

view of the similarity of Sandage and Tammann's¹¹ velocity-magnitude relationship (see their Fig. 4) in the supergalactic centre and anticentre directions, a peculiar anisotropy in the absolute magnitudes of Sc I galaxies which just compensates any anisotropy in the velocities is required if the cosmic expansion is not to be isotropic. We consider such a conspiracy to be less plausible than the hypothesis of isotropic expansion. The issue cannot be finally decided, however, until radial velocities and radial distribution of other kinds of matter at these distances are more accurately known. This will require velocity and magnitude data for several kinds of standard candles ('standard candle' meaning, in this context, a class of objects with an absolute magnitude dispersion $\lesssim 0.50$ mag, corresponding to the inhomogeneity scale $15 h^{-1}$ Mpc at these distances).

Of course, we do not expect the cosmic expansion to be perfectly isotropic in the direction of clusters and clouds of galaxies because these matter inhomogeneities will have perturbed the expansion to some extent. Since the perturbed galaxy velocities near an inhomogeneity are determined by the absolute amount of matter in the inhomogeneity, its mass and hence the mean matter density of the Universe can, in principle, be determined once the galaxy distribution and velocity field near the inhomogeneity are mapped out^{19, 27-29}. As we have shown, the Rubin-Ford data are consistent with an unperturbed galaxy velocity field and hence a low density Universe. Paradoxically, the apparent anisotropy of the radial velocities reported by RFR in ref. 1 may impose a rather strong upper limit to the mean matter density of the Universe. To see this, refer back to Fig. 1. Suppose now that matter is decelerated towards the centre of the supercluster at RA 12 h. Then the matter on this side of the supercluster centre will be closer to us than the distance assigned on the two-cloud model from Hubble's law. The galaxies in this cloud would then appear too bright to be consistent with the Rubin-Ford data. At this stage, we refrain

from carrying out a calculation of the mean matter density on this basis because of the uncertainties inherent in the limited data at hand. In view of the importance of this parameter and the hypothesis of isotropic expansion to cosmology, it would be very desirable to have more velocity and magnitude data for galaxies at these distances.

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Fossil hominids from the Laetolil Beds

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Remains of 13 early hominids have been found in the Laetolil Beds in northern Tanzania, 30 miles south of Olduvai Gorge. Potassium-argon dating of the fossiliferous deposits gives an upper limit averaging 3.59 Myr and a lower limit of 3.77 Myr. An extensive mammalian fauna is associated. The fossils occur in the upper 30 m of ash-fall and aeolian tuffs whose total measured thickness is 130 m.

THE fossil-bearing deposits referred to variously as the Laetolil Beds, Garusi or Vogel River Series lie in the southern Serengeti Plains, in northern Tanzania, 20-30 miles from the camp site at Olduvai Gorge.

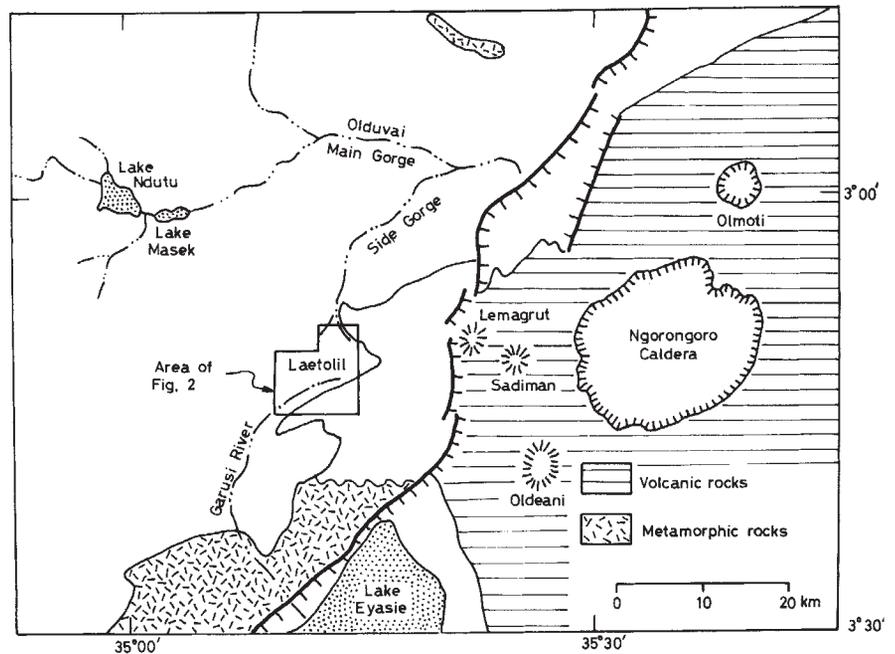
Fossils have been collected from the area on several occasions, the largest collection being made by L. Kohl-Larsen in 1938-39, who also found a small fragment of hominid maxilla which was named *Meganthropus africanus* by Weinert¹. L. S. B. Leakey and M.D.L. visited the area in 1935 and in 1959, while a day trip was made in 1964 in company with R. L. H. The faunal material recovered on these occasions was all collected before the advent of isotopic dating and the age of the fossils remained uncertain until potassium-argon dating was carried

out on samples of biotite obtained during the 1975 field season. In 1974, however, lava flows which unconformably overlie the Laetolil Beds had been dated by G. H. C. at 2.4 Myr.

