

10. Taphonomy and paleoecological context of the Upper Laetolil Beds (Localities 8 and 9), Laetoli in northern Tanzania

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Abstract

The Upper Laetoli Beds at Laetoli in northern Tanzania contain abundant fossil mammalian remains that may help elucidate Pliocene environments and enhance our understanding of the morphological and behavioral adaptations of the Laetoli hominins. The Laetoli vertebrate fossil fauna is also of great interest because its taxonomic composition, especially in the family Bovidae, differs from that of other East African faunas of comparable age. However,

the taphonomic history and paleoecological context of the Upper Laetolil fossil faunal assemblage is not fully understood. Furthermore, the depositional environment of the Upper Laetolil Beds was initially associated with a dry, savanna-like environment characterized by grassland, shrubs, and isolated trees. However, revised stratigraphy and taphonomy at Localities 8 and 9 indicate an existence of more complex depositional environments than those previously described. Fossil faunal remains from the Upper Laetolil Beds are represented by highly variable numbers of skeletal parts dominated by heavily fractured and/or modified distal, proximal, and midshaft fragments of varying sizes, and many isolated teeth. Unlike marine fossil deposits, which furnish thick sections with rich fossil accumulations of invertebrates, the Laetoli deposits are most commonly composed of low-density accumulations with terrestrial faunal assemblages that differ significantly from modern counterparts. Observed changes in faunal composition at Laetoli especially between the Lower and Upper Units have been noted, but their cause has not been established. We present a detailed taphonomic and stratigraphic analysis of fossil faunal assemblages from the Upper Laetolil Beds at Localities 8 and 9 in northern Tanzania

Introduction

The taphonomic history of the Laetoli paleoanthropological site (S3°13', E35°13') in northern Tanzania provides a basis for the formulation of ecological and stratigraphic interpretations. Laetoli, located on the western flank of the Ngorongoro Volcanic Highlands within the Serengeti Plains, consists of fossiliferous sediments that span from 4.3 Ma to 120 Ka. This site is unusual in that its paleobiota is indicative of an upland environmental setting without major rivers or lakes. The Upper Laetolil Beds in particular provide a rich and diverse fossil faunal assemblage, which includes hominins, hominoids, carnivores, rodents, and several bovid species that have been used in ecological interpretations of the ancient landscape.

Paleoecological interpretations of Pliocene Laetoli have been problematic and controversial (Harrison, 2005; Su and Harrison, 2006). For example, Andrews (1989) disputed Leakey et al.'s (1987) suggestion that the Pliocene Laetoli environments were similar to those of the modern Serengeti Plains. Furthermore, Hill's (1987, 1994) analysis of bone weathering from a small sample of Laetoli fossils raised questions about the nature of Laetoli depositional environments. Also, recent paleoecological interpretations of the Upper Laetolil Beds based on the functional morphology of bovid hind limbs

as ecological indicators at Localities 8 and 9 suggested a complex environmental setting for the Upper Laetolil Beds (Musiba, 1999; Musiba and Magori, 2005).

In this paper, we present a new taphonomic history of fossil faunal assemblages from Laetoli in northern Tanzania (Figure 1) and its implications for paleoecological interpretations of the Upper Laetolil Beds at Localities 8 and 9. We focus particularly on the fossil faunal assemblage between the dated horizons of Tuff 8 (3.46 ± 0.12 Ma) and Tuff 1 ($\leq 3.76 \pm 0.03$) (Drake and Curtis, 1987; Hay, 1987; Manega, 1993) exposed at Localities 8 and 9 (Figure 1).

Previous Studies

Past generalized ecological studies of Pliocene Laetoli characterized this site as an open savanna grassland similar to the present-day Serengeti Plains (Hay, 1980; Harris, 1985; Bonnefille and Riollet, 1987). Nevertheless, the rich and diverse faunal assemblage of the Upper Laetolil Beds suggests a much more complex environmental setting (Musiba, 1999; Harrison, 2005; Musiba and Magori, 2005). Most of the faunal assemblage, particularly the bovids, rodents, and primates, are diagnostic of specific environmental settings that are no longer present within the Serengeti region. Evidence from fossil pollen collected near the bottom of the

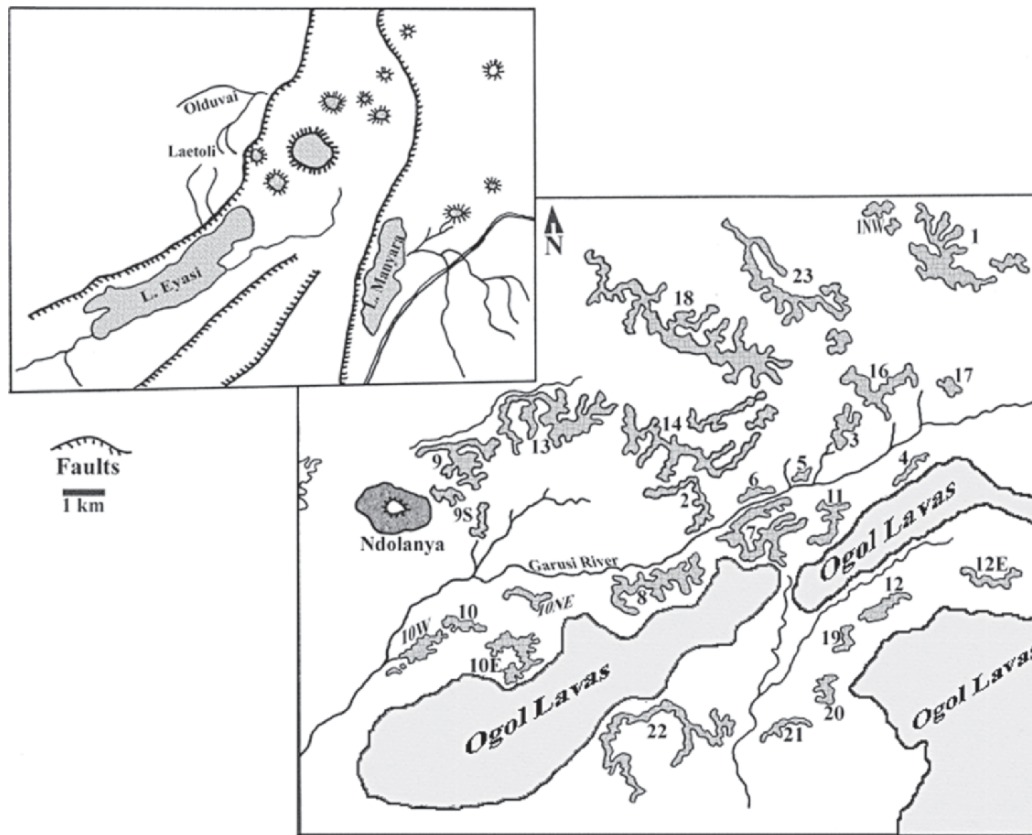


Figure 1. Map of Laetoli showing the paleontological localities with Laetolil Beds.

upper part of the Laetolil Beds, at Tuff 1 and below Tuff 7, suggests vegetational similarities between the Pliocene and the modern Serengeti Plains (Bonafille and Riollet, 1987). However, it has been suggested that the pollen data are diagnostically and stratigraphically very problematic (Andrews, 1989). For instance, pollen samples used in earlier interpretations derive from sediment traps on termite mounds, and the collected samples contained a high proportion of non-descriptive woodland species that are currently not present within the Serengeti. Bonafille and Riollet's (1987) palynological spectra of the Laetoli flora revealed high proportions of unknown pollen. This indicates the possible existence of mosaic environments very different from those of the modern Serengeti landscape.

