

Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania

M. D. Leakey & R. L. Hay*

P.O. Box 7, Ngorongoro, Tanzania

Recent excavation of the tuffs of the Laetolil Beds in Tanzania has revealed the presence of a large variety of footprints from the Pliocene. Many of these prints can be correlated with fossilised remains of Pliocene animals found in the same area.

It was stated previously¹ that the name Laetolil would be used in preference to either Garusi or Vogel River for the area where the Laetolil Beds are exposed. Laetolil, as stated then, is an anglicisation of the Masai word Laetoli and was first used by Kent². The Tanzanian authorities have now asked that the term Laetolil should be dropped in favour of Laetoli. The name Laetoli will be used for the area, but the Pliocene deposits will continue to be known as the Laetolil Beds, as established in 1976¹.

The Laetolil Beds (Figs 1, 2) are dominantly tuffs which have a maximum known thickness of 130 m and are divisible into upper

and lower units. Nearly all the fossils have come from the upper unit which is 45–60 m thick.

In 1975 three marker tuffs had been identified in the upper unit of the Laetolil Beds¹. Since then, more than a dozen widespread air-fall tuffs (Fig. 3) have been recognised, permitting detailed correlations.

Description of the footprints tuff

The footprints tuff is divisible into two units of differing lithology and structure. The lower unit, 7–8.6 cm thick, is relatively uniform in thickness and is characterised by widespread ash layers of even thickness, commonly with rainprinted surfaces. The upper unit, generally 5–7 cm thick, thins over the higher areas of the lower unit and thickens in depressions to eliminate the undulations preserved by the mantle bedding of the lower unit.

Several unusual features of these tuffs can be explained by composite ash falls of natrocarbonatite ash and melilitite lava globules. The ash must have been cemented rapidly to have

* Present address: Department of Geology and Geophysics, University of California, Berkeley, California 94720

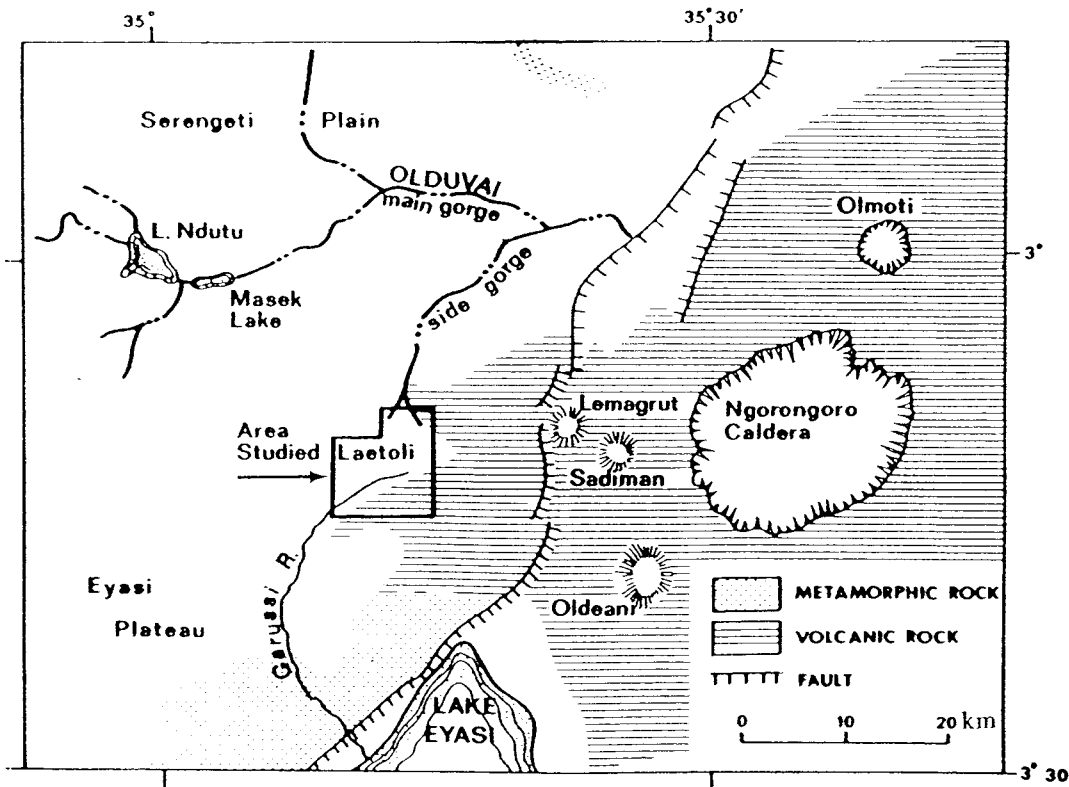


Fig. 1 Map of the southern Serengeti and volcanic highlands showing the position of the Laetoli area.

