11. The paleoecology of the Upper Laetolil Beds at Laetoli

A reconsideration of the large mammal evidence

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Keywords: Ecological diversity analysis, ecovariables

Abstract

Laetoli, in northern Tanzania, is one of the most important paleontological and paleoanthropological sites in Africa. Apart from Hadar, it has yielded the largest sample of specimens attributable to the mid-Pliocene hominin, *Australopithecus afarensis*, including the type specimen. As such, it is important to explore the paleoenvironment at Laetoli, especially the different habitat types that may have been exploited by *A. afarensis*. Previous interpretations of the paleoecology at Laetoli have led to quite different conclusions. Initially, the paleoenvironment was reconstructed as an arid to semi-arid grassland with scattered bush and tree cover, and patches of acacia woodland, similar to the modern-day local setting. However, some aspects of the fauna do indicate that the range of habitats may have included more dense bush cover and more extensive tracts of woodland than seen in the region today. The main objective of this paper is to re-examine this issue by more thoroughly documenting the paleoecological setting by conducting a more detailed and comprehensive comparative analysis of the mammalian fauna. To this end, the ecovariable structure of the mammalian fauna at Laetoli is compared to other Plio-Pleistocene hominin-bearing fossil localities and modern faunal communities from different habitats, including forest, woodland, open woodland, bushland, shrubland, grassland, and desert. Principal components analysis (PCA) and bivariate analyses of predictor ecovariables were conducted. An important finding was the general distinctiveness of fossil assemblages, including Laetoli, from modern communities. Terrestrial mammals were found to have the greatest impact on the uniqueness of fossil communities, with fossil assemblages having very high proportions of terrestrial mammals when compared to modern communities. Furthermore, the high frequency of grazers and terrestrial mammals, combined with the low occurrence of arboreal and frugivorous mammals at Laetoli, indicates affinities with modern mammalian communities living in grassland, savanna, and open woodland settings. Taking into account

R. Bobe, Z. Alemseged, and A.K. Behrensmeyer (eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, 279–313.

the results of this study, and the presence of indicator species, we reconstruct the paleoecology of the Upper Laetolil Beds as a mosaic habitat dominated by grassland and shrubland, with areas of open- to medium-cover woodlands, as well as some closed woodland and possibly gallery forest along seasonal river courses.

Introduction

Laetoli, in northern Tanzania, is renowned as one of the most important paleontological and paleoanthropological sites in Africa. Apart from Hadar, it has yielded the largest sample of specimens attributable to the mid-Pliocene hominin, *Australopithecus afarensis*, including the type specimen, as well as the remarkable discovery of well-preserved trails of hominin footprints (Leakey et al., 1976; White, 1977, 1980a, b, 1981, 1985, 1989; Leakey and Hay, 1979, 1982; Leakey, 1981, 1987a, b, c; Tuttle, 1985, 1987, 1990; Robbins, 1987; White and Suwa, 1987; Tuttle et al., 1991, 1992). An intensive program of research directed by Mary Leakey from 1974 to 1982 laid the foundation for a greater understanding of the geology, geochronology, and paleontology of Laetoli (see papers in Leakey and Harris, 1987). More recent fieldwork at Laetoli has included further excavations and collections (Kyauka and Ndessokia, 1990; Ndessokia, 1990; Kaiser et al., 1995), refinements in the geochronology (Ndessokia, 1990; Manega, 1993), efforts to conserve the fossil footprints (Anonymous, 1995; Agnew et al., 1996), and research on the paleoecology and taphonomy (Musiba, 1999; Kovarovic et al., 2002). In 1998, one of us (TH) began directing renewed paleontological and geological investigations at Laetoli, a project that is currently ongoing. A major aim of this renewed work at Laetoli is to provide a better understanding of the paleoecology, especially the types of habitats that could potentially have been exploited by *A. afarensis*.

Previous interpretations of the paleoecology at Laetoli have led to quite different conclusions. Initially, the paleoecology was reconstructed as an arid to semi-arid grassland with scattered bush and tree cover, and patches of acacia woodland, similar to the modern-day local setting (e.g., Hay, 1981, 1987; Bonnefille and Riollet, 1987; Gentry, 1987; Harris, 1987a; Leakey, 1987a; Meylan, 1987; Watson, 1987). The major lines of evidence that supported this conclusion were derived from analyses and interpretations of the geology, palynology, and vertebrate paleontology. These include: (1) extensive wind transportation of sand-sized ash particles, indicating poor vegetation coverage on land surfaces (Hay, 1987); (2) caliche paleosols with ash particles cemented by phillipsite, most likely formed under alkaline environments favored by semi-arid to arid conditions, at least seasonally (Hay, 1987); (3) the Footprint Tuff (the lower part of Tuff 7) directly overlies a tuffaceous layer containing small roots, interpreted as grass rootlets, while the regularity of the contact between these tuffs implies that the land surface on which the Footprint Tuff was deposited was largely barren of grass, and possibly heavily grazed (Hay, 1987); (4) the base of the Footprint Tuff contains a layer rich in fossil twigs and leaf impressions that resemble modern species of *Acacia* (Hay, 1987); (5) fossil pollen assemblages indicate an arid savanna vegetation characterized by a high diversity of herbaceous plants, dominated by grasses, and with a sparse tree cover, possibly associated with a warmer and drier climate than today (Bonnefille and Riollet, 1987); (6) the snake and avian fauna is typically associated with savanna, bushland, and open woodland habitats (Meylan, 1987; Watson, 1987); (7) several genera of rodents (i.e., *Saccostomus*, *Xerus*, *Thallomys*, and *Pedetes*) as well the leporid, *Serengetilagus*, are indicative of dry grassland–savanna habitats (Denys, 1985, 1987; Davies, 1987a, b); (8) the abundance and taxonomic diversity of herpestids indicate savanna to open woodland conditions (Petter, 1987); (9) the taxonomic composition of large carnivores at Laetoli resembles the community structure seen today in African savannas (Barry, 1987); (10) the predominance of Alcelaphini, Antilopini, and Neotragini in the bovid fauna implies that non-woodland habitats were present (Gentry, 1987); and (11) the occurrence of the large, hypsodont *Notochoerus euilus* as the dominant suid, and the absence or rarity of *Nyanzachoerus kanamensis*, which is otherwise quite common at contemporary East African localities, suggests relative dry conditions (Harris, 1987a, b). It is reasonable to conclude from these various lines of evidence that grassland, savanna, and open woodland habitats were an important component of the ecological setting at Laetoli during the mid-Pliocene.

However, some aspects of the fauna do indicate that the range of habitats may have included more dense bush cover and more extensive tracts of woodland than seen in the region today (Butler, 1987; Harris, 1987a; Meylan, 1987; Petter, 1987; Verdcourt, 1987). Andrews (1989), using ecological diversity analysis, argues that the fauna reflects a more heavily wooded environment than previously recognized, and that some unusual properties of the mammalian community structure are best accounted for either by mixing of faunas from different ecologies or by habitat changes through the sequence. Subsequent studies of the mammalian fauna by Reed (1997) and Musiba (1999), and of stable carbon isotopes (Cerling, 1992), have provided additional support for a greater representation of wooded habitats at Laetoli. For example, Reed (1997) showed that closed woodlands are indicated by the high taxonomic diversity of arboreal and frugivorous mammals present at Laetoli. There are certainly good ecological indicators in the mammalian fauna that suggest that bushland and woodland habitats were a significant component at Laetoli. Among the bovids, Tragelaphini and Cephalophini are typically associated with wooded habitats, while *Madoqua*, which is remarkably common at Laetoli, prefers bush and thorn scrub (Kingdon, 1974c, 1997; Gentry, 1987). The species diversity and abundance of giraffids (belonging to three species and representing more than 16% of all artiodactyl specimens from Laetoli) implies a woodland setting that supports a guild of large browsers not represented in contemporary faunas. The suid, *Potamochoerus*, has a strong preference for forest and woodland habitats (Kingdon, 1974e, 1997; Harris, 1987b). Several species of primates are known from Laetoli, including the bushbaby, *Galago sadimanensis*, and at least three species of cercopithecids, *Parapapio ado*, *Paracolobus* sp., and a colobine monkey somewhat larger in size than the extant *Colobus*, and possibly a larger papionin[1] (Leakey and Delson, 1987; Walker, 1987). The diversity of the primate community is suggestive of closed woodland or forest, at least along river courses. Although cercopithecids occupy a range of habitats from grassland to forest today, they do require stands of trees or rocky outcrops as sleeping sites. Reconstructions of the landscape and topography at Laetoli indicate a gently undulating terrain, with no rock outcrops, implying that larger trees would have been important sites of refuge for cercopithecid primates. The postcranial remains attributed to *Paracolobus* and *Parapapio* also imply a significant component of arboreality. Of the small mammals,

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[1] Ndessokia (1990) lists *Theropithecus darti* in his faunal list of the Upper Laetolil Beds. However, no information is given on the provenience or nature of the find(s) on which this record is based, and we have been unable to locate the original material. No specimens of this taxon have been recovered from the Upper Laetolil Beds by Leakey's or Harrison's teams, so we are inclined to discount this record. However, Mary Leakey did recover *Theropithecus* sp. from the Ngaloba Beds, and it is possible that the record refers to material from this younger horizon.

the occurrence of the bush squirrel, *Paraxerus*, and the giant elephant shrew, *Rhynchocyon*, implies closed woodlands with dense undergrowth and substantial leaf litter (Kingdon, 1974a, b, c, 1997; Butler, 1987; Denys, 1987). The avian community, including at least one small species of francolin, a larger francolin, a guinea fowl, as well as ostriches, implies that the paleoecology at Laetoli was most likely open woodland, bushland, savanna, or grassland (Watson, 1987; Harrison and Msuya, 2005; Harrison, 2005). However, in habitats where grassland predominates, francolins and guinea fowl require low brush and thickets for escape and refuge, as well as trees in which to roost at night. They prefer mosaic ecotonal habitats offering open feeding areas with good visibility, but with dense vegetation cover and patches of woodland nearby (Dörgeloh, 2000; Harrison, 2005). The terrestrial gastropod community at Laetoli includes *Subulona* and *Euonyma* that are found today primarily in evergreen forest (Verdcourt, 1987). Urocyclid slugs are extremely common and ubiquitous, and although they do occur today in dry open woodland and savanna habitats, leaf litter and fallen trees are a necessary requirement as sites for feeding and aestivation. Finally, the greater proportion of Afro-Montane elements in the palynological spectrum compared with the modern pollen rain (Bonnefille and Riollet, 1987), and the density and diversity of macrobotanical remains (such as twigs, leaves, and seeds), indicate that wooded and forested habitats were a more important component of the paleoecology in the Pliocene than they are in the region today.

The balance of evidence implies that the previous emphasis on the predominance of grassland and savanna habitats at Laetoli may have been somewhat overstated. Although one can be confident that grassland and savanna were an important component of the ecological setting, the totality of the faunal and floral evidence suggests that a mosaic of habitats was available, with a greater representation of open and closed woodland than is seen today in the vicinity of Laetoli. Nevertheless, it still remains to be established just what would be the closest modern analog to the paleoecological setting at Laetoli. With a more detailed and comprehensive analysis of the fauna it might be possible to develop a more nuanced interpretation of the paleoecology at Laetoli, one that entails a broader comparison with modern and Pliocene faunas from Africa. This is one of the main objectives of the current study.

However, before the Laetoli fauna can be compared in this way, an initial inference needs to be tested. One possible alternative explanation for the conclusion that Laetoli represents a heterogeneous mosaic of grassland, savanna, and woodland habitats is that the various ecological signals are derived from a composite fauna from different localities that span the entire stratigraphic sequence of the Upper Laetolil Beds. Rather than a complex mosaic of habitats occurring uniformly throughout the sequence, the structure of the fauna might reflect distinct differences in the patterning of vegetation in space and time, of which the composite ‘time-averaged’ fauna merely offers an ecological palimpsest. To test this hypothesis, we analyze the faunas from the different collecting localities and stratigraphic zones separately to see if there are any significant difference in the faunas in space and time. If there are observed differences, then the paleoecology of each locality and/or stratigraphic zone will need to be reconstructed separately and the general paleoecology of Laetoli reconsidered in light of these findings.