Furthermore, some of the fossil faunal remains and other geologic evidence from the

Upper Laetolil Beds are also partly inconsistent with the analogy of the modern Serengeti environments. For example, the Hippotragini are not as abundant at Laetoli as they are in the modern Serengeti (Gentry, 1981, 1987). According to Gentry (1981), "As far as bovids are concerned Laetoli is a strange locality ... its faunal assemblage is less similar to present day Serengeti fauna ...". The Pliocene bovid community from Laetoli is characterized by a low number of species with many incomplete or uncertain identifications. For example, *Aepyceros* and *Reduncini* are rarely represented in the Laetolil Beds. According to Gentry (1981) the absence of these bovids combined with the abundance of *Madoqua* indicates a dry-country fauna. However, the distribution of *Madoqua* species in the fossil assemblage within the Laetolil Beds also differs from their modern counterparts and many have no

modern representatives (Gentry, 1981, 1987). Furthermore, the presence of Tragelaphini, Cephalophini, and two indeterminate Bovini species at some localities suggests that part of Pliocene Laetoli was characterized by wooded habitats (Gentry, 1987; Bobe et al., 2002).

Additionally, the presence of two species of Chelonia (*Geochelone laetoliensis* and *Geochelone brachyularis*) in the assemblage also indicates that Laetoli Pliocene environments might have contained patches of arid grassland (Meylan and Auffenberg, 1987). However, a modern counterpart of the subgenus *Aldabrachelys*, which is represented by a gigantic tortoise currently seen in the islands of the Pacific and Indian Ocean, inhabits coastal woodland or forest (Meylan and Auffenberg, 1987). In addition, the presence of *Python sebae* suggests the existence of a body of water within the Laetoli area (Meylan and Auffenberg, 1987). Fossil gastropods recovered at Laetoli, however, do not conform to continuous woodland forest or open grassland cover (Verdcourt, 1987; Pickford, pers. communication). However, fossil gastropods from Laetoli, which are represented by Achatinidae (*Achatina zanzibarica*), *Burtoa nilotica*, *Limicolaria martensiana*, *Subulona pseudinvoluta*, and *Trochonanina* sp. are mainly inhabitants of open woodland, coastal forest, and upland forest (Verdcourt, 1987). Modern counterparts of the Laetoli gastropods require moist environments with precipitation ranging from 750 to 2000 mm (Verdcourt, 1987).

The conflicting evidence from previous studies presented here suggests a broad spectrum of environmental settings at Laetoli during the Pliocene and may reflect possible taphonomic biases (spatial mixing or environmental condensation) or may indicate a complex mosaic of environments (Andrews, 1989; Harrison, 2005; Musiba and Magori, 2005). An alternative explanation for the contradictory evidence would be sampling biases, and misinterpretation of the almost indistinguishable strati-

graphic events that characterize the sequences in question (Gifford, 1981). Andrews (1989) for example has suggested that sampling biases (mixing by collectors of material from different beds) might be directly responsible for the poor environmental resolution in previous studies of the Laetolil Beds.

The presence of cercopithecines and colobines in the Upper Laetolil Beds (Leakey and Delson, 1987) is also indicative of mosaic environments capable of supporting various primate groups (Kappelman, 1991). In modern African environments it is very rare that more than two closely related cercopithecoid species would occupy the same ecological niche without risking competition and other selective pressures. Of 15 species of rodents represented at Laetoli, *Saccostomus* (a dry savanna inhabitant), *Thallomys* (dependent on *Acacia* woodlands), and *Heterocephalus* (semi-arid inhabitant) dominate the Upper Laetolil fossil assemblage (Denys, 1987). These rodent taxa, if considered as a single community, would support the open-country savanna model at Laetoli 3.5 Ma. However, such a community of several species of rodents occupying a wide range of ecological niches rarely exists in modern savanna ecosystems (Wesselman, 1985). When individually treated, the rodents offer conflicting ecological information (Denys, 1987). The only exception is the naked mole rat (*Heterocephalus*), which can withstand extreme temperatures (Kingdon, 1974, 1997). Therefore, species diversity for rodents is too high for a single community from a very dry savanna habitat (Andrews, 1989).

Additionally, insectivores, which are sparsely represented at Laetoli, contradict the savanna-like model. Only a single species of a giant elephant shrew (*Rhynchocyon pliocaenicus*) has been identified within the Upper Laetolil Beds. This species is somewhat smaller than its living congener (Butler, 1987), which is habitat-specific and requires either gallery forest, woodland and/or closed tree, or bush cover with abundant leaf litter (Corbet and Hanks, 1968).

Evidently, past paleoecological interpretations of the Upper Laetolil Beds present various taphonomic problems including sampling, sediment mixing, and preservation biases. It is however unmistakable that the interpretation of Laetoli paleoenvironments as being drier than today relied exclusively upon the taxonomic distribution of fossil faunal remains and the problematic pollen evidence collected at various localities within the Laetoli area. The fossil faunal assemblages and stratigraphic resolution used in the reconstruction of Laetoli paleoecology represent multiple events of stratigraphically indistinguishable units of well-mixed horizons (Musiba and Magori, 2005). The existence of burrowing animals and termitary mounds within the Laetolil Beds are clearly good indicators of bioturbation and sediment mixing.

Laetolil Beds in Paleoecological Context

The Laetolil sediments, deposited on a basement rock of basalt origin, also provide important information relevant to the discussion of Laetoli depositional environments and are further reviewed in detail here. The Upper and Lower Laetolil Beds were entirely deposited on land, on the crest and flanks of a broadly uplifted dome overlying the Precambrian bedrock in the Eyasi Plateau. The Laetolil Beds occur in a series of shallow outcrops with many discontinuous exposures spreading about 1600 km² to the south and west of Lemagruti, and to the northwest of Lakes Masek and Ndutu (Hay, 1987; Manega, 1993). The Laetolil Beds preserve a unique type of fossil record of hominin footprints and animal trackways that have been dated to 3.5 Ma and provide a snapshot of past environments at Laetoli.

The stratigraphic and taphonomic context of the Upper Laetolil Beds particularly at Localities 8 and 9 is indicative of numerous taphofacies including bioturbation, sediment mixing, and overprinting of short episodes of depositional

environments, especially the last 60 m within the unit (Figure 2). A generalized description of the columnar section of Plio-Pleistocene Laetoli sediments by Hay (1987) indicates that lithologically the area consists of deposits characterized by lava flows, tuffs, and clay stones. The deposits are mainly of nepheline-phonolite, melilitite-carbonatite in composition and/or eolian tuff in origin (Hay, 1978). Because of the varying degrees of exposures and weathering of the Laetolil Beds from one locality to another, the lithologic description provided below is based on observations made at Localities 8, 9, and 9S. Detailed lithologic information has been provided by Manega (1993) and Hay (1987).

The lower unit of the Laetolil Beds consists of graded water-worked tuffs, Lapilli Tuffs, and conglomerates (in the upper 30 m) that are chemically easily identifiable. The unit consists of mudflow deposits, eolian- and water-worked tuffs with channel fillings from the eroded Ogol Lavas, and few layers of conglomerates and breccia (Hay, 1987; Manega, 1993). The topmost part of this unit, however, is about 75% reworked tuff of eolian origin with numerous thin water-worked tuff layers that are 45–60 m thick, indicating the existence of a substantial amount of water in the area during and after their deposition. The remainder of the Upper Laetolil Beds is composed of approximately 20% air-fall volcanic ash. One to two percent of the upper unit consists of easily distinguishable stream-reworked tuffs (Hay, 1987). The water-worked tuffs within the unit are generally composed of fine- to coarse-grained, moderate- to well-rounded, and highly indurated tuffs. They are well sorted with thin laminae that vary in thickness. The water-worked tuffs are also dominated by clastic deposits, which compose about 90% or less of the entire unit. This sedimentary evidence points toward a set of complex depositional environments.