prevented erosion of the sand-sized lava globules by wind in this semi-arid climate in which 80-85% of the sediment was wind-worked. Natrocarbonatite ash would have dissolved incongruently in rainfall to yield soluble carbonates, which would have crystallised under the heat of the Sun to cement the ash layer in a few hours.

Footprints were made on at least six different surfaces but are by far the most common at two levels (Fig. 4). Prints of birds and

hares are common to all levels, but prints more than about 10 cm in diameter have been found only in the upper unit. Particularly striking is the number of elephant prints in the higher levels compared to their apparent absence below.

On the basis of the available evidence a tentative history of the footprint tuff begins near the end of the dry season and continues into the rainy season. The first showers of ash fell on a relatively bare, nearly flat landscape with scattered *Acacia* trees. The ash layers which constitute the lower unit were cemented by intermittent showers near the beginning of the rainy season. A few times between showers extruded eolian sediments, together with some of the air-fall ash, were redeposited by wind. The sharp contact at the base of the upper unit may mark the onset of the rainy season. Stratification in the upper unit is compatible with sheetwash produced by heavy showers, but is unlike that of the lower unit in which individual ash layers vary little in thickness over a distance of 5 km. The smaller amount of calcite in the upper unit may have resulted from either heavy rains or a smaller original content of carbonatite ash, or both. Thus, the abrupt appearance of footprints of elephants and other large animals in the upper unit may represent, at least in part, their migration which accompanies the rainy season.

The 1975 and 1976 field seasons at Laetoli were devoted to study of the geology of the area and the collection and excavation of fossil vertebrates and molluscs from the Laetoli Beds and later deposits. The age of the upper, fossiliferous part of the Laetoli Beds was established at 3.6-3.75 Myr (ref. 1).

While visiting the Laetoli camp during 1976 Dr Andrew Hill observed a number of depressions in the surface of a fine-grained tuff exposed in a river bed. These proved to be footprints of birds and mammals ranging from elephant and rhinoceros to carnivores and hares, which had been exposed by natural erosion and weathering.

The first site where footprints were observed (site A in Fig. 2) lies just south of the Garusi River in fossil Locality 6. An area of ~490 m² has been exposed by natural erosion and by excavation. To the south-west, at a second site (C) there are ~156 m² of the footprint-bearing tuff exposed. Both these localities were studied in detail in 1977. Five further areas where the footprint-bearing tuff is well exposed are also known but have not yet been completely studied.

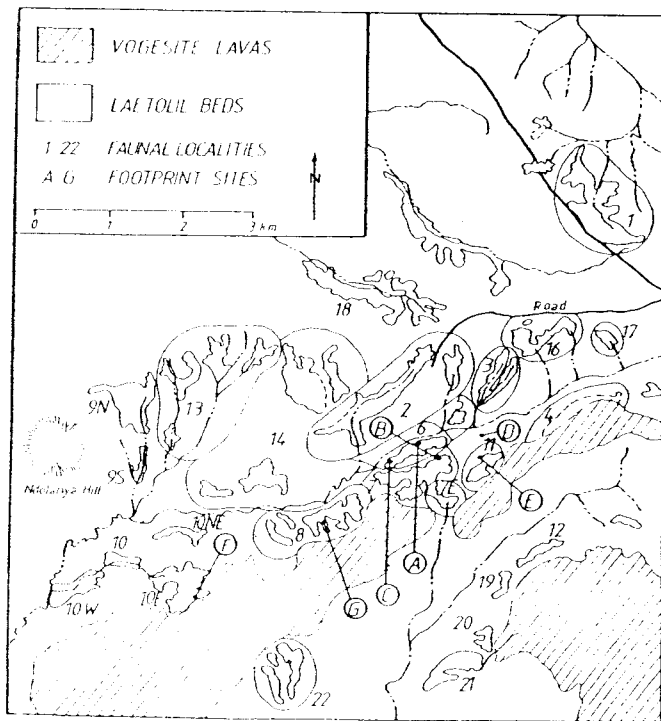


Fig. 2 Map of the fossil localities and footprint sites at Laetoli.