Given these considerations, this paper attempts to answer two critical questions about the paleoecology of Laetoli: (1) Are there significant differences in the composition of the faunas at Laetoli that reflect geographical differences in the local ecology or changes in ecology through time? (2) If the fauna indicates temporal and/or geographical heterogeneity or uniformity, how does this impact on reconstructions of the overall paleoecology at Laetoli? In order to answer these questions we first assess the nature and the degree of differences between the faunas from different localities and stratigraphic zones at Laetoli, then we attempt a reanalysis of the paleoecology based on a more detailed and comprehensive comparative study of the mammalian fauna using ecological diversity analysis.

Geological Context

The stratigraphy and geochronology of Laetoli have been well documented (Kent, 1941; Pickering, 1964; Hay, 1976, 1978, 1987; Drake and Curtis, 1979, 1987; Hay and Leakey, 1982; see Figure 1). Fossil vertebrates have been recovered from throughout the sedimentary sequence, but the most productive units are the Laetolil and Ndolanya Beds (Hay, 1987; Figure 1). The Laetolil Beds rest unconformably on the Precambrian Basement, and are divided into two lithological units – the upper and lower units. The lower unit consists primarily of aeolian tuffs interbedded with air-fall and water-worked tuffs (Leakey et al., 1976; Hay, 1987). It is dated radiometrically from 3.8 Ma to older than 4.32 Ma (Drake and Curtis, 1987), although based on estimated sedimentation rates at Laetoli, the bottom of the sequence could be as old as 4.6 Ma.

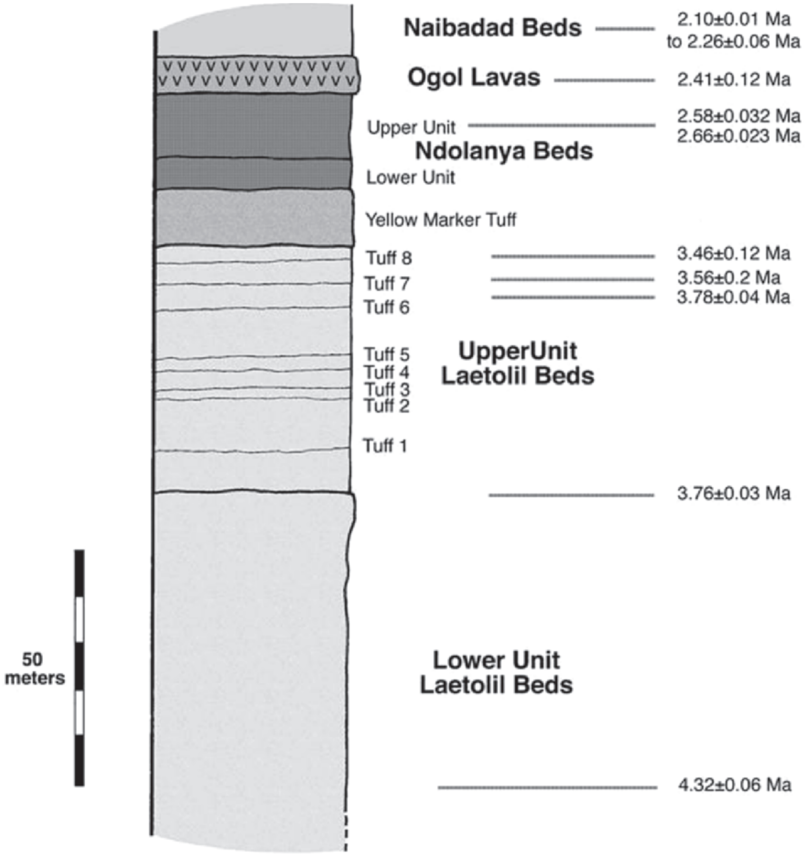

Figure 1. General stratigraphic column of Laetoli (after Hay, 1987; Drake and Curtis, 1987; Ndessokia, 1990; Manega, 1993).

A small fauna has been recovered from the Lower Laetolil Beds (Harris, 1987; Harrison et al., in preparation), but no hominin fossils have yet been found. The Upper Laetolil Beds, from which all of the *Australopithecus afarensis* specimens have been recovered, have been radiometrically dated to ~3.5 to 3.8 Ma (Drake and Curtis, 1987; Figure 1). The sediments consist largely of aeolian tuffs, but also contain a series of air-fall tuffs and some water-worked tuffs (Hay, 1987). Eight of the air-fall tuffs, identified on the basis of their lithology and mineralogical composition, have been identified as marker tuffs (Hay, 1987). These can be used to sub-divide the fauna from the Upper Laetolil Beds into a series of narrow temporal zones (Hay, 1987). Renewed fieldwork at Laetoli since 1998 has allowed a more refined appreciation of the stratigraphical provenience of the fossils at each of the localities at Laetoli, and these data are presented in Table 1.

The Ndolanya Beds consist of a series of tuffs and calcretes, which are subdivided into upper and lower units (Hay, 1987). The lower unit is chiefly clay-rich deposits, with some massive vitric tuffs and limestones. Root markings are common, but no fossil vertebrates have been found. The upper unit is comprised mainly of aeolian- and water-worked tuffs (Hay, 1987). This unit is highly fossiliferous, with a diverse vertebrate fauna, including *Paranthropus aethiopicus* (Harrison, 2002). The fauna from the Upper Ndolanya Beds is consistent with an age of ~2.5 to 2.7 Ma (Harris and White, 1979; Beden, 1987; Gentry, 1987; Hooijer, 1987; Harris, 1987b), and radiometric dates of 2.58 to 2.66 Ma have been reported (Ndessokia, 1990; Manega, 1993). The Ndolanya Beds are overlain by a series of lavas, the Ogol lavas, with an average K-Ar date of 2.41 Ma (Drake and Curtis, 1987; Hay, 1987).

Table 1. Fossiliferous horizons of the Upper Laetolil Beds at all Laetoli localities included in this study

Locality	Fossiliferous horizons
1	Between Tuff 6 and Yellow Marker Tuff
2S	Between Tuffs 5 and 7
2W	Between Tuffs 5 and 7
3	Between Tuffs 7 and 8
	Between 4 and 6
4	Between Tuffs 6 and 8
5	Between Tuffs 3 and 5
6	Between Tuffs 5 and 7
7	Between Tuffs 5 and 8
8	Between Tuffs 5 and 7
	Between Tuff 7 to above Tuff 8
9	Between Tuffs 5 and 7
	Between Tuffs 7 and 8
9S	Between Tuff 2 and below Tuff 1
10	Between Tuffs 1 and 3
10E	Between Tuffs 5 and 7
	Between Tuffs 7 and 8
10W	Between Tuffs 1 and 3
11	Between Tuffs 7 and 8
12	Between Tuffs 5 and 7
12E	Between Tuffs 5 and 7
13	Between Tuffs 5 and 8
	Between Tuffs 3 and 5
15	Between Tuffs 6 and 7
16	Between Tuff 7 to just above Tuff 8
17	Between Tuff 7 and Yellow Marker Tuff
19	Between Tuffs 5 and 8
20	Between Tuffs 6 and 8
21	Between Tuffs 5 and 7
22	Between Tuffs 5 and 7
	Between Tuffs 2 and 5
22E	Between Tuffs 5 and 7

The majority of fossils from the Upper Laetolil Beds have come from a relatively restricted area at Laetoli, covering about 80 km^2, centered on the eastern reaches of the Garusi River valley (Figure 2). Thirty-four collecting localities and sub-localities have now been delimited at Laetoli that expose outcrops of the Upper Laetolil and Upper Ndolanya Beds (Leakey, 1987a; Harrison, unpublished data; Figure 2). These collecting localities, which are quite limited in size (no larger than 1 km^2), are used as the basic geographical unit in this study.

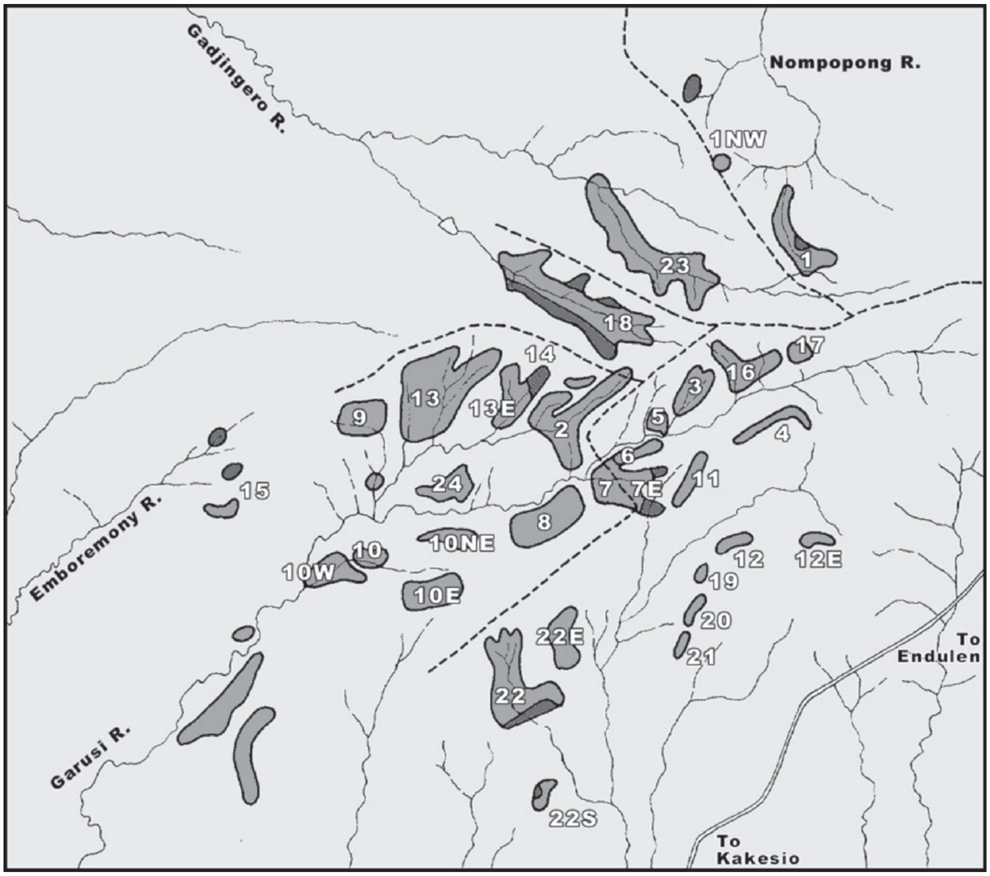

Figure 2. Map of the area of Laetoli and the positions of the localities. The shaded areas are fossiliferous exposures of the Upper Laetolil Beds (light grey) and the Upper Ndolanya Beds (dark grey) (after Leakey, 1987a; Harrison, unpublished data).

Materials

MATERIALS FROM THE UPPER LAETOLIL BEDS

The material studied includes fossil mammals from the Upper Laetolil Beds recovered by Mary Leakey from 1974 to 1981 and by Terry Harrison from 1998 to 2001. The Upper Laetolil fauna is represented by 71 mammalian species. For the analyses conducted in this study, taxa with an estimated weight of under 500 g were excluded due to the relative rarity of micromammals at Laetoli. The exclusion of these taxa resulted in a total of 57 mammalian species, which were compiled from a total of 14,575 individual specimens (Mary Leakey Collection: 8,952; Terry Harrison Collection: 5,623). The number of species recovered from each locality is provided in Table 2. Almost all of the material was recovered by surface collection after the specimens had weathered out of the sediments. Previous attempts at excavation have proved unrewarding (see Leakey, 1987a) because fossils are mostly preserved as isolated and fragmentary specimens that were scattered across the paleoland surface rather than in high-density concentrations. Determination of precise stratigraphic provenience (i.e., depth of horizon below a certain marker tuff) is not possible in most cases. Nevertheless, by

Table 2. The number of species in each locality and sub-locality analyzed in this study. Taxa with estimated weights of less than 500 g are not included. There is a total of 57 (>500 g) species present at Laetoli

Locality	Number of species
1	28
2S	19
2W	21
3	37
4	22
5	34
6	30
7	35
8	32
9	29
9S	28
10	35
10E	38
10W	33
11	32
12	22
12E	16
13	22
13E	10
13 "Snake Gully"	15
15	15
16	29
17	16
19	8
20	15
21	30
22	28
22E	8

careful observation of the provenience of *in situ* bones it has been possible to reconstruct the stratigraphic units that have produced the majority of fossils at each locality. In many cases, fossils come from several horizons, so the collected assemblages may contain fossils derived from strata that span one or more marker tuffs. Although this limitation does not allow us to sub-divide the samples according to horizons separated by consecutive marker tuffs, it is possible to divide the faunas according to five stratigraphic zones (i.e., above Tuff 8, between Tuff 7 and 8, between Tuff 5 and 7, between Tuff 3 and 5, below Tuff 3). Specimens from the Upper Laetolil Beds have been sorted according to collecting locality and stratigraphic zone.