We now report evidence that fossiliferous deposits of several different ages exist in the Laetolil area and that specimens found on the surface are not necessarily derived from the same beds. There are, however, noticeable variations in the colour and physical condition of the surface fossils which provide indications of their origin.

Discrepancies in the fauna were noted by Dietrich² and Maglio³ who both postulated faunal assemblages of two different ages. In view of this, it was proposed for a time that the name Laetolil should be abandoned in favour of the more generalised term Vogel River Series, based on the colloquial German name for the Garusi river, which abounds in bird life. As the early fossiliferous deposits here referred to as the Laetolil Beds are not confined to the Garusi valley, this change of name seems unnecessary. Furthermore, the name Laetolil embraces a larger area, because it is the anglicised version of the Masai name (laetoli) for *Haemanthus*, a red lily that is abundant in the locality. The Laetolil Beds, *sensu stricto*, form a discrete unit, distinguishable from later deposits, and M.D.L. considers that the original name proposed by Kent

Fig. 1 Map of the southern Serengeti and volcanic highlands.



in 1941⁴ should be retained for this part of the sequence.

The relationship of the Laetolil to the Olduvai Beds had been under discussion for some years, but in 1969 R. L. H. noted that they underlay bed I at the Kelogi inselberg in the Side Gorge and established that they antedated the Olduvai sequence. This has been further confirmed when tuffs correlative with bed I as well as an earlier, fossil-bearing series of tuffs were found to lie unconformably on the Laetolil Beds.

Interest in the area was renewed in 1974 after the discovery by George Dove of fossil equid and bovid teeth in the bed of the Gagjingero river, which drains into Lake Masek at the head of Olduvai Gorge. These fossils were found to be eroding from relatively recent deposits, probably the beds named Ngaloba by Kent⁴. Exposures of the Laetolil Beds, not hitherto seen by M.D.L., were found to the east of the Gagjingero river, at the headwaters of the Garusi river and of the Olduvai Side Gorge (referred to as Marambu by Kohl-Larsen⁵). Several fossils, including a hominid premolar, were found at these localities and subsequent visits yielded further hominid remains.

The possibility of establishing the age of the hominid fossils from the Laetolil Beds by radiometric dating and of clarifying the discrepancies in the faunal material led to a 2-month field season during July and August 1975. Samples from the fossiliferous horizons, collected by R. L. H., have now been dated. On the basis of these results the hominid remains and associated fauna can be bracketed in time between 3.59 and 3.77 Myr.

No trace of stone tools or even of utilised bone or stone was observed in the material from the Laetolil Beds, although handaxes and other artefacts occur in conglomerates which are present in certain areas and which are unconformable to the Laetolil Beds.

Stratigraphy of Laetolil area

The bulk of the faunal remains and all of the hominid remains were found within an area of about 30 km² at the northern margin of the Eyasie plateau and in the divide between the Olduvai and Eyasie drainage systems (Fig. 1).

Kent studied this area as a member of L. S. B. Leakey's 1934–35 expedition, and his short paper is the only published description of the stratigraphy. He recognised three main subdivisions of the stratigraphic sequence, which overlies the metamorphic complex of Precambrian age. The lower unit he named the Laetolil Beds and the upper the Ngaloba Beds. The middle unit consists of olivine-rich lava flows and agglomerate, which are much closer in age to the Laetolil Beds than to

the Ngaloba Beds. Kent briefly noted the local occurrence of tuffs younger than the lavas and older than the Ngaloba Beds. He described the Laetolil Beds as subaerially deposited tuffs, and he gave 30 m as an aggregate thickness in the vicinity of Laetolil. The Ngaloba Beds he described as tuffaceous clays, and he gave a thickness of about 5 m at the type locality. Pickering mapped this area as part of a 1:125,000 quarter degree sheet⁶ and extended the known occurrence of the Laetolil Beds. He also recognised that at least some of the tuffs are of nephelinite composition.

This picture was modified considerably by stratigraphic work in 1974 and 1975. The Laetolil Beds proved to be far thicker and more extensive than previously recognised. The thickest section, 130 m, was measured in a valley in the northern part of the area (geological localities A to C, Fig. 2). The base is not exposed and the full thickness of the Laetolil Beds here is unknown. Sections 100–120 m thick and representing only part of the Laetolil Beds were measured about 10 km south-east of Laetolil. The Laetolil Beds are 15–20 m thick at a distance of 25–30 km to the south-west and 10–15 m thick at Lakes Masek and Ndutu, 30 km to the north-west. The Laetolil Beds are tuffaceous sediments, dominantly of nephelinite composition.

The lavas and agglomerates noted by Kent overlie an irregular surface deeply eroded into the Laetolil Beds. The lavas were erupted from numerous small vents to the south, south-west and west of Lemagrut volcano. Although designated as nephelinite by Kent, the flows proved to be vogesite, a highly mafic lava with interstitial alkali feldspar and phlogopitic biotite. The lavas have reversed polarity as determined by field measurements (personal communication from A. Cox). A sample of lava from geological locality D (Fig. 2) gave K–Ar dates of 2.38 ± 0.5 Myr and 2.43 ± 0.7 Myr (Table 1).