Table 1 Mean percentages of mammalian specimens from various sites

Bovidae (of which 15.1% are <i>Madoqua, dik-dik</i>)	43%	Equidae	4.4%
Lagomorpha	14.4%	Suidae	3.6%
Giraffidae (including both a large and small species, as well as <i>Sivatherium</i>)	11.2%	Proboscidea	3.4%
Rhinocerotidae	9.7%	Rodentia	3.3%
		Carnivora	3.1%

Avifauna, Cercopithecidae, Hominae and Pedetinae were omitted from this list.

Deeply worn game tracks or pathways can be seen crossing the footprint areas at two sites. These were clearly used repeatedly by animals to reach some objective and on modern behavioural patterns it is likely that they were made by the game going to and from water holes.

Only a proportion of the animals represented in the fossil prints have been identified so far. Investigation of present-day game tracks in National Parks is underway to provide comparative information. In general, however, the fossil record agrees well with the footprints. A Musukuma tracker was employed to assist in identifications. He assisted considerably in identifying to family and generic levels, particularly in the case of Bovidae, which are commonly represented in both the footprint and fossil records.

A partial breakdown of the mammalian specimens recovered from the Laetoli Beds in 1975 was published¹ and may usefully be given here. Additional material was recovered in 1976 and 1977, but the overall proportions of various groups remain close to the first figures (Table 1).

The footprints that have been recorded are briefly described below, with notes on the fossil material where it seems to be related.

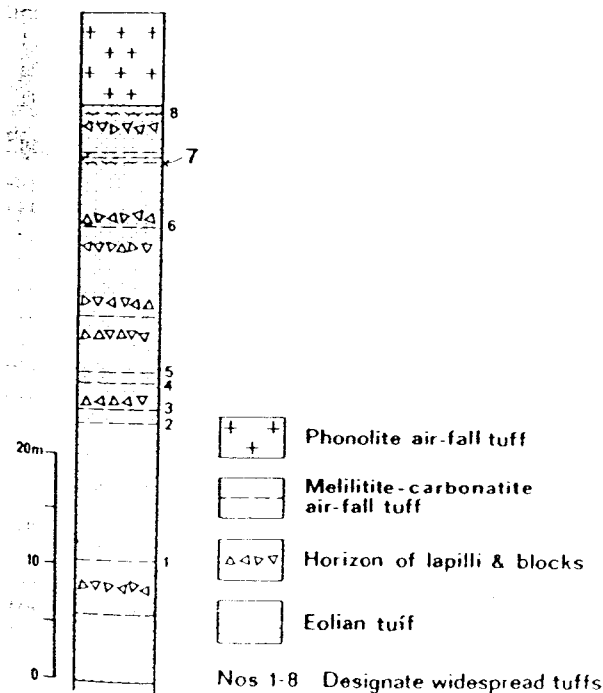


Fig. 3 Columnar section of the upper unit of the Laetoli Beds at Locality 1 showing air-fall tuffs and horizons of lapilli and blocks. The present report is based on studies of the lower part of Tuff 7, termed the Footprint Tuff. Tuffs 6, 7 and 8 were designated Tuffs a, b and c by Leakey *et al.*¹. The pholite tuff was designated Tuff d.

Diplopoda

A single track approximately 20 cm long is known at site (A).

Fossil record: a small fragment of fossilised centipede was found at Locality 4.

Avifauna

(1) *Struthio* sp. Two isolated prints at site (A).

(2) *Phasianidae*, cf. Guinea fowl. Numerous tracks occur at all sites, generally in trails of four or more. They compare closely with tracks of the living helmeted Guinea fowl, common in the Laetoli area today. Average length of eight fossil prints 62 mm, of nine modern prints 60 mm.