The faunal data are examined in two ways: (1) by collecting locality (see list of localities in Table 1 and Figure 2), regardless of stratigraphic unit, which allows us to determine any local geographic differences; (2) by stratigraphic zone (see Table 1), which permits an assessment of whether or not ecological changes occur during the course of the 300 Kyr represented by the Upper Laetolil Beds. Due to the low number of specimens found above Tuff 8, they were combined with specimens found between Tuffs 7 and 8, resulting in four main divisions of the stratigraphic zones. Using these data, faunas can be compared in a three dimensional spatial-stratigraphic framework to determine the nature of any geographical heterogeneity or temporal change in the ecology.

MATERIALS FROM COMPARATIVE LOCALITIES

Modern Localities

Ecological diversity data for modern faunal communities are compared with those from Laetoli in order to assess which modern-day communities are most similar and, therefore, most likely to have a comparable ecology. The modern faunal communities employed in this study can be categorized into seven main habitat types: forest, closed woodland, bushland, open woodland, shrubland, grassland, and desert (Table 3). Definition and categorization of the modern communities follows those of Reed (1996, 1998) and faunal lists are taken from published literature (Swynnerton, 1958; Ansell, 1960, 1978; Lamprey, 1963; Child, 1964; Vesey-FitzGerald, 1964; Rahm, 1966; Sheppe and Osborne, 1971; Smithers, 1971, 1983; Rautenbach, 1978a, b; Behrensmeyer et al., 1979; Happold, 1987; Skinner and Smithers, 1990; Coe et al., 1999).

Table 3. Modern African localities and vegetation types

Locality	Vegetation
Congo Rainforest	Forest
E. of River Niger	Forest
W. of River Niger	Forest
E. of River Cross	Forest
Zambia Lowland Forest	Forest
Zambia Montane Forest	Forest
Kilimanjaro	Closed Woodland
Guinea Woodland	Closed Woodland
Serengeti Bush	Bushland
Rukwa Valley	Bushland
Mkomazi Game Reserve	Bushland
Kafue National Park	Open Woodland
Southern Savanna Woodland	Open Woodland
Okavango	Open Woodland
Botswana Northwest	Open Woodland
Sudan Savanna	Open Woodland
Southwest Arid	Shrubland
Kalahari	Shrubland
Kalahari Thornveld	Shrubland
Sahel Savanna	Shrubland
Chobe National Park	Shrubland
Amboseli National Park	Shrubland
Tarangire National Park	Shrubland
Makgadikgadi Pan	Grassland
Serengeti Plains	Grassland
SS Grassland	Grassland
Namib Desert	Desert

From: Swynnerton, 1958; Ansell, 1960, 1978; Lamprey, 1963; Child, 1964; Vesey-FitzGerald, 1964; Rahm, 1966; Sheppe and Osborne, 1971; Smithers, 1971, 1983; Rautenbach, 1978; Behrensmeyer et al., 1979; Happold, 1987; Reed, 1996, 1998; Coe et al., 1999.

Fossil Localities

Data from African Plio-Pleistocene hominin localities of similar age to the Upper Laetolil Beds are also included in order to situate Laetoli in a broader comparative context, and to determine the diversity of habitats that were available to hominins during the Pliocene. The faunal list for each site was compiled from the literature (Gray, 1980; Harris, 1987a; Feibel et al., 1991; Leakey et al., 1995; Reed, 1996; Leakey and Harris, 2003). Current interpretations of their paleoecology are presented in Appendix 1.

Methods

ECOLOGICAL DIVERSITY ANALYSIS

Ecological diversity analysis, first applied to the fossil record by Andrews et al. (1979), enables comparisons between the ecological attributes (i.e., body size, feeding habits, and locomotor type) of fossil and extant communities across time and geographic regions without regard to taxonomic affinity. Differences between communities in their ecological diversity reflect differences in habitat. It has been shown, for example, that ecological diversity patterns are similar for similar habitats, regardless of species composition, e.g., tropical rainforest communities in Asia and South America are similar even though quite different taxa are represented (Andrews et al., 1979). This is a valuable method for interpreting the paleoecology of fossil communities because it is based on general ecological principles, rather than inference through closely related modern taxa (Andrews et al., 1979; Reed, 1997). Another advantage of this approach is that preservational and taphonomic biases, which are inherent in specimen counts of fossil assemblages, have less impact on the species represented in the community, especially if small mammals are excluded from the analysis (Andrews et al., 1979; Kovarovic et al., 2002). Due to the relative rarity of micromammals at Laetoli, it is highly unlikely that small mammal taxa are well represented in the Laetoli fossil assemblage. As a result, all taxa with an estimated body weight of less than 500 g were excluded from these analyses.

Trophic and locomotor variables in ecological diversity studies are ideally assigned as a result of ecomorphological studies (such as Kay, 1984; Van Valkenburgh, 1985, 1988, 1990; Janis, 1988, 1990; Damuth, 1990; Spencer, 1995; Kappelman et al., 1997). Once these data are compiled, the total spectrum between communities (e.g., Andrews et al., 1979; Andrews, 1989) or the abundance of each ecological variable can be compared (e.g., Reed, 1997). The trophic and locomotor ecovariables used in this study follow those developed by Reed (1996) (Table 4). There are nine trophic categories: browsers, grazers, fresh grass grazers, mixed feeders, root and tuber feeders, carnivores (includes carnivores that consume bone and carnivores that eat insects), insectivores, frugivores (includes frugivorous mammals that have significant insects and leaves in their diets), and omnivores; and five locomotor ecovariables: aquatic, fossorial, arboreal, terrestrial, and terrestrial/arboreal. In some cases, certain ecovariables are combined for a more robust dataset (i.e., total carnivory and total frugivory) (see Table 4). In this analysis, inferred locomotor and dietary behaviors for Laetoli fossil mammals are taken directly from the literature, including ecomorphologic and isotopic studies (see papers in Leakey and Harris, 1987; also Bishop, 1995, 1999; Spencer, 1995; Reed, 1996; Cerling et al., 1999, 2003b; Sponheimer et al., 1999; Harris and Cerling, 2002; Kovarovic et al., 2002) (Table 5). Locomotor and dietary ecovariables for fauna from comparative fossil and modern communities are taken from published papers (Shortridge, 1934; Maberly, 1950; Blamey and Jackson, 1956; Ansell, 1960, 1978; Player and Feely, 1960; Mitchell and Uys, 1961; Eloff, 1964; Grafton, 1965; Mitchell et al., 1965; Bothma, 1966; Wilson, 1966; Goddard, 1968; Kummer, 1968; Schaller, 1968; Pienaar, 1969; Tinley, 1969; Owen, 1970; Jungius, 1971; Milstein, 1971; Smithers, 1971, 1983; Child et al., 1972; Grobler and Wilson, 1972; Owen-Smith, 1973; Dunbar and Dunbar, 1974; Kingdon, 1974a–g, 1997; Williamson, 1975; Joubert, 1976; Melton, 1976; Skinner et al., 1976; Sinclair, 1977; Stuart, 1977; Davidge, 1978; Post, 1978; Rasmussen, 1978; Dieckmann, 1980; Skinner et al., 1980; Sharman, 1981; Sauer et al., 1982; Depew, 1983; Novellie, 1983; Ferreira and Bigalke, 1987; Norton et al., 1987; Barton, 1989; Marean, 1989; Gaynor, 1994; Oates, 1994; Bishop, 1995, 1999; Lewis, 1995; Spencer, 1995; Bronikowski and Altmann, 1996; Reed, 1996; Cerling et al., 1999, 2003b; Sponheimer et al., 1999, 2003; Gagnon and Chew, 2000; Fashing, 2001; Werdelin and Lewis, 2001; Avenant and Nel, 2002; Dankwa-Wiredu and Euler, 2002; Harris and Cerling, 2002; Hill and Dunbar, 2002; Kovarovic et al., 2002).

Table 4. Ecovariable categories used in this study (following Reed, 1996)

Code	Locomotor adaptations	Code	Trophic adaptations
T	Terrestrial	G	Grazer
T-A	Terrestrial–Arboreal	FG	Fresh Grass Grazer
A	Arboreal	B	Browser
AQ	Aquatic	MF	Mixed Feeder
F	Fossorial	Fg	Frugivore
		F-I	Frugivore–Insect
		FL	Fruit and Leaves
		C	Carnivore
		C-B	Carnivore–Bone
		C-I	Carnivore–Insect
		I	Insectivore
		O	Omnivore
		RT	Root and Tuber
		TC	C + C-B + C-I
		TF	F + F-I + F-L

Once ecovariables were assigned, the frequency of each ecovariable was calculated. Before any statistical tests were run, the arcsine transformation was performed on the frequency data in order to normalize the distribution (Zar, 1999). This is because percentages form a binomial, rather than normal, distribution and the deviation from normality is great for small or large percentages (Zar, 1999). A modified chi-square test (Zar, 1999) was used to assess the statistical significance of each ecovariable frequency between collecting localities and stratigraphic zones. For this analysis, only the fossils collected by Harrison were used, because of the greater precision in recording the stratigraphic provenience of the material. In addition, the proportions of each ecovariable from Laetoli were compared with those from other fossil sites and modern communities. In order to do this, principal components analysis

Table 5. List of fossil mammals from the Upper Laetolil Beds (updated from Harris, 1987) and their locomotor and trophic adaptations (see text for references). This list is subject to revision pending further taxonomic studies