The 130-m section of the Laetolil Beds (Fig. 3) is divisible into an upper half consisting largely of wind-worked, or aeolian, tuff⁷ and a lower half consisting of interbedded ash-fall and aeolian tuff with minor conglomerate and breccia. Tephras in the lower half are nephelinite, whereas nephelinite and melilitite are subequal in the upper half. Between these two divisions is a distinctive biotite-bearing coarse lithic-crystal tuff 60 cm thick. Hominid remains and nearly all of the other vertebrate remains are confined to the uppermost 30 m of aeolian tuffs beneath a widespread pale yellow vitric tuff 8 m thick (tuff d of Fig. 3). Several other marker tuffs, between 1 m and 30 cm thick, can be used for correlating within the fossiliferous 30-m thickness of sediments. The three prominent marker tuffs, designated a, b, and c (Fig. 3, column 2), can be recognised

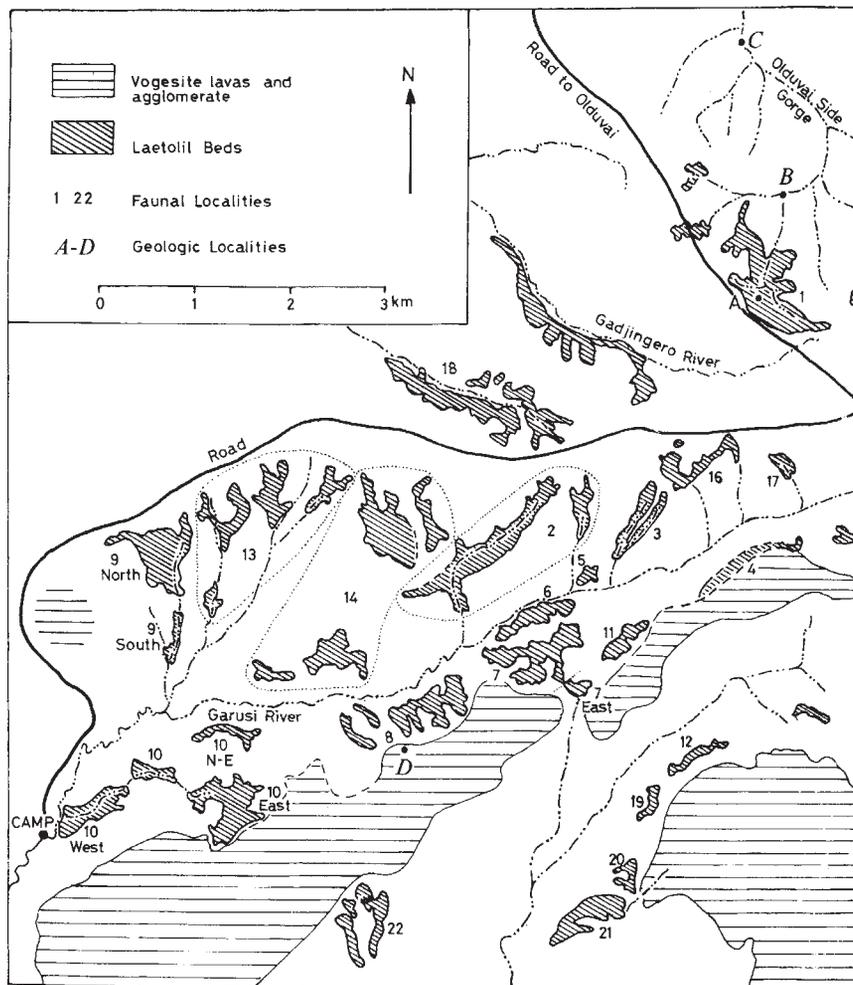


Fig. 2 Map of the Laetolil area showing the fossil beds.

throughout the area shown in Fig. 2. Widespread horizons of ijolite and lava (mostly nephelinite) xenoliths are at several levels in the fossiliferous part of the section and assist in correlating. Biotite is common in some of the ijolite.

Additional fossiliferous deposits, of mineralogical affinity to the Laetolil Beds and 10–15 m thick, lie between tuff *d* and the bed I (?) tuffs at several places. They are locally separated from tuff *d* and the underlying aeolian tuffs of the Laetolil Beds by an erosional surface with a relief of 8 m. These sediments comprise water-worked tuffs, aeolian tuffs, clay-pellet aggregate of aeolian origin and limestone. The tephra are of phonolite and nephelinite composition. It is not yet clear whether or not these sediments should be regarded as part of the Laetolil Beds.

Beds I and II are represented by sedimentary deposits that lie stratigraphically between the lava and the Ngaloba Beds. The bed II deposits locally contain fossils and artefacts.

Sadiman volcano, about 15 km east of the fossiliferous exposures, seems to have been the eruptive source of the Laetolil Beds. The one K–Ar date, of 3.73 Myr, obtained from Sadiman lava, fits with the K–Ar dates on the Laetolil Beds presented here. This date was published previously as K–Ar 2238 (ref. 8), where it was incorrectly assigned to Ngorongoro because of a mistake in listing the sample numbers.

Potassium–argon dating

The vogesite lava is composed of approximately 85–90% olivine and augite. The remainder is principally anorthoclase in the groundmass together with a very small amount of phlogopitic biotite. These two minerals proved too fine-grained and sparse for effective separation, and whole-rock samples were used for dating.