At Locality 8 for example, the exposed Upper Laetolil Unit exhibits a 120°–210° SW strike and a 5° to 10° SW dip with a two-joint system

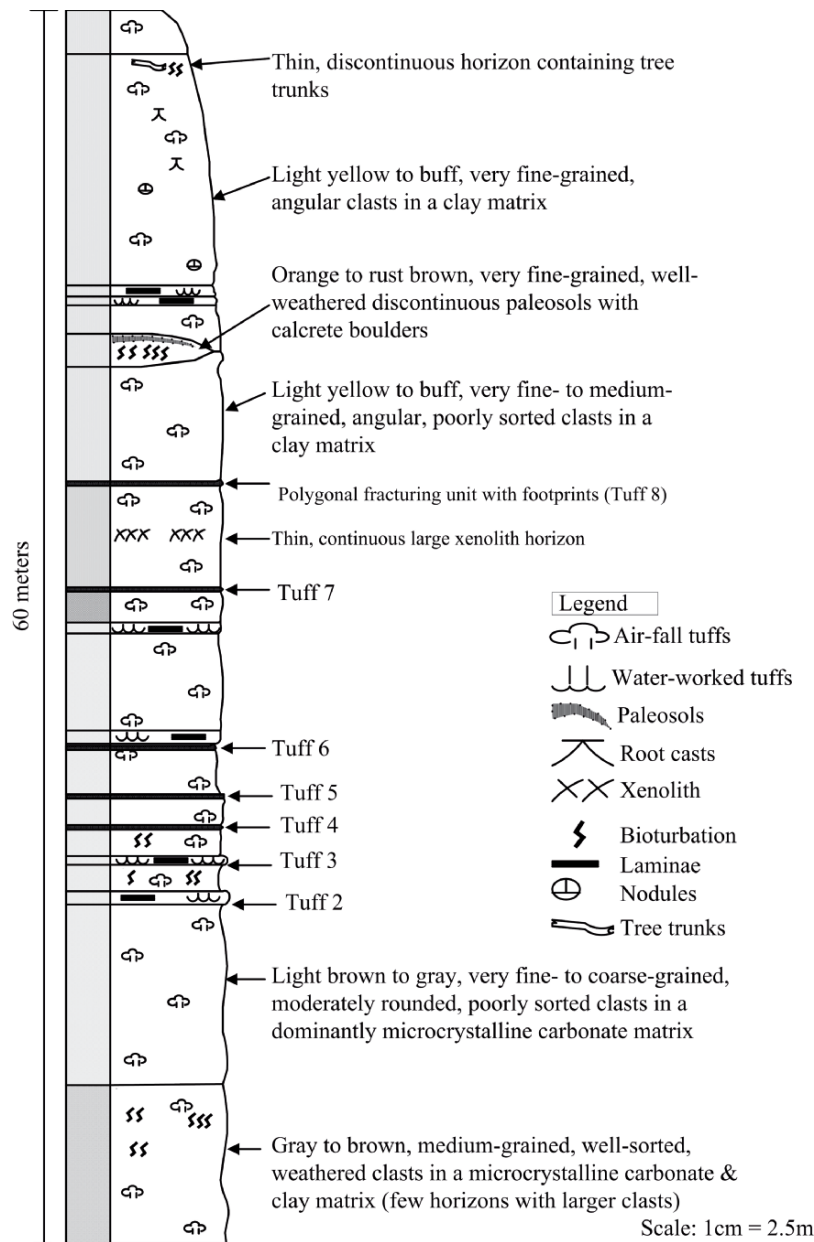


Figure 2. Detailed stratigraphic profile of the Upper Laetolil Beds.

(vertically and horizontally) filled with calcite material of varying size and width ranging from 1 to 60 cm thick. The calcite-filled joints can easily be distinguished within the exposed Upper Laetolil Beds at Localities 8 and 9. The thickness of the two joints at Locality 8 tends to increase as one moves northward towards and beyond the footprint site G. An open joint of about 40 cm thick characterized by a 210° SW and 195° NE striking system with a NE/SW

dipping trend was recorded northeast of the footprint site. Similarly at Locality 9, southwest of Locality 8 the same trend was noted. The sediments here tend to be dominated by air- and water-fall tuffs that are distinctively laminated. The laminae are closely interbedded and vary in thickness (12–15 cm). Therefore, they indicate the possible existence of a substantial amount of water that may well have supported a variety of flora and fauna.

Exposures about 3 m thick located northeast of the footprint site G are composed of sediments that reveal evidence of intensive bioturbation. The sediments in this area consist of deposits that are downgraded, heavily worn, reworked, and loosely packed. These deposits consist of laminated layers with medium- to fine-grain sands. About 150 m southeast of site G, the Upper Laetolil exposures bear a 300° SW strike with a 6° SW magnitude dip. The exposures here consist of a sorted fine to medium topmost layer about 60 cm thick, subdivided into sublayers of 15- to 45-cm thick loosely packed tuffs.

Additionally, stream-worked tuffs occur in several places and they are also very common above Tuff 6, where most of the deposits are lenticular and cross-bedded with channel filling that ranges from 0.15 to 1.2 m deep. These deposits grade from finer- to coarser-sorted sediments consisting of xenoliths, air-fall, and eolian tuffs. Furthermore, Manega (1993) noted that some sediment mixing occurs above Tuff 7 where stream-worked deposits 45 to 60 cm thick consist of material from younger deposits.

Root casts and nodules are also very common throughout the Upper Laetolil Beds. Most of the root casts are grayish in color, cylindrical in shape, and range in diameters from 1 to 13 cm (Figure 2). The infilling of the root casts consists of calcite material (cryptocrystalline) with rare inclusions of volcanic tuffs. The nodules, which are divided into three types, range in diameter from 1 to 45 cm and consist of: (a) microcrystalline calcite nodules that are circular and uniform in composition, (b) well-undulated tuff nodules that are also circular to oval and uniform in composition, and (c) small nodules with massive rings of tuffs that are separated by thin layers of calcite. From a stratigraphic and lithologic standpoint the Upper Laetolil Beds contain very distinctive sediments with depositional histories that are very important in paleoecological inter-

pretations. This is particularly the case with the water-worked tuffs described above.

Material and Methods

The data for this study originated from two sources: an excavation at Locality 9 ($n = 483$) and a systematic surface collection at Localities 8 and 9 ($n = 812$; Figure 3). The fossils were collected using a 100% surface collection method established at Laetoli by Ndessokia (1990). The collection included cranial and postcranial fragments, with few complete and *in situ* bone remains.

At Locality 9, a grid system consisting of three surface collection sections and one trench was established with a north/south bearing datum line. The three surface collection areas (Sections A, B, and C) were established on a 10 × 10 m grid system along the datum line. All exposed bones on each grid were first flagged (Figure 4) and numbered before their orientation relative to the datum line was established and recorded using a Brunton compass. Also the distance from one specimen to the nearest was recorded before the specimens were tagged and bagged. All recovered material, regardless of size, was tagged and recorded. These data were used to generate Rose diagrams of bone orientation. Later on, the sediments within the grid system were swept and screened on a 10 × 10 mm sieve. No floatation recovery technique was used in order to recover fragments that were smaller than 10 mm thick due to lack of sufficient water within the area. The contemporary Laetoli landscape is very dry during the dry season and nearest water sources, which are also used by the nomadic Maasai pastoralists, are located about 20 to 35 km away from Localities 8 and 9. Furthermore, the Ngarusi (Garusi) River, which is a main drainage within the Laetoli area, is seasonal and usually dries out during the dry season.