	Locomotor	Trophic
Artiodactyla		
Bovidae		
aff. *Pelea*, sp. indet.	T	G
Alcelaphini, large sp.	T	G
Parmularius pandatus	T	G
Gazella janenschi	T	B
Simatherium kohllarseni	T	MF
Brabovus nanincisus	T	B
Cephalophini sp. indet.	T	B
Hippotragini sp.	T	G
Praedamalis deturi	T	G
Madoqua avifluminis	T	B
Raphicerus sp.	T	B
Reduncini, sp. indet.	T	G
Tragelaphus sp.	T	B
Giraffidae		
Giraffa stillei	T	B
Giraffa cf. *jumae*	T	B
Sivatherium cf. *maurusium*	T	B
Suidae		
Notochoerus euilus	T	G
Potamochoerus porcus	T	O
Perissodactyla		
Rhinocerotidae		
Ceratotherium praecox	T	G
Diceros bicornis	T	B
Ancylotheriidae		
Ancylotherium hennigi	T	B
Equidae		
Eurygnathohippus sp.	T	G
Proboscidea		
Elephantidae		
Loxodonta exoptata	T	G
?Stegodon sp.	T	–
Deinotheriidae		
Deinotherium bozasi	T	B
Tubulidentata		
Orycteropodidae		
Orycteropus sp.	F	I
Primates		
Cercopithecidae		
cf. *Paracolobus* sp.	T-A	FL
Parapapio ado	T-A	FL
cf. *Papio* sp.	T	FL
Colobinae sp. indet.	A	FL
Hominidae		
Australopithecus afarensis	T	O
Galagidae		
Galago sadimanensis	A	FI
Insectivora		
Rhynchocyon pliocaenicus	T	I
Carnivora		
Felidae		
Megantereon sp.	T-A	C
Homotherium sp.	T	C
Dinofelis sp.	T-A	C
Leo cf. *pardus*	T	C
Leo sp.	T	C
Felis, large sp.	T-A	C
Felis, medium sp.	T-A	C
Felis, small sp.	T-A	C
Felidae gen. indet.	–	–
Canidae		
?Megacyon sp.	T	C
aff. *Canis brevirostris*	T	C-I
Vulpes sp.	T	C
cf. *Otocyon* sp.	T	I
Canidae gen. indet.	–	–
Hyaenidae		
Crocuta sp. nov.	T	C-B
Hyaenidae, *incertae sedis*	T	C-B
Herpestidae		
Herpestes (Herpestes) ichneumon	T	C-I
Herpestes (Galerella) palaeoserengetensis	T	C-I
*_Helogale palaeogracilis_	T	C-I
*_Helogale_ sp.	T	C-I
Mungos dietrichi	T	C
Viverridae		
Viverra leakeyi	T	O
Mustelidae		
*_Propoecilogale bolti_	T	C
Mellivora capensis	T	C-I
Rodentia		
Sciuridae		
*_Xerus_ cf. _janenschi_	T	F
*_Paraxerus_ sp. Indet.	T-A	F
*Sciuridae gen. et sp. nov.	–	–
Cricetidae		
*Gerbillinae gen. indet.	F	B
*_Tatera_ cf. _inclusa_	T	B
*_Dendromus_ sp. indet.	T-A	G
*_Steatomys_ sp. indet.	F	B
*_Saccostomus major_	F	B
Muridae		
*_Thallomys laetolilensis_	A	B
*_Mastomys cinereus_	T	B
Hystricidae		
Hystrix leakeyi	T	R
Hystrix cf. *makapanensis*	T	R
Xenohystrix crassidens	T	R
Bathyergidae		
*_Heterocephalus quenstedti_	F	R
Pedetidae		
Pedetes laetoliensis	F	G
Lagomorpha		
Serengetilagus praecapensis	T	G

*Species less than 500 g, excluded from analyses.

(PCA) was conducted using STASTICA 6.0, and predictor ecovariables (i.e., arboreality, terrestriality, frugivory, grazing) were used in bivariate plots (Reed, 1996, 1997).

FAUNAL SIMILARITY

In addition, a faunal similarity index was used to provide a measure of how similar the Upper Laetolil fauna is to those from other African Plio-Pleistocene sites (see Appendix 1). Several different faunal similarity indices have been devised (e.g., Simpson, 1960; Nakaya, 1994; Reed, 1996), but the most widely used is Simpson's index (Simpson, 1960). The formula is as follows:

Simpson's Index = C/N_1
C = number of taxa in common for both faunas
N_1 = total number of taxa of the smaller fauna

In this study, the unit of analysis is the species. Indices are transformed into percentages by multiplying C/N_1 by 100. Faunal similarity indices are generally used to detect provincial or temporal relationships (Flynn, 1986), rather than habitat similarities, but given that the sites included in this study are regionally and chronologically constrained, it is likely that a significant component of any observed differences is likely to reflect ecological distinctions (Van Couvering and Van Couvering, 1976).

Results and Discussion

COMPARISONS OF THE UPPER LAETOLIL FAUNAS FROM DIFFERENT LOCALITIES AND STRATIGRAPHIC ZONES

The faunas from different stratigraphic zones and collecting localities of the Upper Laetolil Beds presented in Table 1 were compared in order to discern whether there was any evidence of temporal or spatial heterogeneity. Time averaging of faunas over the course of the more than 300 Kyr represented by the Upper Laetolil sequence could produce a composite fauna that reflects a mixture of different habitats. If this is the case, it might account for the high species diversity and unusual composition of the large mammal community. It would also impact on comparisons with present-day mammalian communities, and make it difficult to ascertain the paleoecology of Laetoli based on its closest modern analogs. To test for habitat heterogeneity, the ecological diversity at each of the collecting localities and stratigraphic zones was compared. A modified chi-square test (Zar, 1999) was conducted on the relative proportions of the ecovariables (Table 6).

The results show that there are no significant differences in ecological diversity between the different localities or stratigraphic zones (Table 7). This implies that the composition of

Table 6. Percentages of locomotor and trophic ecovariables for the large mammalian fauna of the Upper Laetolil Beds

	Upper Laetolil (%)
T	79.6
T-A	9.3
A	3.7
F	7.4
AQ	0.0
G	22.2
FG	0.0
B	22.2
MF	1.9
Fg	0.0
FI	1.9
FL	7.4
TF	9.3
C	16.7
C-I	7.4
C-B	5.6
RT	5.6
O	5.6
I	3.7

Abbreviations: T = Terrestrial; T-A = Terrestrial–Arboreal; A = Arboreal; F = Fossorial; AQ = Aquatic; G = Grazer; FG = Fresh Grass Grazer; B = Browser; MF = Mixed Feeder; Fg = Frugivore; F-I = Frugivore –Insects; FL = Fruit and Leaves; TF = Total Frugivory; C = Carnivore; C-I = Carnivore–Insects; C-B = Carnivore–Bone; RT = Root and Tuber; O = Omnivore; I = Insectivore.

Table 7. Significance results for the comparisons of the Upper Laetolil faunas from different localities and stratigraphic zones, using a modified chi-square test (Zar, 1999) where significance is set at $X^2 = 7.815$ ($p < 0.05$). NS = Not significant

Locomotor adaptations			Trophic adaptations		
	X^2	Significance		X^2	Significance
T	0.404016	NS	**G**	1.368645	NS
T-A	0.37787	NS	**FG**	–	–
A	0.421882	NS	**B**	0.092018	NS
AQ	–	–	**MF**	0.118129	NS
F	0.365414	NS	**Fg**	–	–
			FI	3.1933	NS
			FL	1.009128	NS
			C	0.395363	NS
			C-B	0.695276	NS
			C-I	3.1933	NS
			I	0.787727	NS
			O	0.910169	NS
			RT	0.169224	NS

the mammalian community in terms of ecovariables was essentially identical throughout the entire Upper Laetolil sequence, and that the general ecological structure remained uniform throughout this time. This is an important finding, because it demonstrates that the large mammal community remained remarkably stable over an extended period of time, regardless of regional and local perturbations in the ecosystem. We can infer from the geology, for example, that periodic inundations of carbonatite ash from the volcano Sadiman were catastrophic events that would have dramatically affected the local vegetation, and in all probability had severe consequences on the local mammalian community. Heavy ash falls would have blanketed the paleoland surface, burying and killing the herbaceous vegetation, and within a short time, the ashes would have formed well-cemented tuffaceous limestones, killing standing trees, preventing root penetration by germinating seeds, and impeding the long-term regeneration of trees and woody shrubs. During these periods, extensive areas of dry grassland, with few or no trees, would have dominated Laetoli. However, since there are no indications of specialized grassland communities associated with any of the faunal assemblages from the Upper Laetolil horizons, these periods of disruption in the ecosystem were apparently relatively short term (probably on the order of centuries), and grasslands were apparently quickly replaced by the climax vegetation. The uniformity of the mammalian faunal community from Laetoli implies that fossils are almost exclusively preserved in paleosols deposited during periods when the ecosystem was dominated by heavy vegetation, while the very short periods with grassland had relatively low sedimentation rates and produced few vertebrate fossils. The conclusion that can be drawn from these findings is that the general ecosystem at the time of the deposition of the Upper Laetolil Beds was a mosaic of different habitat types (i.e., not a mixture of time-averaged habitats), and one that remained remarkably stable over time, despite the influences of volcanic inundations that probably had only a localized and relatively short-term impact.

For the purposes of this study, given the spatial and geographical uniformity of the faunas from the Upper Laetolil Beds, the composite fauna derived from the entire sequence can now be used to reconstruct the paleoecology of Laetoli. The paleoecological relationships of the Upper Laetolil Beds will be deduced from ecological diversity analyses and faunal similarity indices.

ECOLOGICAL DIVERSITY ANALYSIS

Ecological diversity data from the Upper Laetolil Beds, and comparative data from other Plio-Pleistocene African sites and modern faunas, were analyzed using principal components analysis (PCA). When PCA was performed, 19 factors were extracted, although PC 1 and 2 accounted for 32.8% and 17.7% of the total variance (Table 8). A bivariate plot of

Table 8. Eigenvalue and the percentage of total variance for the first six principal components

PC	Eigenvalue	% Total variance
1	6.238171	32.8
2	3.363629	17.7
3	2.489357	13.1
4	1.637822	8.6
5	1.280560	6.7
6	1.060219	5.6

the first two factors shows three groupings – modern forest communities, modern non-forest communities, and fossil communities (Figure 3). It is interesting to note, in this regard, that, with the exception of forest communities, all other modern habitat types represented in tropical Africa cluster closely together and are not easily differentiated, except for Serengeti Plain and Savanna Grassland, which fall within the range of fossil sites (we will return to this point later in the discussion). This may indicate that either the ecovariables or the multivariate methods of analysis used in this study are too coarse to readily distinguish between non-forest habitat types.

There are three possible explanations for the distinctiveness of fossil assemblages, including Laetoli, compared to all modern large mammal communities: (1) *Fossil sites have no modern analogs*. Since faunal communities change and evolve through time, it should not be unexpected to find that the structure of communities in the Pliocene is somewhat different from that of modern-day communities. For instance, Andrews and Humphrey

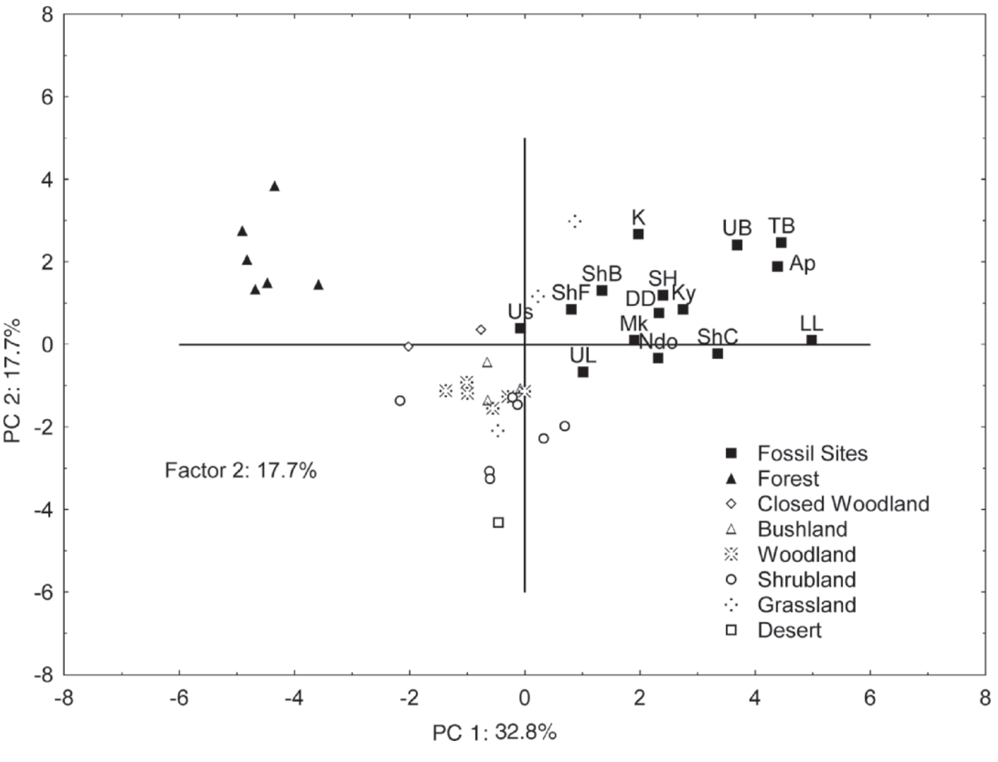

Figure 3. Results of a principal components analysis (PCA). This is a projection of modern and fossil localities on the factor plane (PC 1 × PC 2). There are generally three distinct groupings – modern forest, modern non-forest, and fossil localities. Fossil locality abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Upper Ndolanya Beds; K = Kanapoi; Ap = Apak; Ky = Kaiyumung; SH = Sidi Hakoma; DD = Denen Dora; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; Us = Usno; TB = Tulu Bor; UB = Upper Burgi; Mk = Makapansgat Member 3.