Table 1 K–Ar dates from the Laetolil area

Sample	KA no.	Dated material	Sample weight (g)	% K	mol g ⁻¹ ⁴⁰ Ar radiation × 10 ⁻¹¹	% ⁴⁰ Ar atmosphere	Age yr (Myr)	Remarks
Vogesite lava, location D	2835	Whole rock	10.06588	1.013	0.419	74.0	2.38 ± .05	Unconformably overlying Laetolil Beds
	2837R	Whole rock	11.27408	1.013	0.427	84.4	2.43 ± .08	
	2929	Whole rock	1.98629	6.96 ± .03	4.118	77.5	3.41 ± .08	Treated with dilute HCl
Tuff c, location A	2977	Whole rock	2.544	6.98 ± .04	4.462	78.5	3.68 ± .09	Treated with warm dilute acetic acid
	2979	Whole rock	1.94298	6.95 ± .04	4.454	79.1	3.69 ± .10	
Xenolithic horizon, location A	2930	Whole rock	3.07730	7.58 ± .02	4.771	50.8	3.62 ± .09	Treated with dilute HCl
	2930R	Whole rock	1.83909	7.58 ± .02	4.733	39.7	3.59 ± .05	
Ash-fall tuff, location B	2932	Whole rock	1.05978	6.00 ± .1	3.996	75.0	3.82 ± .16	Crushed, hand picked, treated with dilute HCl
	2938	Whole rock	1.42092	6.49 ± .04	4.182	78.8	3.71 ± .12	

⁴⁰K/K = 1.18 × 10⁻⁴; ⁴⁰K_λ = 5.480 × 10⁻¹⁰ yr⁻¹; ⁴⁰K_{λβ} = 4.905 × 4.905 × 10⁻¹⁰ yr⁻¹; ⁴⁰K_{λε} = 0.575 × 10⁻¹⁰ yr⁻¹.

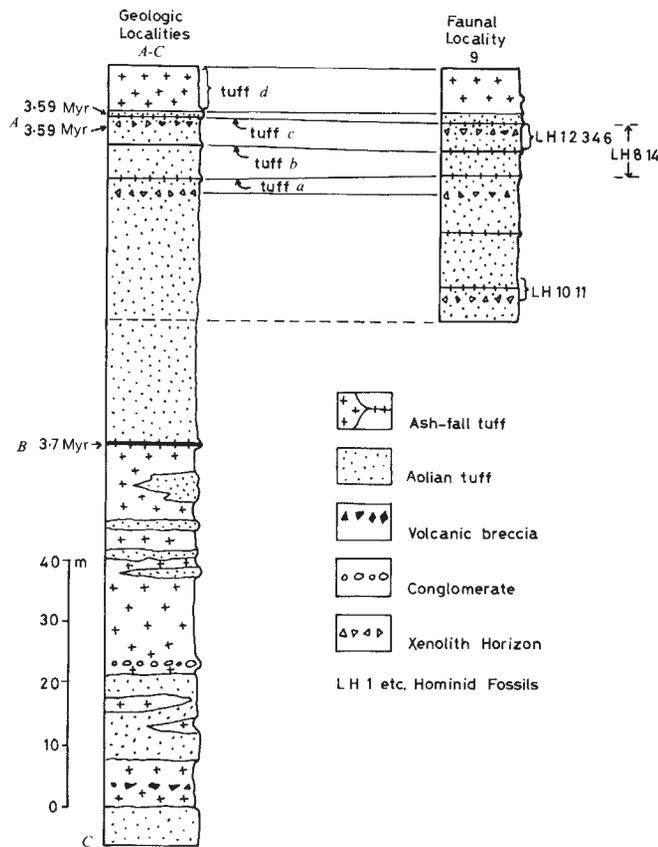


Fig. 3 Stratigraphic column of the Laetolil Beds showing the positions of the dated tuffs and hominid fossils.

In addition to the vogesite lava unconformably overlying the Laetolil Beds, three of the tuffaceous layers within the Laetolil Beds have been dated by the conventional, total degassing K-Ar method (Table 1), and one of these tuffaceous layers has also been dated by the $^{40}\text{Ar}/^{39}\text{Ar}$ method, using incremental heating.

Tuff c is the uppermost of the dated horizons, lying near the top of the fossiliferous deposits. It is a widespread crystal-lithic air-fall tuff cemented with calcite and generally 10–15 cm thick. Abundant biotite crystals 1–2 cm in diameter occur in the upper part of the tuff, which is composed of nepheline and milelitite. The dated crystals were hand-picked from two outcrops of the tuff at locality A (Figs 2 and 3). The cementing calcite adhering to and interleaving the biotite books was removed by treatment with dilute HCl for a few minutes on one sample and with warm dilute acetic acid on two other samples. This treatment was found to have negligible deleterious effects on biotite standard samples. The three dates obtained for tuff c (3.41 ± 0.08 Myr, 3.68 ± 0.09 Myr, and 3.69 ± 0.10 Myr) have about equal precision so were averaged to give a date of 3.59 Myr.