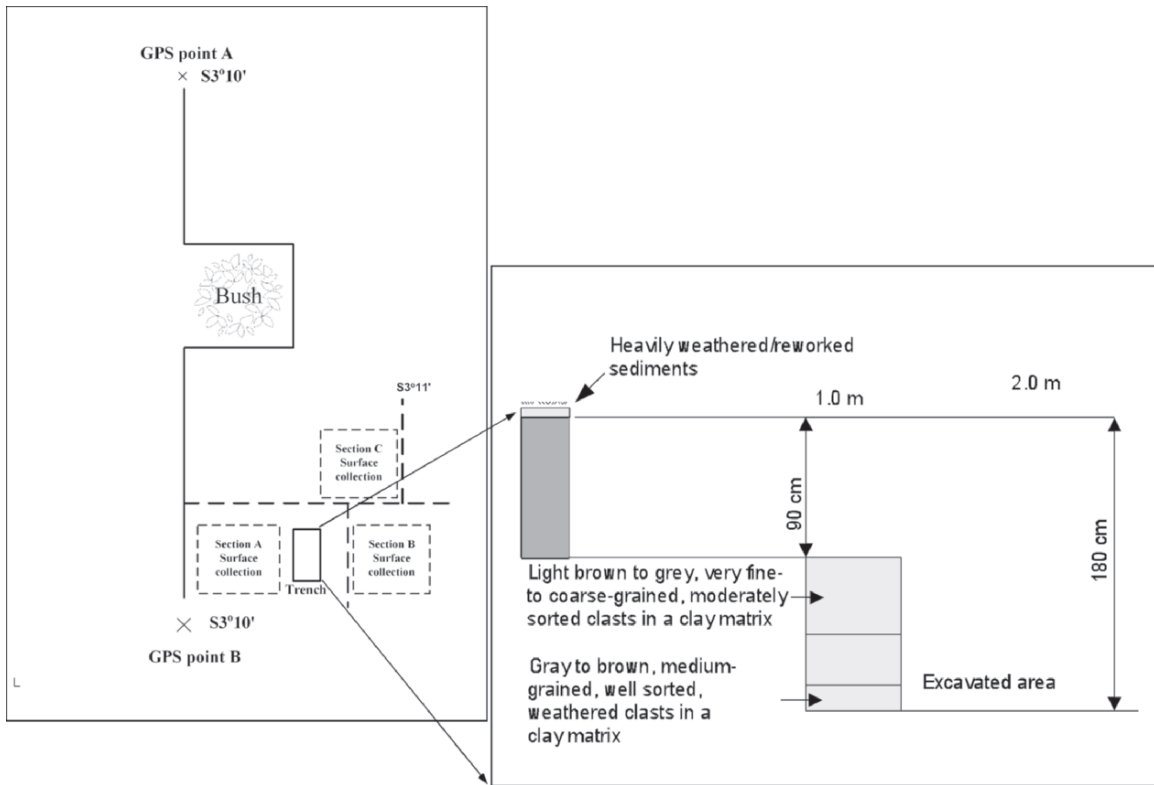


Figure 3. Excavation plan and surface collection grid at Locality 9.



Figure 4. Photo showing flagged and mapped surface finds at Locality 9.

The excavation that was carried out at Locality 9 in 1998 produced numerous complete small mammalian specimens including four pellets of articulated rodents, which are currently under study by Julian Kerbis (at the Field Museum of Natural History in Chicago) and will be published separately in the near future. Small rodents, particularly Gerbillinae and Murinae, dominate most of the burrowing animal assemblages that have been reported from the Upper Laetolil Beds at several localities (Davies, 1987; Denys, 1987). The excavation was conducted in order to establish a control sample to assess the taphonomic biases associated with surface collections at Localities 8 and 9. Taphonomic processes identified and recorded from the assemblage include the following: bone distribution pattern, disarticulation, pitting,

puncture, crenulations, breakage, trampling, etching, root marking, desquamation, and weathering.

Additionally, a small portion of Leakey's (1976–1979) fossil faunal remains was included in the analysis of bone surface modification in our 1998 study. However, Leakey's (1976–1979) field team collected only specimens that were large enough to identify. Small and unidentifiable specimens were collected, counted, and left in piles on the site by her team (Table 1; Figure 5). This method of surface collection produced a sampling bias that favored only robust and easily identifiable bones. Contrary to Leakey's collection strategy, our team systematically recorded all exposed bones in all transects within the established datum line. All bones were tagged, counted, identified, and measured (in terms of length

Table 1. Leakey's table of vertebrate and invertebrate faunal specimens collected and listed from the Laetolil Beds

Taxa	NISP ¹ for collected fragments	NISP for fragments left on site	Total
Gastropoda	316	2	318
Slug (mantles)	171	–	171
Chelonia (complete)	8	–	8
Chelonia (scutes/bones)	6	132	138
Reptilia (various)	16	–	16
Struthionidae (eggshell fragments)	57	–	57
Aves indet.	31	–	31
Soricidae	8	–	8
Lorisidae	5	–	5
Cercopithecidae	87	–	87
Hominidae	25	–	25
Rodentia	331	–	331
Leporidae	1959	902	2861
Pedetidae	191	3	194
Carnivora	261	–	261
Deinotheriidae	23	–	23
Elephantidae	97	131	228
Orycteropodidae	11	–	11
Equidae	171	94	265
Chalicotheriidae	5	–	5
Rhinocerotidae	267	377	644
Suidae	234	90	324
Giraffidae	456	352	808
Sivatheriidae	57	1	58
Bovidae	1,684	1,597	3,281
Totals	6,420	3,738	10,158

¹ Number of Identified specimens.

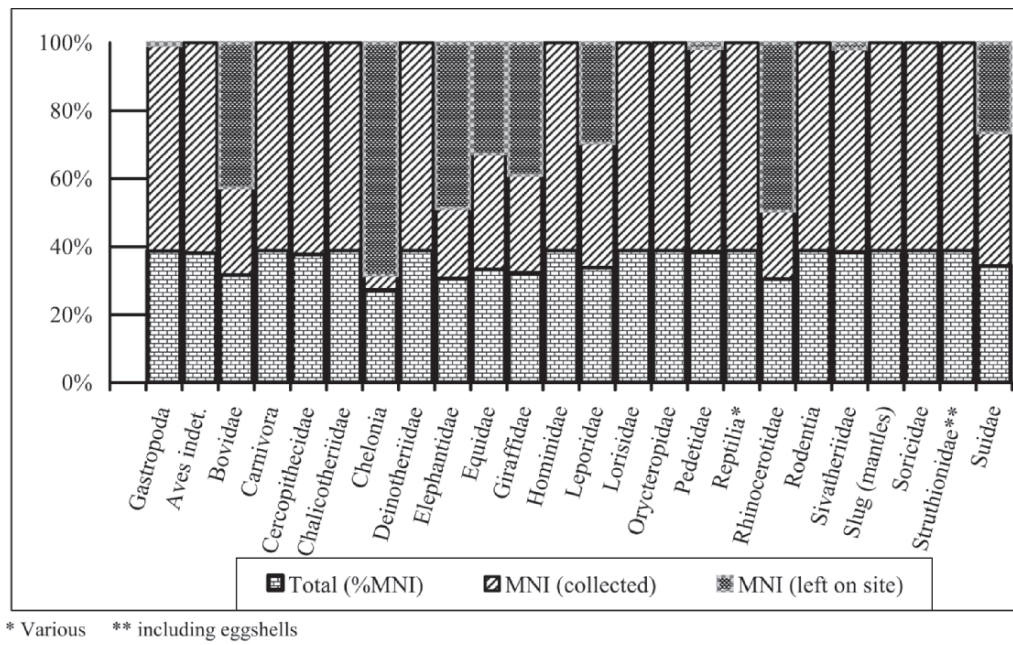


Figure 5 Taxonomic distribution of fossil faunal remains within the Laetolil Beds (including data by Leakey et al., 1987).

and thickness). Only unidentifiable bones that were <1cm long, which could not be identified and used for any taphonomic analyses, were collected but not used in the analyses.

We used Leakey's 1976–1979 Laetoli sample to establish surface bone modification. From that sample, two categories of bone surface modification were established using a scope with a 10× magnification. The two categories we established are physical damage (trampling, breakage on distal ends of long bones such as metapodials, gnawing on distal and proximal ends of long bones, etching, root marks, and boring on shafts of long bones) and chemical alterations (bone surface weathering and exfoliation).