(1999) hypothesize that many Plio-Pleistocene faunal communities have no equivalence to those found in present-day habitats. Although the general ecological attributes associated with mammalian community structure remain broadly similar through time and space, and there are evidently close taxonomic similarities between the modern fauna and flora to those from the Pliocene of East Africa, this need not necessarily imply that the vegetational and faunal communities were constituted in the exactly same way to produce assemblages comparable to those seen today. If this is the case, then fossil localities cluster together because they share aspects of their ecology that are not found in any modern-day large mammal communities. (2) *There is inherent bias in the fossil record*. Since fossil communities include only a fraction of the taxa represented in the original communities, there is an inherent sampling bias that may affect the outcome of comparative analyses (even if small mammals, which are evidently under-represented taxonomically at most fossil sites, are excluded; see Dodson, 1973; Korth, 1979; Andrews and Nesbit Evans, 1983; Andrews, 1990; Fernandez-Jalvo and Andrews, 1992; Fernandez-Jalvo, 1995, 1996; Hoffman, 1988). Other than the original sampling bias, there is also the issue of recovery bias. For example, small fossil specimens are more easily destroyed after exposure or overlooked by collectors. If this is the case, then the fossil localities cluster together because certain taxa are uniformly absent or under-represented in the fossil record. (3) *Ecomorphological analyses may not accurately reflect the range of habitat preferences of fossil taxa*. There is an inherent asymmetry in the manner in which ecovariables are assigned to fossil and extant taxa in ecological diversity analyses. Trophic and locomotor categories of modern species are based on direct behavioral observations, while the behavioral categories of fossil taxa are based on inferences of function derived from the morphology of preserved anatomical parts. While such inferences can generally be expected to yield equivalent results, there might be a lack of precise correspondence between modern and fossil data that affects the outcome of ecomorphological analyses of fossil communities. For example, it is conceivable that some taxa might be coded incorrectly for habitat type if they show specializations for a particular behavior, even though it may represent a relatively minor component of their overall repertoire (i.e., semi-terrestrial monkeys that spend most of their time in trees, or mixed feeders that include a large component of fruits in their diet). If this is the case, the results of ecomorphological analyses of fossil assemblages would tend to exaggerate the terrestrial, cursorial, and folivorous components of a community. A possible means of circumventing this problem would be to use ecomorphology to assign ecovariables to both fossil and modern taxa. Even so, we suspect that this bias is not profound enough to account for the major differences seen between the fossil and modern large mammal communities, but it may be a contributing factor.

A detailed examination of the large mammal fauna from the Upper Laetolil Beds and modern communities provides insights into whether or not the PCA results are due to differences in community structures in the past, taphonomic biases against certain taxa, or a lack of correspondence between ecomorphological data from modern and fossil communities. Identification of the individual ecovariables that drive the distinctions in the PCA helps to isolate the critical factors that differentiate fossil and modern communities. For PC 1, the highest contribution comes from terrestrial mammals. Direct comparisons of the faunal lists show that fossil communities have a higher proportion of terrestrial mammals. For example, terrestrial mammals in modern communities account for 33.3% to 88.8% of the total large mammal fauna, whereas at fossil sites the proportion of terrestrial mammals

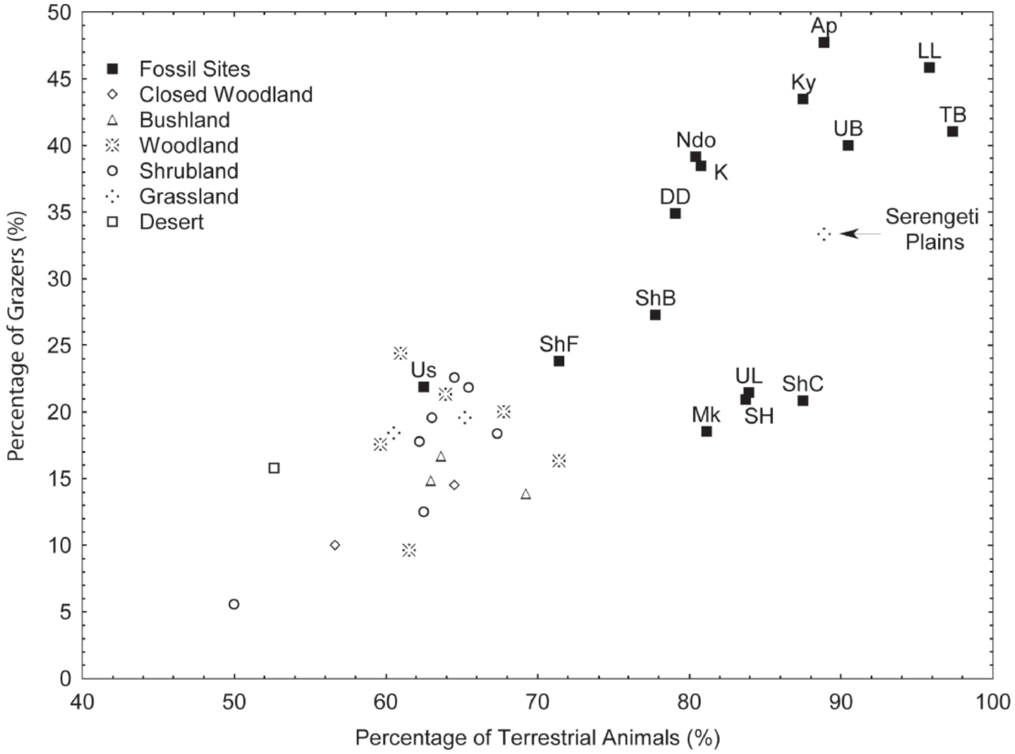

Figure 4. Bivariate plot of the community percentages of terrestrial and grazing mammals from African Plio-Pleistocene localities and modern communities. Note the separation of fossil and modern communities and the placement of the Serengeti Plains (with arrow). The latter is the only modern faunal community to fall within the range of fossil localities. Fossil locality abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Upper Ndolanya Beds; K = Kanapoi; Ap = Apak; Ky = Kaiyumung; SH = Sidi Hakoma; DD = Denen Dora; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; Us = Usno; TB = Tulu Bor; UB = Upper Burgi; Mk = Makapansgat Member 3.

is generally much higher, ranging from 62.5% to 97.4% (Figure 4).

A closer examination of the faunal lists reveals that the large mammal fauna from the Upper Laetolil Beds differs from modern communities primarily in the relative proportions of carnivores and artiodactyls. A higher proportion of carnivore taxa in modern habitats are non-terrestrial when compared with Upper Laetolil. Non-terrestrial taxa include those that exhibit significant arboreal, terrestrial–arboreal, aquatic, and fossorial locomotor behaviors. Only 26.3% of the carnivore species found in the Upper Laetolil Beds are non-terrestrial, compared to modern communities, which have 37.5% to 75.0% (with the exception of the Serengeti Plains, 11.1%). Most non-terrestrial carnivores are felids, mustelids, and viverrids. Almost all non-terrestrial carnivores from Upper Laetolil are felids (with the exception of *Mellivora*), and with nine species identified, it is comparable in diversity to many modern communities; thus, it is unlikely that felids are an under-represented component of the fauna. Mustelids and viverrids, however, are much more impoverished in species number when compared to modern communities, and all of the taxa are classified as terrestrial, except for *Mellivora*. In modern communities, the small carnivore guild is often the most numerous in terms of species numbers and typically includes a large number of non-terrestrial taxa (see Kingdon, 1974d, 1997).

To characterize the relative representation of non-terrestrial carnivores at Laetoli, the Kruskal–Wallis non-parametric significance test was conducted. It showed that there was a statistically significant difference between the proportions of non-terrestrial carnivores of modern and fossil communities ($p = 0.0003$). A whisker plot with 0.95 confidence intervals illustrates the separation of the two sets of communities (Figure 5). The abundance of non-terrestrial carnivores is a significant contributor to the distinctiveness of fossil and modern communities. The relatively low proportion of non-terrestrial carnivores in fossil faunas may be due to ecological differences in community structure between fossil and modern carnivore guilds. The large carnivores from the Plio-Pleistocene of Africa differ from extant communities in having a greater number of species and in exhibiting a different suite of behaviors (Lewis, 1995). It is likely that this taxonomic and paleobiological distinction can also be applied to the small carnivores. Alternatively, the low proportion of non-terrestrial carnivores could possibly be attributed to taphonomic factors. Since many non-terrestrial species are small in size with quite distinctive habitat preferences, preservational or collecting biases may impact on their observed taxonomic diversity. Most likely, the disparity in the proportion of non-terrestrial carnivore species in fossil communities is due to a combination of these factors.

The difference in the proportions of grazing mammals between modern and Upper Laetolil communities can be attributed to artiodactyls, specifically bovids. The proportion of artiodactyl grazers in modern communities

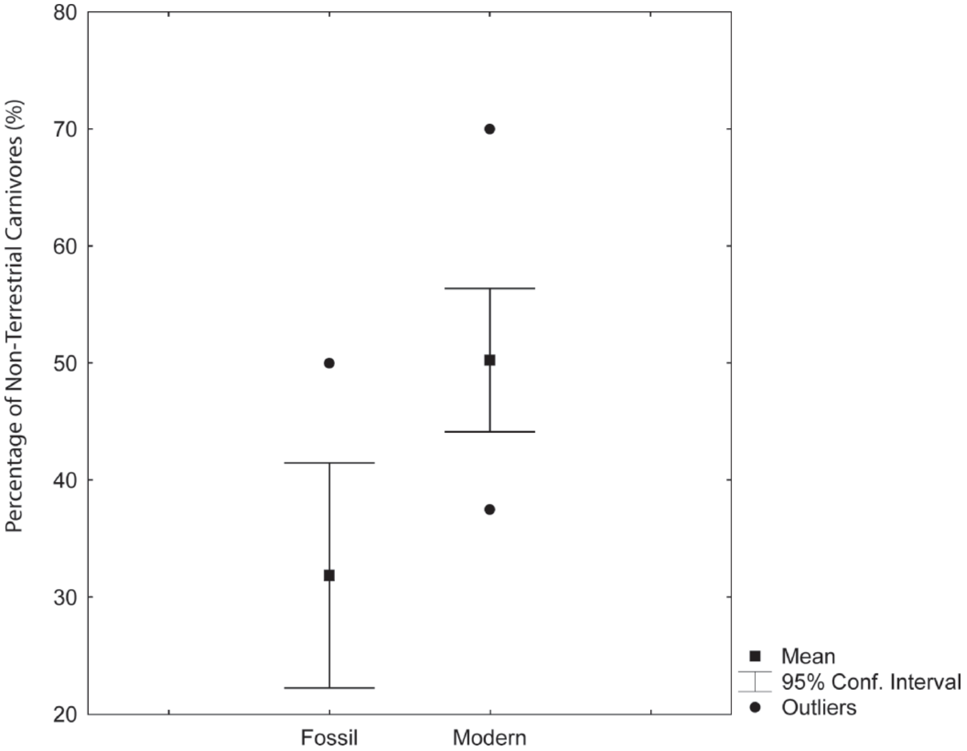

Figure 5. Whisker plot with 0.95 confidence interval of the proportions of non-terrestrial carnivores in fossil and modern communities. There is a clear separation between the fossil and modern communities. The difference is statistically significant (Kruskal–Wallis: $p = 0.0003$).

is relatively low, ranging from 0% to 33.3% (except for Serengeti Plains with 71.4%), compared with 38.9% in Upper Laetolil. The lower frequency of artiodactyl grazers is due to the fact that modern species are classified more often as non-grazers, such as browsers, mixed feeders, and fresh grass grazers, whereas the Laetoli artiodactyls are mostly classified as grazers. As discussed above, ecovariables of modern species are based on direct behavioral observations, while ecovariables of fossil species are based on inferences of function derived from the morphology of preserved elements. This may impact on the accuracy of ecovariable assignment for fossil species. Alternatively, the differences in the proportions of grazers may be due to an ecological difference between modern and fossil communities, such that there is no modern equivalent to the Upper Laetolil fauna. The chance that artiodactyl grazers would have been selectively preserved in the Upper Laetolil Beds compared to browsers or mixed feeders is unlikely, so taphonomic biases can be discounted.

