA trap current and 4.5 kV accelerating potential was about 2.9×10^{-17} mol mV^{-1} for argon on the Daly detector system. Mass discrimination was measured regularly using purified atmospheric argon from a gas pipette; the Daly collector system yielded $^{40}\text{Ar}/^{36}\text{Ar}$ ratios of 289 ± 2 over the course of this work. The irradiation parameter, J , for each unknown was derived by interpolation from the argon isotopic measurements made on gas released from the sanidine fluence monitor crystals (92-176). A minimum of three crystals was measured for each level of fluence monitor in the silica glass tube, with a precision of $\leq 0.3\%$ (standard deviation of the population). The ^{37}Ar and ^{39}Ar were corrected for decay. System blanks and backgrounds in the VG3600 were small to negligible. $\lambda = 5.543 \times 10^{-10} \text{ yr}^{-1}$; $^{40}\text{Ar}^*$ is radiogenic argon, $^{39}\text{Ar}_K$ is K-derived ^{39}Ar . The quoted error for each age includes estimated error in J , the irradiation parameter. ($^{36}\text{Ar}/^{37}\text{Ar}$)_{ca} = 3.49×10^{-4} ; ($^{39}\text{Ar}/^{37}\text{Ar}$)_{ca} = 7.86×10^{-4} ; ($^{40}\text{Ar}/^{39}\text{Ar}$)_K = 0.018 to 0.032, depending on position.

TABLE 3 Results of whole rock dating

Sample number	K wt (%)	Radiogenic ^{40}Ar	$100 \times \text{Rad. } ^{40}\text{Ar}$	Calculated age Myr ± 1 s.d.
		$10^{-12} \text{ mol g}^{-1}$	Total ^{40}Ar	
93-1052	0.959, 0.956	5.17	30.7	3.11 ± 0.04
93-1051	0.871, 0.874	5.16	26.0	3.41 ± 0.04

K-Ar age results on whole rock samples of the Kalokwanya Basalt, near Kanapoi, Kenya. $\lambda_e = 0.581 \times 10^{-10} \text{ yr}^{-1}$; $\lambda_\beta = 4.962 \times 10^{-10} \text{ yr}^{-1}$; $^{40}\text{K}/\text{K} = 1.167 \times 10^{-4} \text{ mol mol}^{-1}$. 93-1052: Basalt capping sandstone and conglomerate, air photo coordinates 0025/122-126. 93-1051: Basalt overlying conglomerate, air photo coordinates 0025/125-073.

tions on single crystals. Thus alkali feldspar was separated from clasts in sample 95-37 from the basal claystone in section CSF94-7 (Fig. 2), the lower of the two tuffaceous horizons. From the stratigraphically higher tephra, two separate samples of claystone (95-36, 95-40) from the same locality, near the base of section CSF94-8 (Fig. 2), provided alkali feldspar concentrates derived from the altered clasts. A further feldspar concentrate was prepared from sample 95-38 collected from a correlative horizon located about 1.3 km north northeast of section CSF94-8 (Fig. 2). Results of total fusion ^{40}Ar - ^{39}Ar dating of 8-10 single alkali feldspar crystals from each sample are given in Table 2, the footnotes of which describe the techniques used. As the uncertainty in each age generally is comparable at about 0.5% standard deviation, a simple mean age was calculated for the results from each sample. Any measured age differing by more than two standard deviations from the mean was eliminated as an outlier and a new mean and standard deviation of the population calculated. For each Kanapoi sample, one single crystal result was excluded by this criterion, and shown in Table 2 in italics. In general we have preferred to quote uncertainties in the

pooled ages as the standard deviation of the population rather than of the mean, as the latter yields values that are misleadingly small, especially when uncertainties in the irradiation parameter, J , of 0.3% are taken into account.

Feldspars from the lowermost tephra-bearing horizon, from sample 95-37, yielded a concordant set of measured ages on 9 crystals with a simple mean of 4.165 ± 0.033 Myr, after excluding one older age (Table 2). The weighted mean age is 4.167 ± 0.004 Myr, where the statistic quoted in this case is the standard deviation of the mean.