Bone surface modification, particularly chemical alteration, of the Laetoli fossils from Localities 8 and 9 was recorded following the classification system of Andrews and Cook (1985). This system distinguishes five categories of modification: little, moderate, intermediate, great, and extreme. Furthermore,

the system takes into account other biogenic and physical modifiers of bone surfaces in archaeological records. Only three categories from Andrews' (1990) method were used in this study: little (L), moderate (M), and extreme (E) to produce a taphonomic history of bone surface modification of fossils from Localities 8 and 9. Because the differences between "great" and "extreme" as well as "moderate" and "intermediate" are difficult to distinguish, the two categories were not used for this study. Additionally, taphonomic variables such as exfoliation, secondary striations and/or scratch marks, and fragmentation were also recorded. Other bone surface modifications such as polishing or abrasion, striations, trampling, cracking, superficial weathering, grooving, pitting, boring, and color variations were also recorded. Behrensmeier's (1978) method of bone-weathering classification was also used to score weathering patterns on the fossils from the Upper Laetolil Beds.

Results and Discussion

FIELD-BASED OBSERVATION OF BONE SURFACE MODIFICATION

Splitting and cracking, which are very common in the Laetoli faunal assemblage, signal time-averaging events. During the 1998 field season at Locality 9, we noticed that newly eroded fossil bones shortly after the rain season in the Serengeti Plains consisted of remains that have distinctive breakage pattern on the distal and proximal ends of long bones (Figure 6). An actualistic pilot study conducted during the 1998 field season revealed that fragments of densely eroding bones, which have partially been exposed, greatly suffer from animal trampling. Broken fragments are easily transported both horizontally and vertically while the remaining, partially buried pieces, are impacted into the ground through compaction and trampling. Trampling is thus responsible for both vertical and horizontal transportation within the Laetoli landscape particularly on dense small- to medium-sized bones.

GENERAL PATTERNS OF BONE ASSEMBLAGE FROM LOCALITIES 8 AND 9

The Laetoli fossil fauna from Locality 9 consists of highly variable numbers of skeletal parts, of which 20% are tali, 18% dentition (including

fragmentary isolated teeth), 13% calcanei, 12% metapodials, about 8% femora, and 6% vertebrae (Figure 7A). Locality 8 however is characterized by highly fragmented long bones, which make up about 71% of the total collection (Table 2; Figure 7B). Furthermore, the assemblage is characterized by highly fragmented bones with varying surface modifications including cracking, sharp breakage, and splitting of proximal and distal ends. The collection is also characterized by 32.5% weathered, 25.2% cracked, 15.1% exfoliated, 8.7% pitted, 4.1% trampled, and 4.5% polished or rounded bones (Table 3; Figure 8). Likewise, bone surface modifications on teeth and horn cores are common and are usually characterized by cracking and splitting.

BONE DISTRIBUTION PATTERN

Overall long bone fragments, particularly midshafts, dominate skeletal representation in the fossil assemblage from Localities 8 and 9. Indeterminate shaft fragments (25%), mostly trampled, weathered, and exfoliated, are very common in the assemblage. At Locality 8, the assemblage consists of 54.8% complete tali, 17.7% distal and proximal radii, 12.8% distal and proximal metapodials, 8% complete calcanei, 3% distal and proximal ends of femora, 1.6% scaphoids, and 1.6% pelvis fragments.

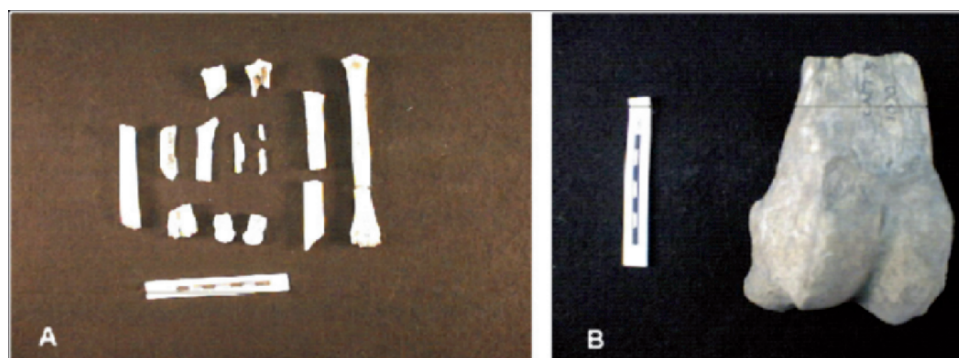


Figure 6. Breakage pattern of long bones at Localities 8 and 9, Upper Laetoli Beds.

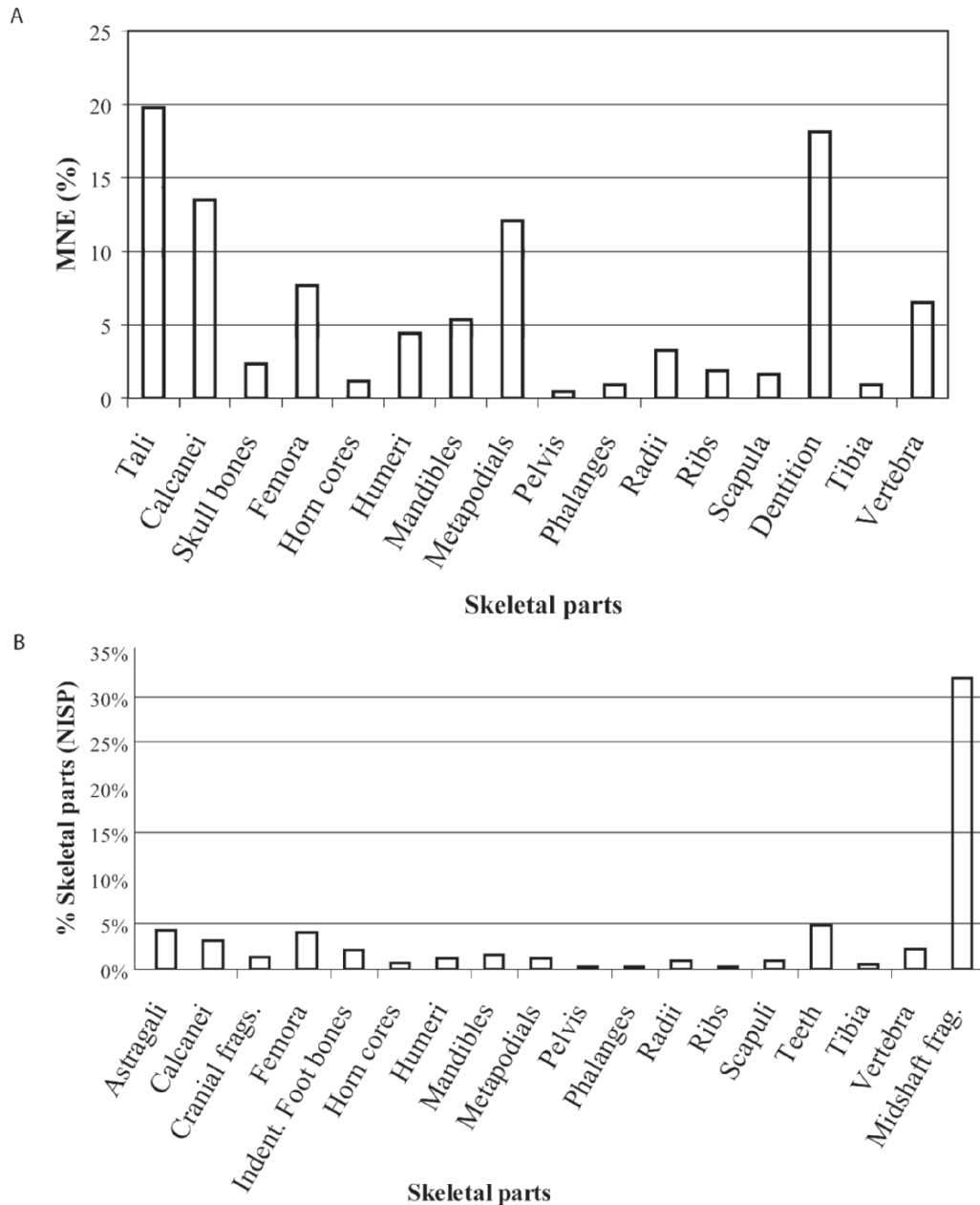


Figure 7. A) Skeletal part representation at Locality 9, Upper Laetolil Beds. B) Skeletal part representation of fossil faunal remains (100% surface collection) at Locality 8, Upper Laetolil Beds.