However, when the Kruskal–Wallis nonparametric significance test was conducted on the proportion of grazers in modern and fossil faunal communities, it was found that there was no statistically significant difference between them ($p = 0.3068$). A whisker plot with 0.95 confidence intervals shows overlapping ranges for fossil and extant communities (Figure 6). This suggests that the abundance of grazing artiodactyls may not be an important factor in the separation of fossil and modern communities in a principal components analysis.

To further examine the separation of modern and fossil communities, we conducted an ecological diversity analysis on artiodactyls only. It is instructive to focus on a group with relatively homogeneous locomotor and trophic adaptations, and see its effect on the distribution of the communities. Artiodactyls are suited for this because they are a large and diverse group, and they are usually the most numerous taxon in a community. A principal components analysis (PCA) conducted on the artiodactyls extracted nine factors. PC 1 and 2 accounted for 37.4% and 28.2% of the total variance, respectively (Table 9). A bivariate plot of the first two principal components shows two distinct groupings – modern forest communities versus all non-forest communities, both modern and fossil (Figure 7). Once again, there is no distinction between modern non-forest communities, and they cannot be readily distinguished from the fossil communities. Even though fossil communities have generally higher proportions of artiodactyl grazers compared to modern communities, they cluster together in this PCA, indicating that grazing is not an important factor in distinguishing the fossil and modern communities. The results of this analysis confirm those of the Kruskal–Wallis significance test and whisker plot. While grazers contribute greatly to the variance seen in PC 1 of the principal components analysis, they do not play a key role in distinguishing fossil localities from extant non-forest localities.

As mentioned above, Serengeti Plains (SP) and Savanna Grassland (SG) are the only two modern communities that fall within the range of fossil communities in the PCA (Figure 3). Their positions on the factor plane projection appear to be the result of a combination of factors – the relatively high frequency of terrestrial animals (SP: 88.9%; SG: 60.5%) and the lack or relatively low proportions of arboreal animals (SP: 0.0%; SG: 0.0%), browsers (SP: 5.6%; SG: 2.6%), fruit and leaf eaters (SP: 0.0%; SG: 5.3%), and omnivores (SP: 11.1%; SG: 2.6%). These ecovariables contribute importantly to PC 1 and 2. However, the displacement of Serengeti Plains from modern communities is mostly driven by its high frequency of terrestrial mammals, surpassed only by those of fossil communities. While other modern communities have similar frequencies for individual ecovariables, they do not exhibit the same combination of frequencies. It is

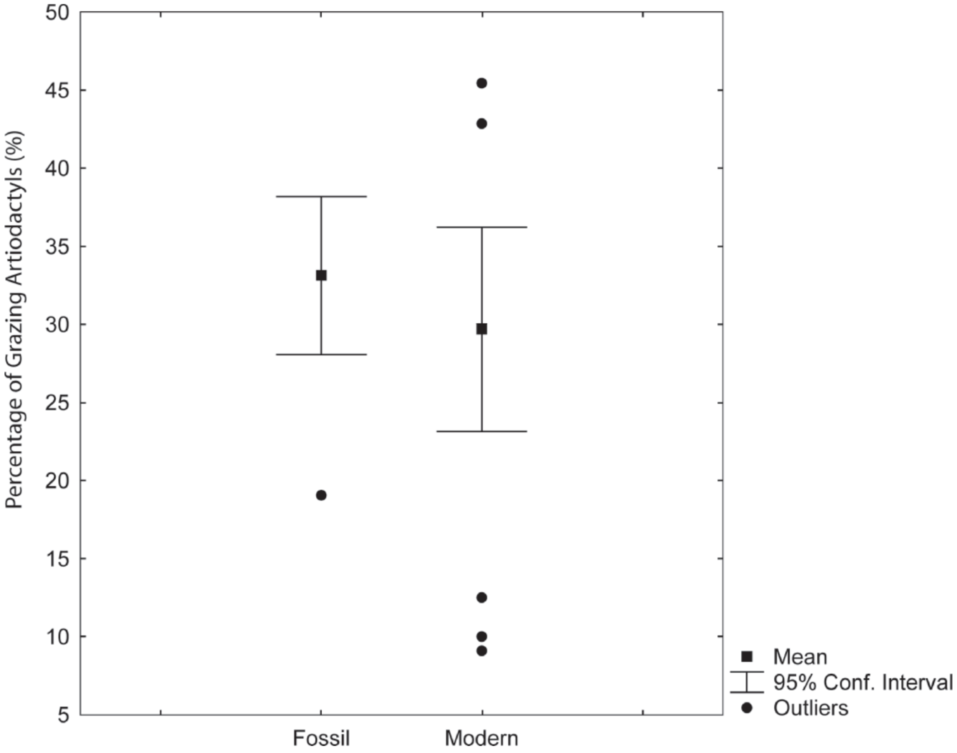

Figure 6. Whisker plot with 0.95 confidence interval of the proportions of grazing artiodactyls in fossil and modern communities. There is no separation between the fossil and modern communities. The difference is not statistically significant (Kruskal–Wallis: $p = 0.3068$).

Table 9. Eigenvalues and percentage of total variance for the first six principal components from the artiodactyl dataset

PC	Eigenvalue	% of Total variance
1	3.366111	37.4
2	2.533995	28.1
3	1.225692	13.6
4	0.799037	8.9
5	0.493679	5.5
6	0.310580	3.5

noteworthy that Serengeti Plains is the only modern fauna to fall within the range of fossil sites in a bivariate plot of terrestrial versus grazing animals due to its high proportion of terrestrial mammals (see Figure 4).

The unique position of the Serengeti Plains among modern communities may relate to the limited diversity and uniformity of its vegetation, which results in a relatively impoverished and ecologically specialized large mammal fauna. Among the comparative faunas used in the study, that from the Serengeti Plains represents a special case because its faunal list is limited to mammals observed in the open grassland habitat of the Serengeti National Park (Swynnerton, 1958). Other faunal lists are derived from the entire area of the national park or game reserve in question, which usually includes multiple habitat types. The faunal list from the Serengeti Plains comprises only 18 species from 8 families and 4 orders (Swynnerton, 1958). Of these, 6 species are medium- to large-bodied bovids and 9 species are carnivores that prey on them (resulting in an extremely low proportion of non-terrestrial carnivores). When the Serengeti Plains faunal list is extended to include all of the Serengeti National Park, it no longer clusters with the

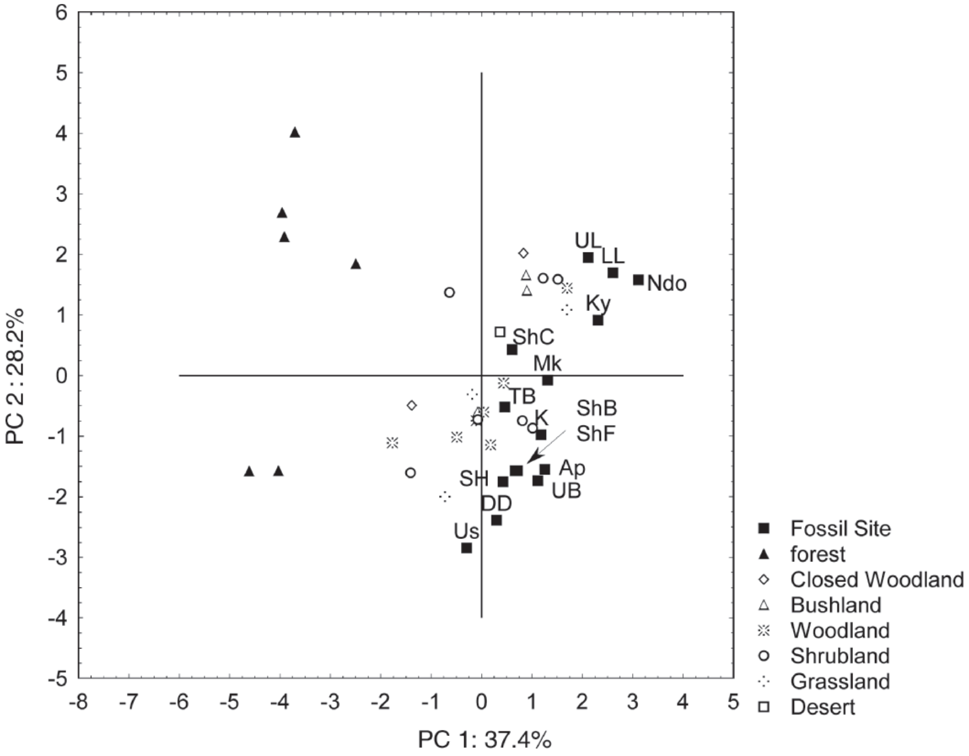

Figure 7. Results of a principal components analysis (PCA) of artiodactyls. This is a projection of modern and fossil localities on the factor plane (Factor 1 × Factor 2). There are two distinct groupings – modern forest and modern and fossil non-forest localities. Fossil locality abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Upper Ndolanya Beds; K = Kanapoi; Ap = Apak; Ky = Kaiyumung; SH = Sidi Hakoma; DD = Denen Dora; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; Us = Usno; TB = Tulu Bor; UB = Upper Burgi; Mk = Makapansgat Member 3.

fossil localities. Given the balance of evidence, it is unlikely that the faunas from fossil sites are from such constrained habitat types as the Serengeti Plains or that they are representative of communities from homogeneous grassland habitats, but the results of the PCA may imply that extensive grasslands were an important part of the paleolandscape of Africa during the Plio-Pleistocene.

Following Reed (1996, 1997, 1998), predictor ecovariables were used in bivariate plots to examine the habitat types to which the Upper Laetolil Beds may be most similar. Predictor ecovariables are those that are most useful in discriminating habitat types, such as terrestriality, arboreality, frugivory, and grazing. Modern forest communities are excluded from the bivariate analyses because their community structure is readily distinguishable from all other habitat types. In this case, total frugivory (TF) is used as the fruit-eating category because it encompasses all mammal species with significant proportions of fruit in their diet. The fauna from the Upper Laetolil Beds is characterized by the following distinctive properties: (1) a relative low occurrence of fruit-eating (9.3%) and arboreal (3.7%) mammals; (2) a high frequency of terrestrial mammals (79.6%); and (3) grazers are the most common mammals (22.2%) (Table 6). The Upper Laetolil fauna clusters with those from modern open woodland habitats. This is especially clear when the predictor ecovariables of frugivory and arboreality are used (Figures 8 and 9). Modern open woodland faunas are characterized by relatively low proportions of arboreal (1.6% to 4.4%) and frugivorous (6.6% to 13.5%) taxa and relatively high frequency of terrestrial (59.7% to 71.4%) and grazing (9.6% to 24.4%) mammals. However, there is overlap between faunas from open woodland and shrubland habitats in terms of their ecovariable structure. Among fossil localities, Upper Laetolil is generally grouped with Makapansgat and Sidi Hakoma, both of which have been reconstructed as having mosaic habitats. Makapansgat is considered to have been woodland with some bushland and grassland (Dart, 1952; Wells and Cooke, 1956; Vrba, 1980; Reed, 1996). Sidi Hakoma is reconstructed as having bushland to forested habitats with areas of open grassland (Gray, 1980; Bonnefille et al., 1987, 2004).