(3) Similar but smaller tracks, averaging 45 mm in length, possibly of francolin.

Fossil record: numerous fragments of ostrich eggshell are known but no skeletal remains. Clutches of eggs comparable in size to those of modern Guinea fowl have been found at Locality 10.

Primates

Cercopithecidae: Tracks are known at three localities.

At site (C) there is a single trail comprising six hind foot prints with a digit protruding to one side. Each of these prints is accompanied by a roughly circular impression, always to the left (Fig. 5). When first discovered these prints were interpreted as knuckle impressions, but more thorough cleaning has revealed traces of the palms of the hands and they are undoubtedly prints of the forefeet. In the hind feet the longest digit is central and the prints range in length from 20.1 to 14.7 cm with an average of 17 cm. The width varies from 10.9 to 8.1 cm with an average of 9.9 cm (excluding the great toe). Stride length varies from 34 to 46 cm with an average of 41 cm. (Stride is here interpreted as the distance between the posterior margin of successive heel prints of the same foot.)

The second trail is at site (D). It was made by a single animal and is 4 m long. There are prints of both hind and forefeet. All are lightly imprinted on a surface which was clearly wet and slippery when the animal walked over it. The average length of the hind prints is 14.5 cm and of the forefeet prints 11 cm. Stride length averages 27.7 cm. These prints are not only smaller than those at site (C) but are relatively broader, with very narrow heel impressions.

At site (F), in fossil Locality 10, there are at least four sets of tracks going in slightly different directions, as do the tracks of present-day baboons when they move in a troop. The average measurements of the hind feet in each of the four trails range from 15.2 to 10 cm and of the forefeet prints from 7.6 to 4 cm (excluding the great toe).

Fossil record: a number of cercopithecoid mandibles and teeth and a few postcranial fragments have been provisionally attributed to *Papio* sp. and a colobine. Most are as small or even smaller in size than those of a living female baboon, but two mandibular fragments, a calcaneum and the distal ends of a humerus and femur are considerably larger than in any living baboon and compare in size with *Theropithecus oswaldi*. The difference in size between the prints described above is compatible with that of the known fossils, although age and sex differences are factors to be considered.

Hominae: Three trails believed to be hominid are known at sites (A) (Fig. 6) and (G) (Figs 7, 8), in fossil Localities 6 and 8. (1) At site (A) there are five prints in a trail 1.5 m long (Fig. 6). Natural erosion has almost entirely exposed two of the prints, but the remaining three are still filled with matrix of the overlying deposits. The exposed prints are short and broad, 15.5 cm long and 10.5 cm wide. The stride is also short with an average length of 31 cm. The gait was somewhat shambling, with one foot crossing in front of the other. Unlike the cercopithecoid prints, the longest digit is the great toe, situated as in the human foot.

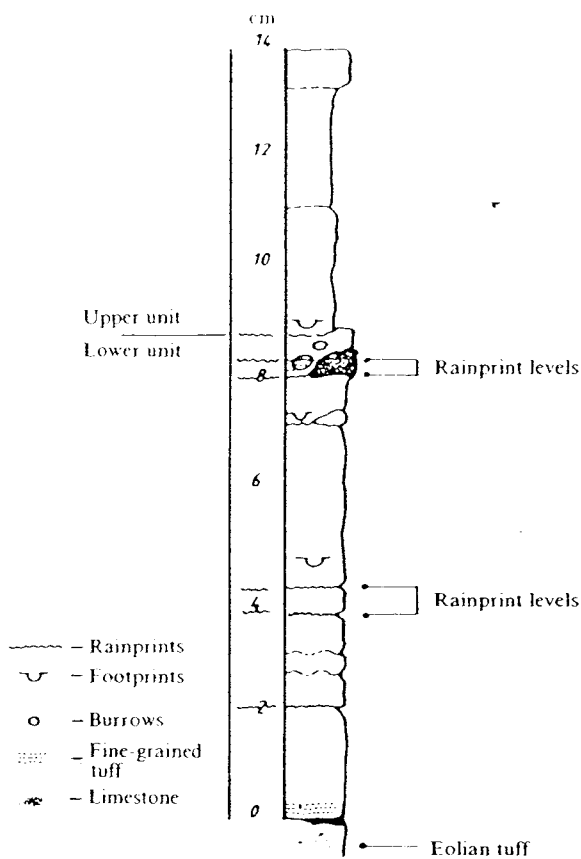


Fig. 4 Generalised columnar section for footprint tuff at site A.