Two conventional K-Ar dates and one $^{40}\text{Ar}/^{39}\text{Ar}$ were obtained from a single biotite crystal from a xenolithic horizon at locality A (Figs 2 and 3) approximately 1–2 m below the youngest tuff dated (tuff c). This horizon lies within the upper part of the fossiliferous beds and is distinguished by its ejecta of ijolite xenoliths together with nephelinite lava xenoliths. Although the biotite occurs in some of the ijolite clasts, a large single free crystal picked from the tuff was used for dating. The good agreement between the two conventional K-Ar dates for this sample (3.62 ± 0.09 Myr and 3.59 ± 0.05 Myr) and the $^{40}\text{Ar}/^{39}\text{Ar}$ date which yielded an isochron age of 3.55 Myr (Fig. 4) indicates that initial excess ^{40}Ar is not a problem with this sample, and that these dates give an average age for this horizon of 3.59 Myr.

Two dates were obtained from a biotite-bearing crystal-lithic tuff 60 cm thick lying approximately 50 m below tuff c near the middle of the thickest section of the Laetolil Beds at location

B (Fig. 2). The tuff is of nephelinite composition, containing abundant augite and altered nepheline and 2–3% of biotite, some crystals of which are as much as 1 cm in diameter. Calcite cements the crystals and fragments together. Biotite was separated by crushing, screening and hand picking and was cleaned of calcite with dilute HCl. Two dates, 3.82 ± 0.16 Myr and 3.71 ± 0.12 Myr, average 3.77 and give a lower limit to the age of the hominid remains (which occur below but close to the dated xenolithic horizon higher in the section) in the 30 m section at locality A (Fig. 2) whose base projects approximately 20 m above this tuff at locality B (Fig. 3).

Fauna

The fossiliferous deposits in the Laetolil area have been subdivided, for purposes of collecting, into 26 localities. These subdivisions are based on existing topographic features such as grassy ridges, lines of trees, stream channels and so on. This has provided a means of dividing the fossiliferous area into units of restricted size, but does not relate to the former topography.

Eighteen of these localities are in the Garusi valley, one in the valley at the head of the Olduvai Side Gorge, one in the Gadjingero valley, five in a valley to the south of the Garusi river and one in an isolated position to the west (Fig 2).

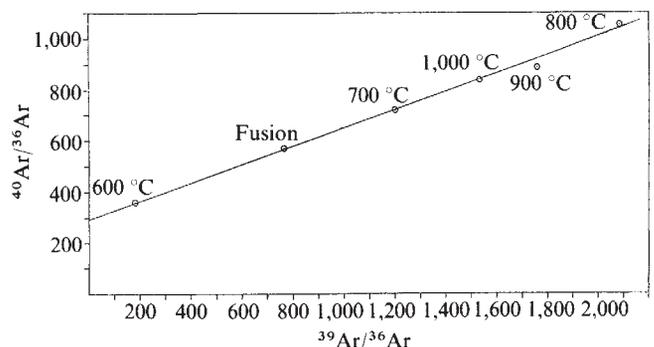
Identifiable fossils noted on the exposures were either collected and registered or listed on the sites. Specimens from the Laetolil Beds were distinctively cream coloured or white and sometimes chalky in texture, but the surface material also included brown, grey or black specimens, often rolled. These have been excluded from the material under review, together with fossils which have adhering matrix clearly dissimilar from the tuffs of the Laetolil Beds. Among these are all remains of *Hippopotamus*, *Equus*, *Theropithecus*, *Phacochoerus* and *Tragelaphus*, formerly included in the Laetolil fauna, with the exception of *Hippopotamus*.

The fossil material from the Laetolil Beds is dispersed and fragmentary and it is not possible to assess the number of individuals represented. In this article, 'numbers of fossils' refer to individual bones and teeth, except in the case of clear association, confined almost entirely to remains of *Serengetilagus* and *Pedetes*, some of which were associated and even articulated.

Table 2 shows the mean percentage frequency of the more common vertebrate groups at several of the richer localities. A total of 6,288 fossil specimens was identified from the localities considered here.

Reptiles are represented by snake vertebrae at three localities and by tortoises at all localities. The latter have an average frequency of 2.2% and include several giant specimens. Avian remains occur widely and at several localities birds' eggs were completely preserved. There is one example of a shattered clutch of at least eight eggs, rather smaller in size than eggs of domestic fowl. Primates were found at 15 localities, and in one area they constitute 3.8% of the fauna. Both cercopithecines and colobines are present (M. G. Leakey, personal communication).

Fig. 4 $^{40}\text{Ar}/^{39}\text{Ar}$ incremental heating of biotite from xenolithic horizon, locality C. Isochron age, 3.55 Myr; $[^{40}\text{Ar}/^{39}\text{Ar}]_0 = 294$; $^{40}\text{Ar}/^{39}\text{Ar} = 0.35318$; $J = 0.005204$.



Rodents are fairly well represented, although not abundant. Of the specimens identified by J.J. Jaeger, the most common are *Pedetes*, *Saccostomus* and *Hystrix*. The carnivore fauna is characterised by a high percentage of viverrids, constituting 32% of all the carnivore specimens. Large carnivores are represented by hyaenids, of which there are several genera, by felids and a machairodont.

Proboscidea include *Deinotherium* and *Loxodonta sp.* (M. Beden, personal communication). There is no evidence that the equid material (other than that derived from later deposits) includes any genus except *Hipparion*. The suids consist only of two genera, *Potamachoerus* and *Notochoerus* (J. Harris, personal communication). The presence of *Ancylotherium* and *Orycteropus*, noted in previous collections, is confirmed and the existence of two rhinocerotids has been established by the discovery of skulls of both *Ceratotherium* and *Diceros*, although only the former was listed previously.