The results of the bivariate analyses presented here contradict those presented by Reed (1997), who reconstructed Upper Laetolil paleoecology as being closed to medium density woodlands. This difference is accounted for by Reed's use of a different dataset and ecovariable coding for certain taxa. Reed (1997) utilized a selective list of mammalian taxa from Localities 1 and 7 only, in order to better constrain the temporal and geographical range of the fauna to be analyzed. However, since there are no significant differences in the community structure of the faunas from the entire Upper Laetolil Beds, regardless of their stratigraphic zone or collecting locality, we have been able to use the

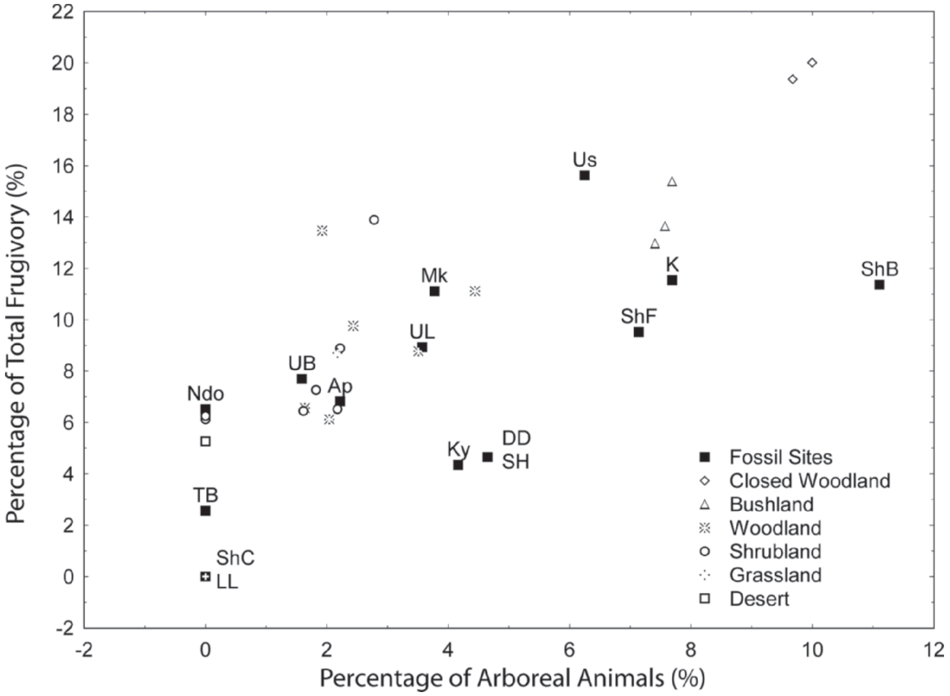

Figure 8. Bivariate plot of the percentages of arboreal and frugivorous mammals from African Plio-Pleistocene localities and modern communities. Upper Laetolil clusters with modern woodland communities, although there is overlap between the shrubland and woodland habitats. Fossil locality abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Upper Ndolanya Beds; K = Kanapoi; Ap = Apak; Ky = Kaiyumung; SH = Sidi Hakoma; DD = Denen Dora; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; Us = Usno; TB = Tulu Bor; UB = Upper Burgi; Mk = Makapansgat Member 3.

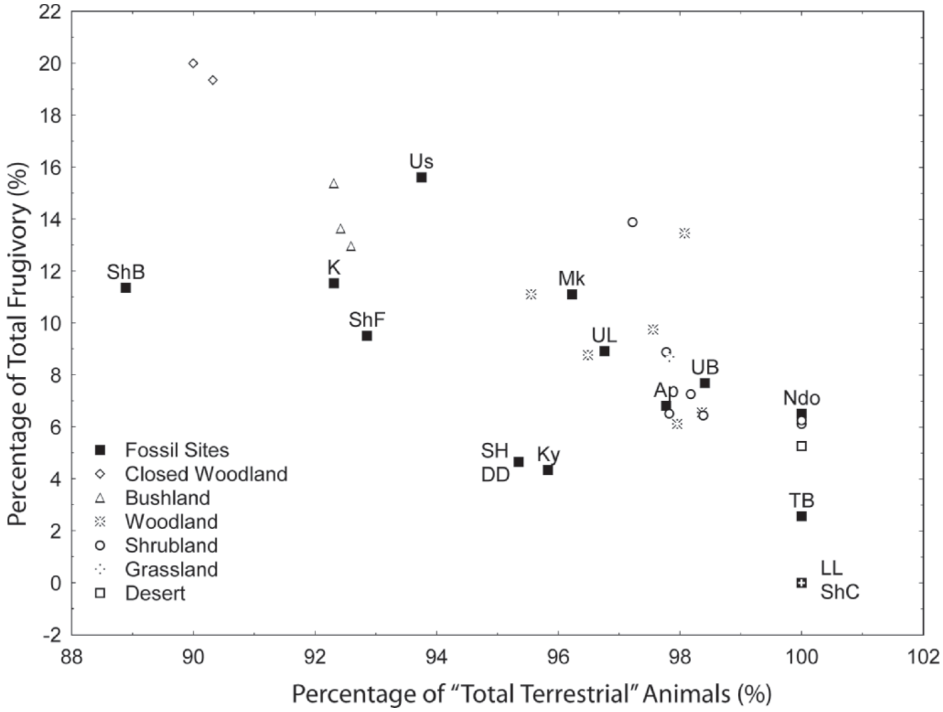

Figure 9. Bivariate plot of the percentages of "total terrestrial" (TT) and frugivorous mammals from African Plio-Pleistocene localities and modern communities. Upper Laetolil clusters with modern woodland communities, although there is overlap between the shrubland and woodland habitats. Fossil locality abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Upper Ndolanya Beds; K = Kanapoi; Ap = Apak; Ky = Kaiyumung; SH = Sidi Hakoma; DD = Denen Dora; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; Us = Usno; TB = Tulu Bor; UB = Upper Burgi; Mk = Makapansgat Member 3.

larger composite fauna in our analysis. As a consequence, while the number of arboreal and frugivorous species remained the same in both analyses, the number of taxa in other ecovariable categories increased, thereby decreasing the overall percentage of arboreal and frugivorous species. Obviously, sampling of taxa is an important consideration in ecological diversity analyses, and as long as the fauna can be shown to be relatively uniform in space and time, the most inclusive faunal list is preferable, and likely to yield the most accurate inference about paleoecology. In this case, Upper Laetolil can be shown to be most similar to modern mammalian communities that live in medium to open woodlands, rather than in closed woodlands.

FAUNAL SIMILARITY

Simpson's Similarity Index was used to calculate the similarity of the mammalian fauna from the Upper Laetolil Beds to those from other Pliocene localities (Table 10). In this case, all mammals identified to the species level, regardless of size, were included in the analysis. The results show that the mammal fauna from the Upper Laetolil Beds was most similar to the faunas from the Lower Laetolil Beds (82%) and Upper Ndolanya Beds (59%). This demonstrates that the faunas from Laetoli, regardless of their age, resemble each other more closely in their taxonomic composition than do penecontemporaneous faunas from other regions of Africa (Table 10). For example,

Table 10. Faunal similarity matrix of African Plio-Pleistocene sites

	UL	LL	Ndo	A	KM	TB	UB	ShB	ShC	ShF	U	SH	DD	K	Mk3
UL	100	82	59	36	50	28	18	13	28	19	50	35	29	38	18
LL	82	100	73	50	33	43	29	14	14	14	21	29	43	31	21
Ndo	59	73	100	27	33	30	30	15	16	15	43	25	33	31	15
A	36	50	27	100	55	27	14	9	9	9	14	25	32	54	9
KM	50	33	33	55	100	50	17	25	25	25	17	33	42	25	8
TB	28	43	30	27	50	100	48	24	28	24	43	45	42	46	7
UB	18	29	30	14	17	48	100	31	40	34	36	50	38	31	15
ShB	13	14	15	9	25	24	31	100	76	48	28	35	33	23	18
ShC	28	14	16	9	25	28	40	76	100	69	34	25	25	15	20
ShF	19	14	15	9	25	24	34	48	69	100	31	25	25	15	19
U	50	21	43	14	17	43	36	28	34	31	100	36	36	15	43
SH	35	29	25	25	33	45	50	35	25	25	36	100	73	31	35
DD	29	43	33	32	42	42	38	33	25	25	36	73	100	54	17
K	38	31	31	54	25	46	31	23	15	15	15	31	54	100	8
Mk3	18	21	15	9	8	7	15	18	20	19	43	35	17	8	100

Abbreviations: UL = Upper Laetolil Beds; LL = Lower Laetolil Beds; Ndo = Ndolanya Beds; A = Apak; KM = Kaiyumung; TB = Tulu Bor; UB = Upper Burgi; ShB = Shungura B; ShC = Shungura C; ShF = Shungura F; U = Usno; SH = Sidi Hakoma; DD = Denen Dora; K = Kanapoi; Mk3 = Makapansgat.

the faunas from the Upper Laetolil Beds and Sidi Hakoma Member at Hadar (~3.4 Ma), which are similar in age, only share 35% of their fauna.

Other Plio-Pleistocene fossil localities exhibit a similar relationship, in which geographical location is more important in determining faunal similarity than age (Table 10). The Apak and Kaiyumung Members of the Nachukui Formation at Lothagam are most similar to each other (55%) relative to other Plio-Pleistocene sites, even though the reconstructed habitats of these two members are quite different (see overview of Plio-Pleistocene sites). Kanapoi, which is comparable in age and geographical close to the Apak Member at Lothagam shares 54% of its fauna with the Apak Member. The mammalian faunas of the Shungura Formation are most similar to each other, ranging from 48% (Member B and Member F) to 69% (Member C and Member F) to 76% (Member B and Member C), even though there is evidence of changing paleoenvironmental conditions throughout the formation. The hypothesized paleohabitats of the Shungura Formation exhibited gradual aridification and opening up of habitats in the sequence (Eck, 1976; Gentry, 1976; Bonnefille, 1983; Bonnefille and DeChamps, 1983; Eck and Jablonski, 1985; Wesselman, 1985; Reed, 1997). Finally, the Sidi Hakoma and Denen Dora Members at Hadar share 73% of their fauna. They are more similar faunally to each other than to other fossil localities, even though there was a change in vegetation through the sequence from deciduous and evergreen forest or bushland (lower Sidi Hakoma) to woodland (upper Sidi Hakoma) to wet and dry grassland (Denen Dora) (Bonnefille et al., 1987, 2004).

Clearly, local ecosystems have the potential to remain relatively stable in terms of faunal composition over long periods of time. This suggests that local and regional environmental and ecological conditions exert more influence over the composition of faunas than do large-scale ecological and climatic changes through time. The reconstructed paleoenvironment of the Upper Laetolil Beds, Lower Laetolil Beds, and Upper Ndolanya Beds are inferred to be distinct, but the general taxonomic composition of the fauna retains its overall integrity.

This implies that there were critical aspects of the Laetoli ecosystem that remain stable over time that buffer the mammalian community from faunal turnover. It has been theorized that intrinsic species constraints, such as genetics, development, and behavior, may be more important to species survival than ecological factors of the environment, but that, within the selective environment, local environmental conditions, including climate, geology, flora, and other fauna, may have more effect on a species than regional climate and geology, which in turn, has greater influence than global conditions (McKee, 1999). Thus, as long as a species is not highly specialized and restricted to a narrow set of ecological conditions, it would not be drastically affected by local environmental alterations caused by changes in regional or global conditions.

Conclusion: Paleoecology of Laetoli Reconsidered

There has been no clear consensus on the paleoecology of Laetoli over the last 15 years, especially for the Upper Laetolil Beds. It has been reconstructed from arid to semi-arid grassland (see papers in Leakey and Harris, 1987) to dense woodland (Reed, 1997). The goal of this paper was to develop a better understanding of the Upper Laetolil paleoecology, based on a more detailed and comprehensive analysis of the large mammal fauna. The major findings of this paper are summarized below.

Time averaging was a significant unresolved issue from previous paleoenvironmental reconstructions of the Upper Laetolil Beds. Given the 300 Kyr time span of the Upper Laetolil Beds, it is conceivable that the fauna represents a composite assemblage that reflects a mixture of different habitats. In order to determine the existence of heterogeneity in the Laetoli large mammal community, the ecological diversity at each of the collecting localities and stratigraphic zones was compared. The results show that there were no statistically significant differences in ecological diversity among the different localities or stratigraphic zones, which allowed for the use of a combined fauna from the entire sequence to reconstruct Upper Laetolil paleoecology. Moreover, this also implied that the general ecological structure throughout the Upper Laetolil sequence remained relatively stable and that the general ecosystem throughout the time of deposition was a mosaic of different habitat types, rather than a mixture of time-averaged habitats.