It has been suggested that these prints might have resulted from the superposition of a hind on forefoot impression, or vice versa, either of a quadrupedal animal or a knuckle-walking primate. Careful examination of the original prints *in situ* reveals no indication of superposition, while the last interpretation invokes the hypothetical existence of an animal which is not present in over 5,000 fossil specimens.

(2) At site (G) there are trails left by two individuals travelling north (Figs 7-9). The trails are parallel and ~25 cm apart, too close for the hominids to have walked abreast. They followed the same line or pathway but it is possible that they did not pass by at the same time as there is a noticeable difference in the conditions of the two sets of prints. Those of the smaller individual are sharp and well defined, indicating a firm, compact surface, whilst those of the larger individual, with one notable exception, are blurred at the edges and enlarged, as would be the case if the surface had been dry and dusty. At one point the smaller individual appears to have paused and made a half-turn to the left before continuing in a northerly direction.

In a number of prints the original surface in which they were made has been eroded, leaving only indentations in the underlying deposits. Thus, the measurements of these prints do not accurately reflect the dimensions of the original impressions and are not included.

The site is now being excavated and the trails have so far been found to extend for a distance of 23.54 m. Trail 1 contains 22 prints and Trail 2 contains 12 prints. The average length/breadth of the prints in Trail 1 is 18.5 × 8.8 cm and in Trail 2 is 21.5 × 10 cm. Average stride length in Trail 1 is 38.7 cm and in Trail 2 is 47.2 cm. Note that the longitudinal arch of the foot is well developed and resembles that of modern man, and the great toe is parallel to the other toes (Figs 7, 8 and 9).

Fossil record: two mandibles, parts of 2 maxillae, partial deciduous and permanent dentitions as well as a partial infant

skeleton and a number of isolated teeth have been recovered from the Laetoli Beds. They bear considerable resemblances to the material collected from the Afar in Ethiopia, although the Ethiopian material is substantially later.

Leporidae

Innumerable tracks of hares occur at all sites.

Fossil record: mandibles and other remains attributed to *Serengetilagus* sp. are abundant.

Carnivora

(1) Viverridae, indet. Series of small carnivore prints with non-retractile claws occur at all sites. They are generally lightly imprinted and rather faint. Average length/breadth 34 × 27 mm. Other small, rounded prints without claw marks, suggest genets. Average length/breadth 28 × 27 mm.

Fossil record: a variety of Viverridae are known among the fossils, some were described by Dietrich³, those from the recent collections are being studied by Mme G. Petter.

(2) Hyaenidae. Hyenas have left a series of well-defined and relatively long trails containing large numbers of prints. Eight trails are known and two gaits are represented. Subject to research on living hyenas, these appear to be a walk and a slow canter or lope. There is uniformity in size, depth and stride within each of the four trails measured, although it is evident that the animals varied in individual size. Average length/breadth/depth measurements:

Trail C.22 (19 prints)	122 × 94 × 12 mm
Trail C.27 (30 prints)	125 × 102 × 22 mm
Trail C.31 (11 prints)	102 × 87 × 13 mm
Trail C.39 (18 prints)	111 × 100 × 18 mm

Fossil record: in a preliminary report, M. G. Leakey noted the existence of three species of hyena from the Laetoli Beds: (1) *Hyaena bellax* (Ewer 1954); (2) *Hyaenictis* cf. *preferfor* (Hendey 1974); and (3) *Lycyaena* sp.

(3) Felidae. One trail of 12 prints at site (A), and several isolated prints appear to correspond in size to those of a serval



Fig. 5 Print of cercopithecoid fore and hind foot at site C.