Among the giraffids, *Sivatherium* and a small form of giraffe are equally common. *Giraffe jumae* is also present but is much

Table 2 Mean percentage frequency of bones of more common vertebrate groups

Group	Mean percentage	Range	Nos of localities
Bovidae	43.0	29.5–57.9	18
Lagomorpha	14.4	5.6–24.0	18
Giraffidae	11.2	6.8–23.2	18
Rhinocerotidae	9.7	5.7–17.3	18
Equidae	4.4	1.7–7.1	18
Suidae	3.6	1.0–7.1	18
Proboscidea	3.4	1.0–5.1	18
Rodentia	3.3	0.9–7.2	17
Carnivora	3.1	0.8–8.2	17

less well represented. The bovid fauna is chiefly characterised by the very high percentage of *Madoqua* (dikdik). In 18 localities dikdik range from 1.5 to 37.7% of all bovid specimens, with a mean percentage of 15.1%.

The 1975 field season, although mainly confined to surface collection, has established that previous collecting had sampled faunas of several time periods. It is now possible to exclude some genera from the published lists of fauna from the Laetolil Beds^{2,9}, such as *Theropithecus*, *Tragelaphus*, *Equus* and *Phacochorus*.

Fossil hominids

Thirteen new fossil hominid specimens were recovered from the Laetolil site during 1974 and 1975. The remains include a maxilla, mandibles and teeth. This sample displays a complex of characters seemingly demonstrative of phylogenetic affinity to the genus *Homo*, but also features some primitive traits concordant with its great age.

The hominid specimens are listed in Table 3. Provisional stratigraphic correlation and dating have placed the hominid remains as shown in Fig. 3. With the exception of Laetolil hominids (LH) 7 and 8, all specimens retain the matrix characteristic of the Laetolil Beds from which they have been weathered or excavated. There is no reason to doubt that all the specimens derive from the Laetolil Beds as reported.

The Laetolil hominid sample consists of teeth and mandibles. Important features of these specimens are described here, followed by a brief preliminary discussion regarding the phylogenetic status of the fossils.

Remains of deciduous and permanent dentitions have been recovered. The dentitions consist of two maxillary and four mandibular partial tooth rows. Compared with the rest of the East African Pliocene/early Pleistocene hominid sample, the Laetolil anterior teeth are large and the postcanine teeth of small to moderate size.

Deciduous dentition

Canines (LH 2, 3) Single upper and lower deciduous canines are known. The lower is a slightly projecting, sharp conical tooth in its damaged state. It is smaller but its overall morphology is similar to its permanent counterpart.

First molars (LH 2, 3) The upper first deciduous molar displays spatial dominance of the protocone and a well-marked mesio-buccal accessory cusp defined by a strong anterior fovea. The lower first deciduous molar is molarised, with four or five main cusps depending on hypoconulid expression. There is a spatially dominant protoconid with a large flat buccal face, a lingually facing anterior fovea, and an inferiorly projecting mesio-buccal enamel line. Vertical dominance of the protoconid and metaconid is marked in lateral view.

Second molars (LH 2, 3, 6) Upper and lower deciduous second molars take the basic form of the analogous permanent first molars but are smaller in overall size. The dM_2 of LH 2 is the only lower molar in the Laetolil sample bearing any indication of a tuberculum sextum.

Table 3 Hominid remains recovered in 1974–75

Laetolil hominid (LH)	Locality	Specimen consists of	Discovered by
1	1	RP ⁴ fragment	M. Muoka
2	3* ¹	Immature mandibular corpus with deciduous and permanent teeth	M. Muluila
3 (a–t)	7*	Isolated deciduous and permanent teeth, upper and lower	M. Muoka
4	7	Adult mandibular corpus with dentition	M. Muluila
5	8	Adult maxillary row: I ² to M ¹	M. Muluila
6 (a–e)	7*†	Isolated deciduous and permanent teeth, upper	M. Muoka
7	5	RM ¹ or ² fragment	M. Muoka
8	11	RM ² , RM ³	E. Kandindi
10	10W	Fragment left mandibular corpus with broken roots	E. Kandindi
11	10W	LM ¹ or ²	E. Kandindi
12	5	LM ² or ³ fragment	E. Kandindi
13	8	Fragment right mandibular corpus with broken roots	M. Jackes
14	19	Isolated permanent teeth, lower	E. Kandindi

LH 9 was not valid.

**In situ*.

†LH 3 and 6 associated in mixed state.