Ecological diversity data from Upper Laetolil were compared with other African Plio-Pleistocene fossil localities, as well as modern communities, using principal components analysis (PCA). An important finding was the general distinctiveness of fossil assemblages, including Laetoli, from modern communities. Predictor ecovariables (i.e., terrestriality, arboreality, frugivory, grazing) were used in bivariate plots to examine the factors that contributed to the distinctiveness of fossil communities. Terrestrial mammals were found to have the greatest impact on the uniqueness of fossil communities. Fossil assemblages had very high proportions of terrestrial mammals, as well as grazers, when compared to modern communities. The high frequency of terrestrial mammals in the Upper Laetolil Beds was apparently determined mainly by the under-representation of non-terrestrial small carnivores, such as mustelids and viverrids. The over-representation of grazing artiodactyls, particularly bovids, mostly accounted for the high proportion of grazers in the Upper Laetolil Beds. However, the result of a non-parametric Kruskal–Wallis significance test showed that the difference between the proportions of extant and fossil non-terrestrial carnivores was statistically significant, while the abundance of fossil and modern artiodactyl grazers was not significantly different.

Three possible explanations were proposed to account for the distinctiveness of the Upper Laetolil Beds from modern large mammal communities: (1) fossil sites have no modern analogs; (2) there is inherent bias in the fossil record such that certain taxa are absent or under-represented in the fossil record; and (3) ecomorphological analyses may not accurately reflect the range of habitat preferences of fossil taxa.

A key finding of this study is that the Laetoli fauna remained remarkably stable over a long period of time. It was found that there were no statistically significant differences in the ecological diversity among Upper Laetolil localities and stratigraphic zones. This implies that the ecological structure remained relatively uniform throughout the Upper Laetolil sequence, for a period of about 300 Kyr, regardless of regional or local environmental disturbances and changes. Furthermore, faunal similarity measures provide evidence that a certain degree of taxonomic stability extended to the Lower Laetolil Beds and to the Upper Ndolanya Beds, which covers a period of more than 1.6 Myr. This does not imply that the Laetoli faunas did not change over the course of this period as a consequence of regional and global climatic shifts or as a result of community turnover, but shows, relative to other contemporary faunas in East Africa, that the Laetoli mammalian fauna maintained long-term taxonomic affinities that distinguish it regionally, regardless of age. Clearly, fundamental aspects of the Laetoli ecosystem remained stable over time, which buffered the mammalian community from dramatic episodes of taxonomic turnover.

A major goal of this study was to approach the paleoenvironment of the Upper Laetolil Beds from the perspective of a more detailed and comprehensive comparative analysis of the mammalian fauna. Results from predictor ecovariables indicate that Upper Laetolil was unlikely to have been predominantly a closed woodland or forested habitat, since these have a higher proportion of arboreal or semi-arboreal mammals with browsing or frugivorous adaptations. Instead, the high frequency of grazers and terrestrial mammals, combined with the low occurrence of arboreal and frugivorous mammals, indicates affinities with modern mammalian communities living in grassland, savanna, and open woodland settings. Overall, the Upper Laetolil large mammal fauna exhibits characteristics that most closely approximate modern open woodland communities. Taking into account the results of this study, and the presence of indicator species, we reconstruct the paleoecology of the Upper Laetolil Beds as a mosaic habitat comprising of open woodland, grassland, and shrubland, as well as closed woodland along seasonal river courses. Evidence from the composition and distribution of tuffs, suggests that this climax vegetation was periodically disrupted and replaced for brief periods by extensive tracts of grassland following episodes of volcanic activity. Although these inundations of volcanic ash would presumably have had a profound effect on the local vegetation and mammalian community, the remarkable homogeneity of the Upper Laetolil fauna throughout the stratigraphic sequence suggests that the mammalian community was rapidly reconstituted in its entirety once the climax vegetation re-established itself.

Acknowledgments

We would like to thank the following individuals for their participation in the expeditions to Laetoli that contributed to the recovery of the material discussed here: P. Abwalo, P. Andrews, E. Baker, M. Bamford, R. Chami, M. Duru, C. Feibel, S. Hixson, J. Kingston, K. Kovarovic, A. Kweka, M. Lilombero, M. Mbago, K. McNulty, C. Msuya, S. Odunga, C. Robinson, W. Sanders, and L. Scott. We thank the Tanzania Commission for Science and Technology and the Unit of Antiquities in Dar es Salaam for permission to conduct research in Tanzania. Special thanks go to N. Kayombo (Director General), P. Msemwa (Director),

F. Mangalu (Director), A. Kweka and the staff at the National Museums of Tanzania in Dar es Salaam and Arusha for their support and assistance. The Government of Kenya and National Museums of Kenya are thanked for permission to study the collections in Nairobi. We would also like to acknowledge R. Bobe and the three reviewers (P. Andrews, M. Tappen, C. Musiba) for their invaluable comments on this paper. We are grateful to the editors of this volume (K. Behrensmeyer, R. Bobe, and Z. Alemseged) for inviting us to contribute to this volume. Fieldwork at Laetoli was supported by grants from National Geographic Society, the Leakey Foundation, and NSF (BCS-9903434 and BCS-0309513). Data collection and analysis were supported by a grant from NSF (BCS-0216683).

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Appendix 1. Summary of current interpretations of other fossil Plio-Pleistocene localities

Nachukui Formation, Lothagam, Kenya (~5.0 – <3.9 Ma)

There is a rich aquatic fauna, including crabs, fish, turtles, crocodiles, waterfowl, and hippopotamids (Leakey and Harris, 2003; Stewart, 2003). While the fish assemblage from the Apak Member (4.22–5 Ma) appears to be river adapted, the Kaiyumung Member (<3.9 Ma) has a predominantly lake fauna (Stewart, 2003; McDougall and Feibel, 2003). Evidence from oxygen isotope analyses of paleosols and mammalian tooth enamel indicate a mosaic of habitats (Cerling et al., 2003a). The Apak mammalian fauna points to a woodland habitat with abundant grassland nearby and the presence of a river, while the Kaiyumung assemblage suggests an open habitat with relative increase in grasslands and bushlands and the presence of a lake (Leakey and Harris, 2003).

Lower Laetolil Beds, Laetoli, Tanzania (~4.6–3.8 Ma)

There has not been much attention given to the paleontology or paleoecology of the Lower Laetolil Beds. Harris (1987) described the presence of fish and crocodiles in the lower unit; however, there is only a single confirmed crocodile specimen in the Mary Leakey collections and no aquatic vertebrates have been recovered subsequently. Based on the similarity of the Lower Laetolil mammalian fauna to that of the Upper Laetolil Beds, Harris (1987) suggested that the two units had comparable environmental conditions, although the presence of aquatic vertebrates indicates that the lower unit had standing water.

Kanapoi, Kenya (~4.2–3.9 Ma)

The mammalian fauna from Kanapoi indicates a dry woodland or bushland environment (Leakey et al., 1995). The primate fauna is dominated by Parapapio cf. ado, but it also includes colobines and Galago senegalensis. Bovids are dominated by Kobus and Aepyceros, species found near water and in edge habitats between grasslands and woodlands, respectively. The sediments were deposited by a large river, confirmed by the abundance of aquatic vertebrates (Leakey et al., 1995). The large river would have supported a wide gallery forest along the main river course (Leakey et al., 1995).

Hadar, Ethiopia (~3.4–2.3 Ma)

There have been various alternative reconstructions of the paleoenvironment of Hadar ranging from an open grassland with humid conditions (Harris, 1991), a wooded to treeless savanna (Boaz, 1977), to an evergreen bushland with forest nearby (Bonnefille, 1983). Bonnefille et al. (1987, 2004) using palynological data, noted a change in habitat over time. During the Sidi Hakoma Member (3.4–3.22 Ma), there were elements of deciduous and evergreen forest or bushland, later replaced by a succession of montane forest and woodland. The habitat becomes more open with the Denen Dora Member (3.22–3.18 Ma), which is characterized by wet and dry grassland. At 2.9 Ma, evergreen bushland and montane forests reappeared, but conditions were not as humid as in the Sidi Hakoma Member. Reed (1997), using community structure and ecological diversity analyses, contends that there were no open, arid habitats before the Denen Dora Member. There is evidence of a lake with marshes in the early part of the Denen Dora Member that changed to floodplains and deltas later in the member (Aronson and Taieb, 1981). Combined with the faunal data, Reed (1997) concluded that during this period the environment was generally woodland, with forests around the margins of the lake, and edaphic grassland.

Shungura Formation, Omo, Ethiopia (~3.5–1.3 Ma)

Fossil wood from the Shungura Formation shows that precipitation became more variable and lower in amount above Member C (2.95–2.6 Ma), causing more open and drought-resistant woodland–grassland communities to replace riverine forest communities (Eck and Jablonski, 1985). Pollen spectra also indicate that arboreal taxa were prevalent in Members B and C, but that they decrease after Member C (Bonnefille and DeChamps, 1983), although Bonnefille (1983) had noted the dominance of grassland during Member B. Micromammals in Members B and C indicate that there was a forest block with humid woodland–grassland, and some dry woodland–grassland (Wesselman, 1985). However, by Member F (2.35–2.33 Ma), the environment had shifted to a dry woodland–grassland and semi-arid steppe (Wesselman, 1985). The bovids indicate a change from a closed environment to one of a more open nature somewhere between Members B and G (Eck, 1976; Gentry, 1976). Reed (1997) ascertained that there was closed woodland with riverine forest and edaphic grasslands during Member B, but by Member C, and into Member F, habitats were dominated by bushland–woodland, even though riverine forest and edaphic grassland still existed. Recent study of the mammalian fauna in the Shungura Formation found that there was a steady decline of forest and closed woodland indicators after 3.2 Ma, while taxa indicating open woodland and grassland habitats increased moderately until after 2.5 Ma when they are more abundant that those associated with forests (Bobe et al., 2002). In his recent study of faunal change in the Shungura Formation, Alemseged (2003) suggests that while there is faunal composition change due to habitat change throughout the sequence, the most important faunal shift occurs during Member G at around 2.3 Ma when grasslands become an important part of the paleolandscape.

Usno Formation, Omo, Ethiopia (3.36–3.0 Ma)

The paleoecology of the Usno Formation is less intensively studied than the Shungura Formation. Reed (1997) concluded that the environment was probably a closed habitat with bushland and thicket areas, as well as riverine forest and woodland.

Koobi Fora Formation, Koobi Fora, Kenya (~4.0–1.3 Ma)

Evidence from stable isotopes (Cerling et al., 1977), palynology (Bonnefille, 1986a, b; Vincens, 1979), and faunal studies (Harris, 1983, 1987b) indicate that Koobi Fora was cooler and more humid during the Pliocene and early Pleistocene than at the present time, but it became progressively more arid throughout the sequence (Harris, 1983). Based on pollen and faunal data, the Tulu Bor Member (3.4–2.64 Ma) was probably a floodplain with gallery forest, while the Burgi Member (2.64–1.90 Ma) was closed woodland to the north becoming more open to the south (Harris, 1991). According to Reed (1997), the ecology during the Tulu Bor Member was scrub woodland on a riverine floodplain. The Burgi Member, in contrast, was open woodland with edaphic grassland and riparian woodland (Reed, 1997).

Members 3, Limeworks Cave, Makapan Valley, South Africa (~3.2–2.7 Ma)

The habitat of Member 3 has been variously reconstructed as woodland (Vrba, 1980), forest (Cadman and Rayner, 1989), and open savanna with nearby bushland (Dart, 1952; Wells and Cooke, 1956). Reed (1997) has suggested that Member 3 was a mosaic habitat with riparian woodland, bushland, and edaphic grassland.

Upper Ndolanya Beds, Laetoli, Tanzania (~2.5–2.7 Ma)

Analyses of the mammalian fauna from the Upper Ndolanya Beds, especially the equids and bovids, suggest an arid, grassland habitat. The equids are more hyposodont than those from the Laetolil Beds, and the bovid fauna is dominated by alcelaphines and antilopines (Harris, 1987). Recent analysis of the Upper Ndolanya large mammal fauna using ecological diversity analysis indicates that the paleohabitat was semi-arid bushland (Kovarovic et al., 2002).