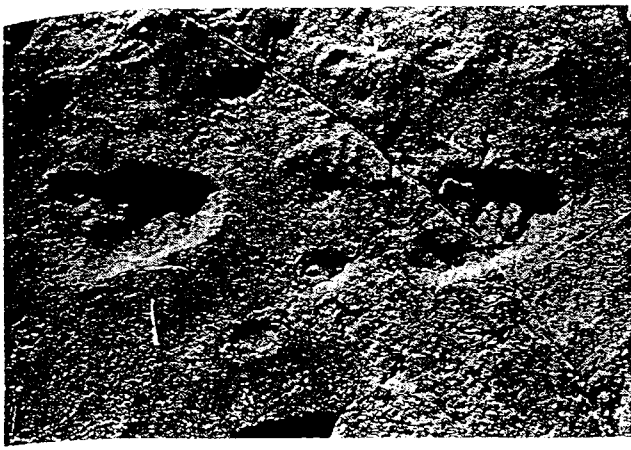


Fig. 6 Hominid footprints at site A.

cat. Average length/breadth/depth $65 \times 52 \times 13$ mm. Average length of stride 29 mm.

Fossil record: remains comparable to *F. serval* and *F. caracal* have been noted in the 1974–76 collections.

(4) *Machairodontinae*. Two prints at site (A), measuring 134×115 mm and 110×115 mm probably belong to a large sabre-tooth cat, as no other felid of comparable size occurs in the fossil material.

Fossil record: The presence of a large sabre-tooth cat, cf. *Homotherium* is indicated by two teeth.

Proboscidea

The proboscidean prints appear to belong to *Loxodonta exoptata* with the exception of one particularly well-preserved print in a trail of four at site (C) in which the phalanges and metapodials were more nearly vertical than in other known proboscidean prints and may be of a *Deinotherium*. The *Loxodonta* prints include a number made by juvenile animals as well as some that are usually large by present-day standards. The average for 15 measured prints, mostly adult, is $420 \times 346 \times 34$ mm.

Fossil record: both *Loxodonta exoptata* and *Deinotherium* cf. *bozasi* occur in the Laetoli Beds, but the latter is relatively scarce. A high proportion of the *Loxodonta* teeth are from juvenile animals.

Equidae

Only two equid trails are known. They have only recently been discovered and have not yet been fully studied. Both are at site (G), one on either side of the hominid trails but travelling in an opposite direction, to the south. The best preserved trail is 4.97 m long and contains 15 prints, nine of which can be measured. They range in length from 9.9 to 7.8 cm with an average of 8.6 cm and in width from 10.6 to 8.3 cm with an average of 8.8 cm. The animal appears to have changed gait during this trail.

Fossil record: numerous teeth, postcranial material and some incomplete mandibles have been found. All can be attributed to *Hipparion* sp.

Rhinocerotidae

Both *Ceratotherium* and *Diceros* must be represented among the many prints of rhinoceros, but no distinguishing features have been observed to date except on the basis of size. A trail at site (A) is one of the longest known, measuring 22 m in length. It contains 31 prints, 23 of which are double, with the hindfoot superimposed on the front. At the western end of the trail, where the animal changed gait, the prints become single and are irregularly spaced. Comparison with modern prints of *Diceros bicornis* at Olduvai show very close similarity. Average length/breadth/depth of double prints in trail: $416 \times 273 \times 31$ mm. Single prints, forefoot $246 \times 248 \times 25$ mm, hindfoot

$256 \times 228 \times 37$ mm. Isolated single fore and hind prints in the adjacent game trail are unusually large and may be of *Ceratotherium*. They measure $285 \times 310 \times 42$ mm and $400 \times 270 \times 33$ mm respectively.

Fossil record: on the basis of the early collections only *Ceratotherium* was believed to be present in the Laetoli fauna. But a skull of *Diceros* has now been found, as well as numerous teeth and some postcranial material.

Chalicotheriidae

Two Chalicothere prints were found at site (C). They are deeply indented and measure $250 \times 155 \times 63$ mm and $243 \times 110 \times 46$ mm. The prints comprise impressions of three digits and of the palm. The digits have left symmetrical rounded grooves and the emplacement for a claw can be seen on one. The prints are 1.30 m apart.

Fossil record: a few specimens which can be referred to *Ancylotherium* cf. *hennigi* have been recovered. They include a calcaneum, astragalus and some phalanges.

Suidae

Thirteen suid prints at site (A) have been measured. They are comparable in size to prints of the living warthog. Average length/breadth/depth measurements are $55 \times 47 \times 11$ mm.