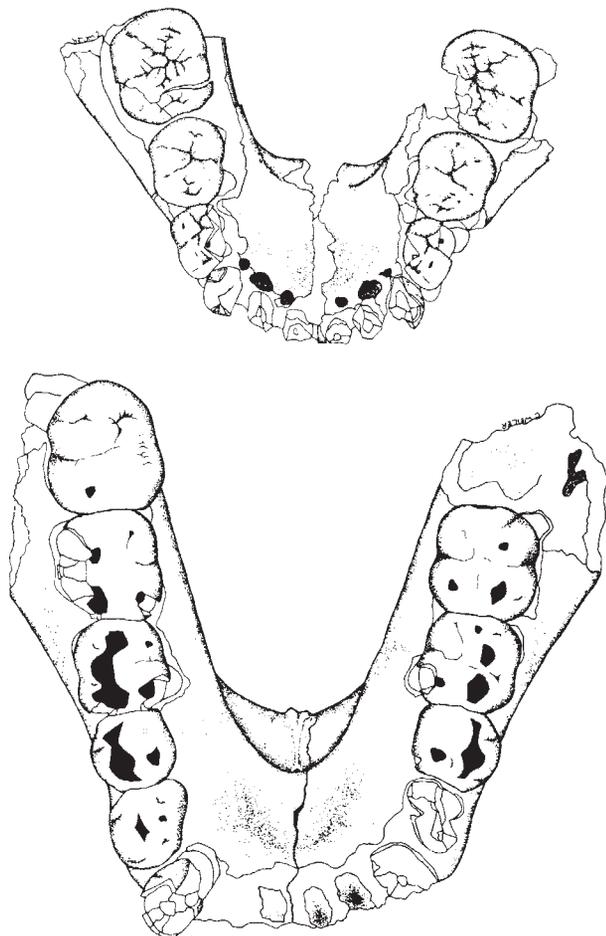


Fig. 5 Occlusal views of juvenile and adult mandibles (LH 2 and 4).

Permanent dentition

Incisors (LH 2, 3, 5, 6, 14) The single upper central incisor is very large and bears pronounced lingual relief. The upper lateral incisors are smaller, with variable lingual relief. The lower incisors are narrow and very tall, with minimal relief.

Canines (LH 2, 3, 4, 5, 6, 14) The incompletely-developed upper canine LH 3 is large, stout and pointed, bearing pronounced lingual relief. LH 6 is slightly smaller, with less lingual relief and a tall, pointed crown. LH 5 bears an elongate dentine exposure on its distal occlusal edge but does not project beyond the occlusal row in its worn state. The lower canines are similar to the uppers in their great size, height and lingual relief.

Premolars (LH 1, 2, 3, 4, 5, 6, 14) The upper premolars tend to be buccolingually elongate and bicuspid, with the lingual cusp placed mesially and an indented mesial crown face. The two lower third premolars each have a dominant buccal cusp with mesial and distal occlusal ridges, and a weak lingual cusp placed mesial of the major crown axis. The long axis of the oval crown crosses the dental arcade contour from mesiobuccal to distolingual, donating a 'skewed' occlusal profile to the tooth. The lower fourth premolars are fairly square in shape with major buccal and lingual cusps and moderate talonids.

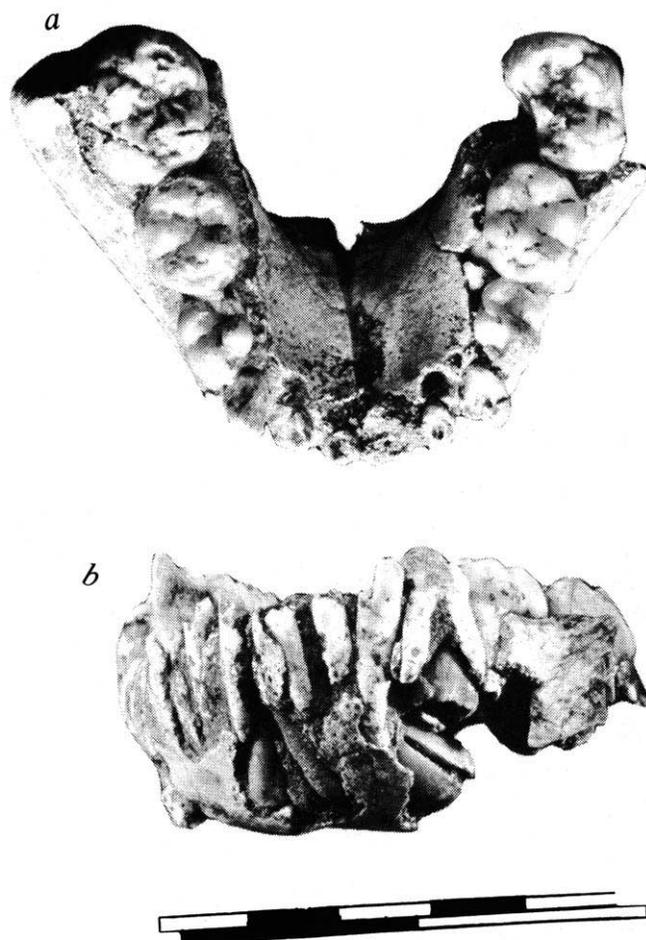
Molars (LH 2, 3, 4, 5, 6, 7, 8, 11, 12, 14) The upper molars are of moderate size, their relative proportions unknown. They show a basic four-cusp pattern with spatial dominance of the protocone and typical expression of a pit-like Carabelli feature. The lower molars display progressive size increase from first to third in LH4. They have a fairly square occlusal outline with hypoconulid appressed anteriorly between hypoconid and entoconid and no trace of a tuberculum sextum. The Y-5 pattern of primary fissuration is constant.

Mandibles

Juvenile mandible (LH 2) This specimen (Figs 5 and 6) is incompletely fused at the midline, and the developing crowns of the permanent canines and premolars are exposed in the broken corpus. The first molars have just reached the occlusal plane. Only the posterior aspect of the symphysis shows fairly intact contours, with a concave post-incisive planum and incipient superior transverse torus. The genioglossal fossa is obscured by midline breakage. Associated distortion has artificially increased the bimolar distances.