Single crystal alkali feldspar ages from the three samples (95-36, 95-38, 95-40) from the stratigraphically higher tuffaceous horizon at Kanapoi yield simple mean ages of 4.112 ± 0.022 , 4.123 ± 0.025 and 4.119 ± 0.005 Myr, respectively (Table 2). These mean ages cannot be distinguished from one another at the 95% confidence level, consistent with sampling a homogeneous population of feldspars in each case, as was expected from the stratigraphic position. Thus it is legitimate to combine all 21 accepted single crystal results from this horizon to yield a simple mean age of 4.118 ± 0.019 Myr (weighted mean age is 4.121 ± 0.004 Myr).

Statistical analysis of the ^{40}Ar - ^{39}Ar ages for the two pumiceous horizons from the lowermost stratigraphic unit at Kanapoi shows that they are readily distinguishable at the 95% confidence level; note that the results are in accord with the stratigraphic order.

It is inferred that these alkali feldspars are volcanic in origin, having crystallized from rhyolitic magmas that erupted explosively. The measured ages are considered to record the cooling of the feldspar crystals at the time of eruption. Deposition of the pumiceous material in the Kanapoi sequence is likely to have occurred very soon after explosive eruption.

TABLE 4 Fossil mammals from Kanapoi

Order	Family	Subfamily/tribe	Genus	Species
Macroscelidea	Macroscelididae		<i>Rhynchocyon</i>	sp.
Primates	Lorisidae	Galaginae	<i>Galago</i>	cf. <i>senegalensis</i>
	Cercopithecidae	Colobinae	gen. nov.	sp. nov.
		Cercopithecinae	<i>Parapapio</i>	aff. <i>ado</i>
	Hominidae		<i>Australopithecus anamensis</i>	
Rodentia	Scuiridae			
	Cricetidae		<i>Tatera</i>	sp.
	Muridae			
	Hystriidae		<i>Hystrix</i>	sp.
Carnivora	Mustelidae		<i>Enhydriodon</i>	sp.
	Viverridae		gen. indet.	
	Hyaenidae		<i>Parahyaena</i>	sp.
Proboscidea	Deinotheriidae		<i>Deinotherium bozasi</i>	
	Gomphotheriidae	Anancinae	<i>Anancus kenyensis</i>	
	Elephantidae	Elephantinae	<i>Loxodonta audorora</i>	
Perissodactyla	Equidae		<i>Hipparion</i>	sp.
	Rhinocerotidae	Rhinocerotinae	<i>Ceratotherium praecox</i>	
Artiodactyla	Suidae		<i>Nyanzachoerus kanamensis</i>	
			<i>Nyanzachoerus jaegeri</i>	
	Hippopotamidae		<i>Hexaprotodon</i>	cf. <i>protamphibius</i>
	Giraffidae		<i>Giraffa</i>	aff. <i>jumae</i>
			<i>Giraffa</i>	aff. <i>stillei</i>
	Bovidae	Tragelaphini	<i>Tragelaphus kyaloe</i>	
		Bovini		
		Reduncini	<i>Kobus</i>	sp. nov.
		Hippotragini		
		Alcelaphini	? <i>Damalacra</i>	sp.
		Aepycerotini	<i>Aepyceros</i>	sp.
		Antelopini	<i>Gazella</i>	sp.
		Neotragini	<i>Madoqua</i>	sp.
			<i>Raphiceras</i>	sp.

Within the deltaic interval, a vitric tephra, termed the Kanapoi tuff (Fig. 2), has been correlated with the Sutejun Tuff of the Chemeron Formation in the Baringo Basin¹⁵. Although not dated, this tephra is about 20 m below a geochemical correlative of the Lokochot Tuff (3.5 Myr¹⁶). A younger limit for the deposition of the sedimentary rocks at Kanapoi is given by K–Ar ages of 3.11 ± 0.04 Myr and 3.41 ± 0.04 Myr on whole-rock samples of the Kalokwanya basalt from the scarp northeast of Kanapoi (Fig. 2, Table 3). The measured ages on the basalts are regarded as reliable minima, as they contain a mesostasis, which may not retain radiogenic argon quantitatively. The combined isotopic dating evidence, therefore, indicates that deposition of the Kanapoi sedimentary sequence occurred during the interval from ~ 4.17 Myr to >3.4 Myr ago in the Pliocene.