Scattered long bone and flat bone fragments occur, some *in situ*, and constitute about 95% of the assemblage at Localities 8 and 9 with a NE–SW orientation at Locality 9, and NW–SE bearings at Locality 8 (Figure 9). Isolated teeth and dental fragments of medium- to large-sized bovids (tentatively identified

as *Alcelaphus* and *Redunca*) are also common, as are mandibular fragments of small to large ungulates (Gentry, 1987). Small rodents, carnivores, and burrowing animals are also present at Localities 8 and 9. Burrowing animals provide the most complete skeletal remains at Laetoli.

Table 2. Skeletal parts representation from fossil faunal assemblage at Locality 8 (surface collection, $n = 812$)

Skeletal parts	NISP
Astragali	35
Calcanei	25
Cranial fragments	10
Femora	33
Indent. tarsal bones	17
Horn cores	5
Humeri	9
Mandibles	13
Metapodials	9
Pelvis	2
Phalanges	2
Radii	7
Ribs	2
Scapulae	7
Teeth	39
Tibiae	4
Vertebrae	18
Midshaft fragments	263
Indet. long bones	312
Total	812

Table 3. Frequencies of taphonomic processes observed on the fossil faunal assemblage from Upper Laetolil fossils ($n = 483$) at Localities 8 and 9

Taphonomic process	Total frequency
Boring	12
Cracking	122
Desquamation	73
Gnawing	6
Pitting	42
Polishing	17
Root-marks	9
Rounding	22
Trampling	20
Staining	3
Weathering	157
Total	483

The dispersal pattern of fossil faunal remains at Laetoli, especially between Tuffs 6, 7, and 8, indicates that the assemblage was time averaged. However, intense volcanism within the Laetoli area during the Pliocene caused short episodes of deposition that resulted in rapid burial, entrapment, and fossilization of small burrowing mammals. Such events, which have been documented

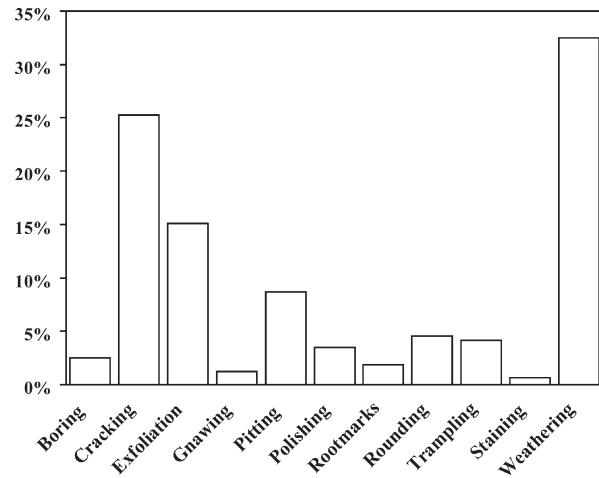


Figure 8. Observed patterns of bone surface modification of the Upper Laetolil fossil faunal assemblage at Locality 9.

by Hay (1987), Drake and Curtis (1987), and Manega (1993), tend to create high fidelity fossil faunal assemblages. For example, rapid sediment deposition in the Upper Laetolil Beds (above Tuff 6) might have caused a maximum amount of spatiotemporal resolution because the rate of bone destruction we observed is lower than that recorded by Leakey and her coworkers in 1987. Fossils recovered above Tuff 6 show no signs of chemical and physical alteration, and they are less fragmented. A similar phenomenon was also observed at various localities within the Laetolil Beds by Leakey and her coworkers in 1987.

Peculiarly, very few immature individual bones (unfused) were recorded for the fossil assemblages from Localities 8 and 9 (<10%). Furthermore, the assemblage is of attritional nature, comprising 95% of bones from mature and 5% from immature individuals of highly diverse species of bovids, leporids, and giraffids. Remains of equids, suids, lagomorphs, rodents, and carnivores are few at Localities 8 and 9.

SURFACE MODIFICATION

Broad contiguous shallow scrap marks on proximal and distal ends of long bones were observed on the fossil assemblage from Localities 8 and

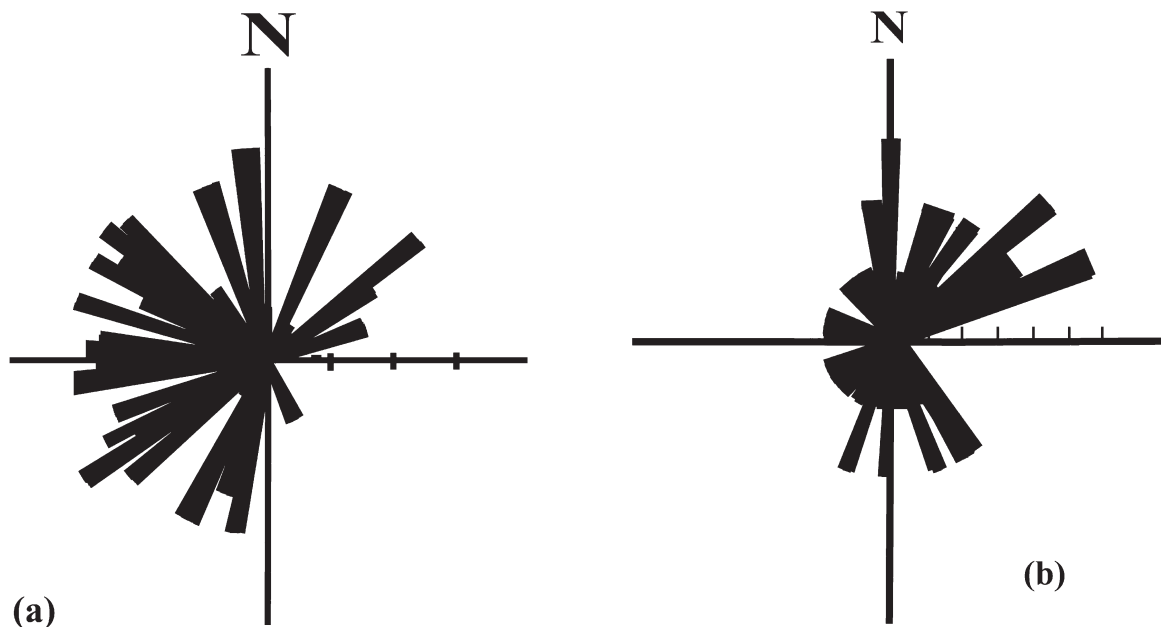


Figure 9. Bone orientation (surface collection) from (left) transects A and B and (right) transect C at Locality 9 (Upper Laetolil Beds).

9 by our team. Such bone surface modifications are normally associated with porcupine bone accumulations (Brain, 1981). However, porcupine species are not common in the Upper Laetolil Beds. Therefore, it is difficult to associate porcupines alone with the surface modification of the fossil assemblages. However, insectivores and carnivores are fairly well represented in the Laetoli fossil fauna (Table 1). The precise identity of the gnawing agent(s) for the Upper Laetolil Beds assemblage is not definitively known, but the gnawing marks on the bones resemble those of carnivorous animals. Perhaps a detailed study of gnawing marks on the Laetoli fossil assemblages will help elucidate some of the taphonomic agents responsible for surface modification and accumulations on the paleolandscape.

It is apparent that damage on long bones from the assemblage indicates that a predator or scavenger with a powerful masticatory apparatus must have applied extensive pressure on both proximal and distal ends of these long bones after they were disarticulated. In modern savanna environments this pattern of bone damage is associated with hyena scavenging activities (Blumenschine,

1989; Hill, 1979, 1980; Selvaggio and Wilder, 2001). Although Laetoli hominid remains are part of the assemblage, their presence does not suggest that they were agents of bone accumulation at Localities 8 and 9. So far there is no conclusive evidence to support such hominid activities at Laetoli. No cut marks on fossil bones from these localities have so far been documented.