Adult mandible (LH 4) The adult mandibular corpus is well preserved, with the rami missing (Figs 5 and 7). The dental arcade is essentially undistorted, and presents fairly straight sides which converge anteriorly. The anterior dentition has suffered *post mortem* damage and loss, except for the right lateral incisor which seems to have been lost in life. Largely resorptive alveolar pathology has obliterated its alveolus and has affected the adjacent teeth. There is development of wide interproximal facets for the canine teeth but no C/P₃ contact facet. This combines with observation of extensive wear on the buccal P₃ face to suggest that C/P₃ interlock has prevented mesial drift from eliminating the C/P₃ diastema. Judging from the preserved posterior incisor alveoli, these teeth were set in an evenly rounded arcade, projecting moderately anterior to the bicanine axis. The internal mandibular contour is a very narrow

Fig. 6 Juvenile mandible from the Lactolil Beds (LH 2). *a*, Occlusal view; except for the first molars all the teeth are deciduous. *b*, Front view showing the central incisors, canine and P₃ in the bone.



parabola in contrast to the wider basal contour which displays great lateral eversion posteriorly. There are weak to moderate superior and inferior transverse tori, the latter bearing strong mental spines.

The anterior root of the ramus is broken at its origin, lateral to M_2 . Occlusal and basal margins diverge strongly anteriorly, resulting in a deep symphysis. The symphysis is angled sharply posteriorly and the anterior symphyseal contour is rounded and bulbous. The lateral aspects of the corpus have very flat posterior portions and distinctive hollowing in the areas above the mental foramina at the P_3 to P_4 position. The corpus is tall and fairly narrow, especially in its anterior portion.

Implications of the specimens

The Laetolil fossil hominid sample, including the original Garusi maxillary fragment⁹, seems to be representative of only one phylogenetic entity or lineage. The variations observed in the material seem to be primarily size-based and stem from individual and sexual factors.



Fig. 7 Adult mandible from the Laetolil Beds (LH 2), occlusal view.

The deciduous teeth, particularly the lower deciduous first molars, display remarkable similarity to hominid specimens from South Africa (Taung; STS 24)¹⁰ as well as to individuals tentatively assigned to *Homo* in East Africa (KNM ER 820, 1507)^{11,12}. They depart strongly from the pattern of molarisation displayed in the South African "robust" specimens (TM 1601; SK 61, 64)¹⁰ as well as from East African specimens generally assigned to the same hominid lineage (KNM ER 1477)¹³.

The Laetolil permanent canines and incisors are relatively and absolutely large and bear a great deal of lingual relief. They ally themselves similarly to earlier hominid specimens such as STS 3, 50, 51, 52; MLD 11; OH 7, 16; KNM ER 803, 1590 (refs 10, 15, 18–21), as well as to the younger African and Asian specimens usually assigned to *Homo erectus*. These features set the Laetolil specimens apart from the sample including SK 23, 48, 876 and so on; Peninj; KNM CH 1; OH 5,

38; KNM ER 729, 1171 (refs 10, 15, 18–21). The Laetolil permanent premolars show none of the molarisation seen in the latter specimens and bear particularly strong resemblances to South and East African material (STS 51, 52, 55; OH 7, 16, 24; KNM ER 808, 992 (refs 10–12, 14)).

The Laetolil permanent molars are consistent in aligning with the South African "gracile" australopithecus and the East African *Homo* material in both size and morphology. The molars do not display the increased size, extra cusps or bulging, expanded, "puffy" development of the individual cusps seen in high frequency among South and East African "robust" forms (SK 6, 13, 48, 52; TM 1517; Peninj; KNM CH 1; KNM ER 729, 801, 802) (refs 10, 17–20). The adult mandible has resemblances to certain East African specimens such as KNM ER 1802, with similar corpus section and basal eversion.

The Laetolil fossil hominids have several features possibly consistent with their radiometric age. These traits include the large crown size and lingual morphology of the permanent canines; the morphology and wear of the C/P₃ complex; the buccolingually elongate upper premolars; the overall square occlusal aspect of the lower permanent molars; the low symphyseal angle; the bulbous anterior symphysis; the relatively straight posterior tooth rows; the low placement of the mental foramina, and the distinctive lateral corpus contours including small, superiorly placed extramolar sulci.

Preliminary assessment indicates strong resemblance between the Laetolil hominids and later radiometrically-dated specimens assigned to the genus *Homo* in East Africa. Such assessment suggests placement of the Laetolil specimens among the earliest firmly dated members of this genus. It should come as no surprise that the earlier members of the genus *Homo* display an increasing frequency of features generally interpreted as "primitive" or "pongid like", which indicate derivation from as yet largely hypothetical ancestors.

Much of the recently discovered comparable fossil hominid material from the Hadar region of Ethiopia shows strong similarity to the Laetolil specimens²³, and further collection combined with detailed comparative analysis of material from both localities is essential for the further understanding of human origins. The Laetolil collection adds to the developing phylogenetic perspective of the early Hominidae and emphasises the need for taxonomic schemes reflective of and consistent with the evolutionary processes involved in the origin and radiation of this family.

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