Fossil record: only two Suidae are known from the Laetoli Beds, *Potamochoerus* sp. and *Notochoerus euilus*. *Hylochoerus* and *Phacochoerus* were previously believed to be present in the early fauna, but during 1974–77 have only been found in the more recent deposits. On size, the prints are probably of *Potamochoerus*, as *Notochoerus* was a larger animal than the living warthog.

Giraffidae

(1) Three trails made by single animals are known. They consist of 6, 7 and 11 prints respectively. There are also 19 other prints attributed to giraffe. In one trail, the animal has dragged its feet after each step and left scuffed grooves up to 96 cm long. Average length/breadth/depth measurement for the prints in the trails are $190 \times 151 \times 29$ mm, $202 \times 144 \times 10$ mm, $211 \times 150 \times 17$ mm and $205 \times 150 \times 28$ mm. Averages for the isolated prints are $208 \times 155 \times 19$ mm.

Fossil record: the prints are of similar size to those of the modern giraffe and can be attributed to *G. jumae* which occurs as a fossil.

(2) Small giraffe cf. *G. stillei*. There are no prints which can positively be allocated to this animal, although its fossil remains are by far the most common giraffid. However, there are many prints, including three trails, which were identified as 'eland' by the tracker. No eland is known in the fossil fauna, nor is there any other bovid in the collection of a size suitable to have made these prints. For the present, it seems justifiable to assign these prints to the small giraffe. They are abundant at site (A), where there are three trails consisting of 21, 14 and 5 prints, as well as 72 isolated prints. The average length/breadth/depth measurements for the prints in the three trails are $140 \times 107 \times 14$ mm, $139 \times 104 \times 13$ mm and $128 \times 94 \times 16$ mm.

Fossil record: if the prints are correctly identified, they would belong to the animal originally named *Okapia stillei*, now known as *Giraffa stillei*.

(3) *Sivatherium*. No prints could be identified. The fossils consist mostly of isolated teeth and foot bones.

Bovidae

(1) Bovini cf. *Simatherium kohllarseni*. These prints consist of large, rounded and generally deeply indented tracks resembling those of the living African buffalo. They are clearly made by Bovini and can be attributed to *S. kohllarseni*, as this is the only bovine in the fossil record. The prints are represented by four trails containing 16, 12, 10 and 5 tracks, as well as 40 additional



Fig. 7 Dual trail of hominid footprints at site G.

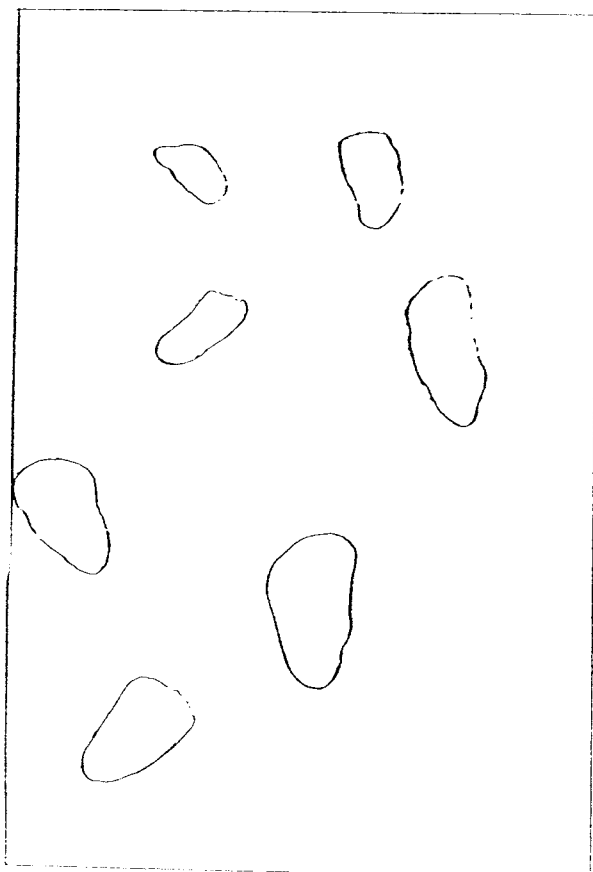


Fig. 8 Outline of footprints shown in Fig. 7.

prints, either single or in pairs. The average length/breadth/depth measurements for the 43 prints in the trails are $185 \times 149 \times 25$ mm.