WEATHERING PATTERN

The Laetoli fossil assemblage is dominated by heavily to moderately weathered bone fragments with polishing (abrasive) signatures that indicate prolonged periods of surface exposure. Prolonged exposure also resulted in exfoliation and rounding particularly on the proximal and distal ends of long bones. Exfoliation usually occurs in alkaline environments and has been reported at Olduvai Gorge (Fernández-Jalvo et al., 1998). Following Behrensmeier (1978) and Tappen (1994), four stages of bone weathering have been recorded at Laetoli. Most of the surface collection is heavily affected by stage IV of bone weathering

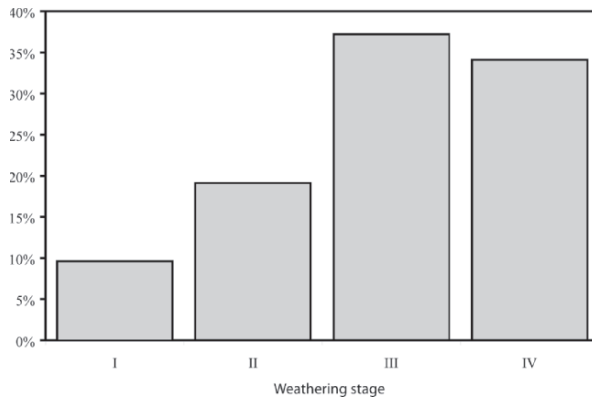


Figure 10. Observed stages of weathering patterns on fossil faunal assemblage from Upper Laetolil Beds (Localities 8 and 9).

(Figure 10). While remains from the excavated trench at Locality 9 show weathering stages II and III, most of the surface collection at this locality is characterized by stages III and IV. This weathering pattern is a good indication of prolonged exposure and time-averaging, especially when combined with cracking and superficial striation.

BIOTURBATION AND SEDIMENT MIXING

Significant signs of bioturbation were observed at Localities 8 and 9 and have been reported by Hay (1987). Extensive burrowing by termites and land snails is very common and frequent in the Upper Laetolil Beds (Verdcourt, 1987). Burrowing as a taphonomic process has an impact on bone distribution particularly on small, dense, and compact skeletal remains (Behrensmeyer, 1983; Behrensmeyer and Kidwell, 1985). Burrowing and bioturbation generate mixed assemblages. Bioturbation by earthworms, burrowing animals, and termites results in massive reworked sediments that are loosely packed. They can easily allow denser skeletal parts from small mammals (rodents and insectivores) to settle down as loosely packed material within the sediments, thus creating highly mixed assemblages. This kind

of mixing process was previously reported at other upland archaeological sites (Martin, 1982; Grant, 1983; Stein, 1983; Armour-Chelu and Andrews, 1994).

Taphonomy and Paleoecological Interpretations

Stratigraphic, geologic, and biological evidence from Localities 8 and 9 indicate that varying depositional conditions occurred at Laetoli around 3.5 million years ago. For example, the presence of fine laminae and volcanoclastic sediment deposits rich in clay indicates wet climatic conditions, whereas the occurrence of a thin layer of calcite within the Laetolil Beds indicates extreme dry conditions sometime during the middle Pliocene. Also the data derived from different taphofacies and lithofacies in Localities 8 and 9 do not entirely support the suggested savanna-like paleoecological models. For example, rich and diverse floral and faunal assemblages that are diagnostic of specific environmental conditions pose a challenge in constructing assemblage fidelity and stratigraphic acuity (Kidwell and Behrensmeyer, 1988; Behrensmeyer, 1991; Behrensmeyer and Hook, 1992; Behrensmeyer and Chapman, 1993).

The Upper Laetolil Beds, made up of thick layers of air-fall tuff deposited in at least six series of volcanic eruptions from a single source at Lemagruti, represent a time-averaged sequence characterized by weathered sediments and mud cracks produced by extended periods of exposure. The presence of intensely weathered paleosols within this layer suggests that Laetoli experienced highly variable climatic cycles characterized by extremely wet and dry conditions. The weathering of the paleosols reflects substantial precipitation, while bioturbation indicates that the environment may have been highly productive to sustain a wide range of insects. Bioturbation in the Upper Laetolil Beds implies that leaf litter of light to heavy vegetation cover may have characterized the environment. This is further supported by the

presence of tree stumps, root casts, and water-worked tuffs of varying degrees. Termitary impressions also support this scenario, while the presence of tree trunks confirms the existence of woodlands within the Laetoli area.

Sedimentological, lithological, and fossil evidence at Localities 8 and 9 indicate that during the Pliocene Laetoli experienced moist and more productive environments than today. The frequency of runoff tuffs with their massive thickness and the high density of termitary tunneling in the Upper Laetolil Beds suggest that sufficient water was available to rework the tuffs over prolonged periods. The presence of exfoliation and root marks, overlapped by striations and cracks on bones, indicates that the assemblage experienced periods of exposure long enough to alter their surface structure. This exposure, however, may not be used to indicate the existence of dry or open country habitats at Laetoli during the Pliocene; these periods of exposure might represent short episodes of extremely variable temperatures followed by wet and cooling phases.

Sedimentation processes in the Laetolil Beds produced stratified sequences of varying degrees of time-averaging (Drake and Curtis, 1987; Hay, 1987). This is consistent with geological observations by other workers. Several episodes of overprinted depositional environments in the footprint tuffs are well documented through sediment mixing by Hay (1987, 1980) and Manega (1993). Furthermore, stratigraphic descriptions by Manega (1993) also provide signs of massive erosion, sediment mixing, reworking, and eventually redeposition that would mask various time-averaged hiatuses.

Although small mammals are good climatic indicators, their representation in the Laetoli fossil assemblages seems to be obscured because they were heavily affected by many taphonomic processes including weathering, fragmentation, predation, and both biological and physical mixing (Hay, 1987; Hill, 1987). Transportation and mixing by biological and

geophysical agents obscured the specific composition of small-mammalian remains in the fossil assemblages. This conclusion is supported by evidence from fossilized owl-pellets of regurgitated small mammals indicating the occurrence of long-distance bone transportation within the Laetoli area.

Unfortunately, slow-rate accumulations tend to smooth out short-term shifts in ecological conditions. Changes in faunal compositions at Laetoli have been noted (Harris, 1985; Harrison, 2005; Gentry, 1987), especially between the Lower and Upper Units as well as between the Upper Laetolil and the Ndolanya Beds (Kovarovic et al., 2002). Yet, the cause of these changes has not been fully established. It is unclear whether these faunal changes through time were caused by tectonic, taphonomic, or climatic factors.

Consequently, repeated depositions of volcanic tuffs followed by prolonged periods of precipitation resulted in varying degrees of sedimentary weathering and bone surface modification within the Laetolil Beds. The varying degrees of sedimentary weathering, especially in the Upper Laetolil Beds, may represent several climatic cycles with significant changes that might have taken place during the Pliocene. These changes are also reflected in the distribution of fossil assemblages. For example, the Upper Unit of the Laetolil Beds is richer in fossil remains than the Lower Unit, with the highest fossil faunal concentration occurring just above and below Tuff 6. However, the fauna is composed of highly fragmented long and flat bones. The assemblage includes fragmented mandibles, isolated teeth, fragmented cranial bones, and occasionally articulated small burrowing mammals.