However, there are good reasons for suggesting that the hominid fossils are derived from a more restricted time interval, based upon palaeogeographic evidence. The fossils come from the lower part of the Kanapoi sequence (Fig. 1), which is correlated with the Lonyumun Lake phase of the Turkana Basin²⁵. The upper fossiliferous zone is in sediments regarded as reflecting local deltaic infill of the lake. Our age measurements from Kanapoi show that the Lonyumun Lake came into existence about 4.2 Myr ago, consistent with data from elsewhere in the Turkana Basin²⁵. The Lonyumun Lake sediments are overlain by the Moiti Tuff, which has an age of 3.9 Myr (see below). Although the Moiti Tuff has not been found at Kanapoi, it occurs overlying the Lonyumun Lake sediments at Nakoret, about 50 km north of Kanapoi, as well as elsewhere in the Turkana Basin²⁵. On this basis we believe that the hominid fossils from Kanapoi are most probably confined to an age interval from 4.2 to 3.9 Myr.

Most of the vertebrate fossils at Kanapoi come from two stratigraphic levels. The lower level is the channel sandstone and overbank mudstone complex associated with the pumiceous tephra dated at 4.17 ± 0.02 and 4.12 ± 0.02 Myr. The upper fossiliferous zone is the distributary channel associated with the Kanapoi tuff (>3.5 Myr). Many of the hominid fossils, including the holotype mandible (KNM-KP 29281) and the maxilla (KNM-KP 29283), are from the lower level, and are thus tightly constrained in age between 4.17 Myr and 4.12 Myr. The tibia (KNM-KP 29285), the distal humerus (KNM-KP 271) and two

mandibular fragments (KNM-KP 29287) are from the upper level, older than 3.5 Myr and younger than 4.1 Myr.

The hominids from Allia Bay derive from beneath or within the Moiti Tuff¹⁷. Single crystal dating of 9 feldspar crystals from a pumice collected from the Moiti Tuff in the Koobi Fora region provided an essentially concordant set of ages with a simple mean of 3.92 ± 0.04 Myr (Table 2) or a weighted mean of 3.94 ± 0.01 Myr. This is younger than our previously published best estimate of $\leq 4.10 \pm 0.07$ Myr¹⁸ based on K–Ar age measurements on bulk alkali feldspar separates from three pumices. White *et al.*¹⁹ reported a ^{40}Ar – ^{39}Ar weighted mean age of 3.89 ± 0.02 Myr for feldspars from tuff VT-1 in the Maka area of Ethiopia. This tuff is regarded as a correlative of the Moiti Tuff on geochemical grounds. The age measurements are consistent with this suggested correlation.

Palaeoecology and fauna

The Kanapoi fossil vertebrates include over 30 mammalian taxa (Table 4), but fish and aquatic reptiles are common. A small *Parapapio*, *Parapapio* cf. *ado*, dominates the cercopithecids; only two colobine specimens were found. The most common carnivore was a precursor of the brown hyaena, cf. *Parahyaena*. The dominant bovid was a medium sized tragelaphine, *Tragelaphus kyalaoe*. Kudus and impalas (in the ratio 12:1, respectively) account for over half of the bovids, with antelopes and alcelaphines making up a further third, and bovines the remainder (J. M. Harris, personal communication).

Early hominids were apparently not restricted to a narrow range of habitats. Dry, possibly open, wooded or bushland conditions are indicated by the Kanapoi mammalian macro- and microfauna, although a wide gallery forest would have almost certainly been present on the large river that brought in the sediments. At Allia Bay there is a fauna that appears to be associated with the large proto-Omo river¹⁷, and a gallery forest is also indicated there by the presence of several large catarrhine species. These sites stand in contrast to Aramis, which is interpreted to have been closed woodland³. At Aramis, aquatic species and large mammals are rare, and colobines make up over 30% of all vertebrate specimens collected. The Laetoli palaeo-environment is believed to have been rather open with grassland, scattered trees and nearby woodland²⁰. A changing mosaic of habitats existed at Hadar, including closed and open woodland, bush and grassland²¹. □

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