Fossil record: a number of horn cores and teeth have been found, including a cranium associated with both horn cores. (2) *Hippotragus* sp. Seven single prints from sites (A) and (C) were identified by the tracker as 'roan antelope'. They are characterised by widely splayed, elongate hoof-marks. The average length/breadth/depth measurements are $109 \times 95 \times 16$ mm.

Fossil record: three horn cores and some teeth, collected during 1975 are believed to be a hippotragine and have



Fig. 9 Left footprint of larger individual in dual trail at site G.

provisionally been attributed to *Praedamalis deturi*. A horn core and teeth in the earlier collections may also belong to this species which is smaller than the living roan antelope.

(3) Alcelaphini. Eighteen prints at site (A) and two at site (C) were identified by the tracker as hartebeest. The prints at site (A) are both smaller and shallower than those at site (C). Average length/breadth/depth for the former are $80 \times 60 \times 14$ mm and for the latter $103 \times 80 \times 23$ mm.

Fossil record: *Pannularius* sp. has been identified on a frontlet with horn cores, teeth and other fragmentary horn cores. There is also a cranium collected in 1959 which has been attributed to a larger species of alcelaphine. A third species may also be represented.

(4) Small antelopes and gazelles. Prints of dik-dik (*Madoqua*) are rare although dik-dik are the most abundant single species of fossil Bovidae. This anomaly may be explained by the fact that dik-dik are one of the Bovidae who do not require to drink.

water, subsisting on moisture from vegetation, while tracks of other Bovidae were probably made going to or from water holes.

Fossil record: *Neotragini*? and *Raphicerus* sp. (Steenbuck) are provisionally identified. *Madoqua* is very abundant. *Antilopini*: the gazelle appears to be *G. janenschii*.

Conclusions

The greater part of the fossil fauna from the Laetolil Beds is recorded in the fossil tracks. In all, over 20 taxa are represented. The preservation of the footprints can be attributed to an unusual and possibly unique combination of climatic, volcanic and mineralogic conditions. The available evidence indicates that the episode took place during a brief period, probably during the onset of a single rainy season which happened to coincide with the eruption of light ash showers from the nearby volcano Sadiman.

The locomotor pattern displayed by the trails of hominid footprints is still under examination but it is immediately evident that the Pliocene hominids at Laetoli had achieved a fully upright, bipedal and free-striding gait; a major event in the evolution of man which freed the hands for tool-making and eventually led to more sophisticated human activities. Moreover, evidence supplied by cranial parts of the somewhat later but related hominid fossils from the Afar in Ethiopia (dated between 2.6 and 3 Myr) indicates that bipedalism outstripped

enlargement of the brain. To have resolved this issue is an important step in the study of human evolution, as it has long been the subject of speculation and debate.

With the hands free and available for purposes not connected with locomotion it is perhaps surprising that no form of artefact has been found. But the concept of tool-making may well have been beyond the mental ability of these small-brained creatures. Any 'tools' or weapons used must have been solely of perishable materials as the Laetolil Beds are devoid not only of artefacts but of all stones other than volcanic ejecta.

Further exploration of sites and analysis of material will continue in 1979, but it is evident that Laetoli will give an unique perspective into hominid environment during Pliocene times.

We thank the United Republic of Tanzania for permission to continue research at Laetoli, the National Geographic Society, Washington, D.C. for financial support, A. A. Mturi, Director of Antiquities, Tanzania and A. J. F. Mgina, Conservator, Ngorongoro Conservation Authority, for their help, Philip Leakey and Peter Jones for organising field seasons, Drs A. W. Gentry, J. Harris and M. G. Leakey for identifying the bovid, giraffid, primate and carnivore fossils and all those who participated in the fieldwork.

Received 28 September 1978; accepted 2 February 1979.

1. Leakey, M. D. *et al.* *Nature* **262**, 460-466 (1976).
2. Kent, P. E. *Geol. Mag.* **78**, 173-184 (1941).
3. Dietrich, W. O. *Palaeontographica* **94**, 44-133 (1942).