The geologic and stratigraphic information of the Upper Laetoli Beds at Localities 8 and 9 supports a mosaic environmental setting characterized by grassland and galleries of woodland for Pliocene Laetoli. In addition, studies based on functional related morphological characters of bovid femoral heads and

metapodials by Musiba (1999) also favor the model of mosaic environments at Laetoli, especially at Localities 8 and 9. Therefore, hominins from the Upper Laetoli Beds, though not so abundant, were part of a mosaic environment. The Upper Laetoli Beds preserve a record of prolonged changes in the environmental settings with a continuous presence of hominins and other mammals. The Laetoli mosaic environment and its varying relief may have been very crucial in preserving the ichnofossil record that documents evidence of hominin footprints and animal trackways during the Pliocene. Its complex geology and stratigraphy makes Laetoli an important site for detailed paleoanthropological studies in the future, especially of the ecological settings and the affinities of the Laetoli footprint makers.

Conclusion

The fossil faunal assemblage from Laetoli is dominated by heavily fragmented long bones, particularly on the distal and proximal ends, and midshafts (Table 2). Few complete bones were recovered at Localities 8 and 9 in the Upper Laetoli Beds during our fieldwork. Bone modifications on this assemblage include boring, tunneling, exfoliation, cracking, and weathering (Table 3). Trampling and bone weathering (stages II–IV) were the most dominant processes affecting the fossil assemblage at Localities 8 and 9. However, small mammalian bones were much more affected than bones from medium to large mammals. Rounding and polishing due to water transportation on proximal and distal ends of long bones is common in the Upper Laetoli fossil assemblage. Exfoliation tends to affect both exposed and *in situ* bones by staining them to appear as if they were charred. This process, which is very common at Laetoli, is attributed to mineral leaching from the sediments into bone matrix. In general, bone modifications of the faunal assem-

blage point towards the presence of streams or channels.

Taphonomic observations and stratigraphic interpretations of the fossil assemblage from Upper Laetoli Beds at Localities 8 and 9 are summarized below. Localities 8 and 9 consist of highly fragmented bone assemblages that point toward multiple depositional events during the Pliocene. Taphonomically, these assemblages are characteristic of active mass accumulation that may have been created by carnivores, rodents, and in some cases predatory birds.

Bone distribution is sparsely scattered and heavily dominated by compact, round, and dense bones as well as long bones. Tali (20%) and radii (18%) dominate the assemblage as the most common skeletal parts. Calcanei and metapodials represent about 14% of the total skeletal parts in the fossil assemblage. Scaphoids and pelvis fragments are least represented in the assemblage, while isolated teeth, which are highly fragmented, make up only about 18%. The highly fragmented teeth are also heavily exfoliated, probably as a result of secondary mineralization after reexposure.

The disarticulation pattern is also non-specific, with the exception of occasional trap specimens from burrows. The Upper Laetoli faunal assemblage from Localities 8 and 9 reflects several phases of cyclic environmental conditions dominated by phases of low-energy regimes. In addition, the assemblage indicates a high degree of predation and scavenging activities as reflected in bone-breakage patterns, gnawing, and tooth marks. In general, the order of disarticulation of the assemblage influenced other processes such as bone surface modification, transportation, and spatial patterning of bones on the landscape. Of particular interest in regard to disarticulation pattern is chemical and physical weathering, which is indicative of a prolonged surface exposure.

High frequencies of bone weathering (stages III–IV), pitting, and burrowing indicate that the

disarticulated bones were not rapidly buried after death. There were prolonged periods of carcass exposure, followed by rapid decay and bone disarticulation and weathering. The prolonged carcass exposure is reflected through bone surface modifications and damages on proximal and distal ends of long bones. Other factors that had considerable effect on the assemblage are insect boring and bioturbation. Animal trampling, rodent gnawing, grooving, root marking, and bacterial and algal staining also suggest that the Laetoli death assemblages suffered prolonged exposure.

Taphonomically, the Upper Laetolil Beds are characterized by a low density of time-averaged fossil accumulations. The beds record a fairly stable sedimentation rate (Drake and Curtis, 1987), but are also characterized by brief episodes of rapid deposition from volcanic eruptions from nearby sources at Lemagruti (Hay, 1987; Manega, 1993). Based on surface bone modifications and other observed taphonomic modifications, the Upper Laetolil faunal assemblage was partially accumulated by carnivores before fossilization. Thereafter the assemblage was exposed and reworked through physical and chemical processes. The assemblage was further modified and vertically and horizontally dispersed via bioturbation, trampling, and compaction.

Overall, classification of the Laetoli fossil bovid assemblage by Musiba and Magori (2005) and Musiba (1999) in a discriminant function analysis of fossil bovid limb morphologies as eco-indicators points towards mosaic-like environments. Using discriminant function analysis and PNN (Probabilistic Neural Network protocol in MatLab) statistics for bovid limb morphologies, Musiba (1999) placed the analyzed bovid limb elements in four habitat types: open, intermediate, woodland, and forest. This interpretation of the Laetoli Pliocene environment is consistent with the geological and stratigraphic information provided in this study for Localities 8 and 9 within the Upper Laetoli Beds.

Fossil bovid remains from the Upper Laetolil Beds at Localities 8 and 9 provide an interesting picture of their evolutionary and behavioral ecology. Gentry (1987) acknowledged the peculiarity of the taxonomic composition of the Laetoli bovinds. These fossils differ in their overall morphology and composition from their extant sister groups (Gentry, 1981). The Laetoli fossil bovinds present a mosaic of femoral morphologies with implications ranging from open country habitat to woodland or woodland/forest mix. Their morphologies reflect the locomotor behaviors favored by the Laetoli bovinds, which range from *Simatherium kohlarseni*—a large-size Bovini that may have favored an intermediate habitat type—to species of Cephalophini (rarely found as fossils), which may have preferred forested or wooded habitats at Laetoli. This broad spectrum of habitats during the Pliocene makes Laetoli very different from other East African paleoanthropological sites (such as Koobi Fora in Kenya and Hadar in Ethiopia) of comparable age, in that its faunal composition was highly diverse.

Furthermore, Laetoli fossil Neotragini, a tribe that is abundant in the Upper Laetolil Beds, may be represented by *Madoqua avifluminis* and probably a *Raphicerus* species (Gentry, 1987). Their extant counterparts tend to favor rather open country habitats. Nevertheless, the appearance of Neotragini in the Upper Laetolil Beds as an abundant taxon would be consistent with open country habitats characterized by galleries of mixed vegetation of light to dense woodland. But *Madoqua* species (extant dik-diks), which are mainly browsers, prefer light to heavily wooded habitats consisting of *Acacia* trees, bush, and thorn scrub, and tend to avoid open grasslands (Kingdon, 1982).

Previously proposed paleoenvironmental models for Pliocene Laetoli placed it in open country grassland environments similar to the present-day Serengeti (Leakey et al.,

1987). However, Laetoli's complex faunal remains and its geology and stratigraphy as discussed in this paper point towards a mosaic environment. For example, *Madoqua* is the most common bovid taxon in the Upper Laetoli Beds (Gentry, 1987) and its modern counterparts prefer light cover habitats. Additionally, the existence of *Tragelaphus* sp., *Simatherium kohllarseni*, *Cephalophus* sp., *Hippotragus* sp., and sp. indet. aff. *Pelea* in the fossil assemblage is also in contrast with the open country or savanna grassland models. Furthermore, viverrids, *Herpestes*, and several mollusk species within the Upper Laetoli Beds also point towards a mosaic type of ecological settings. The geologic and stratigraphic evidence further contradicts the savanna grassland interpretation of Laetoli's Pliocene environments, especially at Localities 8 and 9.

This study represents a small fraction of the entire Laetoli site. Therefore, the results presented here may not be used to generate an overall interpretation of the greater Laetoli paleoanthropological site (200 km²) without taking into account the size of the area and the variable topography that existed during the Pliocene. Therefore, systematic and uniform studies of the entire site in the future are recommended in order to model overall Pliocene environments for the entire site. We believe that the taphonomic history of Laetoli is much more complex than previously considered in that it is characterized by episodes of highly variable time-averaged bone accumulations. Some of these accumulations between Tuffs 6, 7, and 8 occurred over a time span of approximately 300,000 years and are separated by multiple depositional events.

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