Chapter 19
Large Mammal Evidence for the Paleoenvironment of the Upper Laetolil and Upper Ndolanya Beds of Laetoli, Tanzania

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Abstract There has been much debate on the environment of Pliocene Laetoli. These disagreements reflect the complexity of the paleoenvironment and the difficulties in reconciling contradictory evidence. In this paper, the community structure of the large mammal fauna at Laetoli is compared to that of modern faunal communities and the relative abundances of bovid tribes are examined. The results of these analyses are interpreted within the context of other lines of evidence, including those based on rodents, gastropods, phytoliths, stable isotopes and mesowear. The balance of evidence suggests that the ecology of the Upper Laetolil Beds was a mosaic of grassland-shrubland-open woodland habitats with extensive woody vegetation in the form of shrubs, thickets, and bush. There was also a significant presence of dense woodland and possibly riverine forest habitats. The results also indicate that the ecological conditions in the Upper Laetolil Beds became progressively drier and less wooded through time. There is no clear consensus as to the paleoenvironment of the Upper Ndolanya Beds. While there is evidence to suggest that it was drier and more open than the Upper Laetolil Beds, there is contrary evidence indicating that it was at least as humid and wooded as the Upper Laetolil Beds.

Keywords Community analysis • Pliocene • Bovidae • Indicator species • Relative abundances.

Introduction

There has been much debate regarding the paleoenvironmental reconstructions of the Upper Laetolil Beds of Laetoli, Tanzania. Past reconstructions have ranged in a continuum from open, dry savanna habitats (Leakey and Harris 1987) to woodland-grassland habitats (Su and Harrison 2007, 2008) to medium-density woodland (Reed 1997) and to dense woodland and forest habitats (Kovarovic and Andrews 2007). Based on previous faunal and paleoecological analyses (papers in Leakey and Harris 1987; Reed 1997; Kovarovic and Andrews 2007; Su and Harrison 2007, 2008), it is clear that Pliocene Laetoli was most likely ecologically heterogenous, but it is unclear as to the proportion and the changes in the geographical and temporal distribution of the different habitats. Taphonomic and geologic analyses suggest that the heterogeneity seen in the Laetoli large mammal fauna was not the result of time-averaged and transported assemblages, but rather a reflection of the mosaic nature of the environment at the time of deposition (Su and Harrison 2007, 2008). The lack of higher-level resolution in the data and the difficulty in resolving and integrating the contradictory inferences from different lines of evidence are major factors in the debate. In this paper, the large mammal evidence will be examined using a variety of methods, including indicator species (specifically species of the family Bovidae), relative abundances of bovid taxa, and community analysis using ecovariable proportions. The results are then integrated with other lines of evidence to provide a better understanding of the paleoenvironment of Pliocene Laetoli.

Materials and Methods

The analyses presented in this paper are derived from fossil specimens recovered from the Upper Laetolil Beds (ULB; 3.85–3.6 Ma) and Upper Ndolanya Beds (UNB; 2.66 Ma) at Laetoli by Terry Harrison and his team from 1998–2005. All specimens are from surface collections. All anatomically identifiable specimens were collected; however, only dental specimens were included in these analyses to minimize biases in sampling and element representation due to taphonomic factors (Su and Harrison 2008).

Community Structure

In this analysis, an attempt is made to compare and contrast the Laetoli faunas to known extant community structures

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from different habitat types. The goal of this analysis is to determine to which modern habitat types the Upper Laetolil and Upper Ndolanya Beds are most similar in community structure. The method is based on the observation that differences in community structure reflect differences in habitats, and represents an approach that is commonly used in paleoecological analyses (for examples, see Reed 1997; Kovarovic et al. 2002; Su and Harrison 2008; Su et al. 2009). Andrews et al. (1979) have shown that patterns of community structure based on dietary and locomotor variables (=ecovariables) are similar in similar habitats, regardless of species composition. This is a method for interpreting the paleoecology of fossil communities based on general ecological principles, rather than on using inferences from closely related modern taxa (Andrews et al. 1979; Reed 1997). The method is based on faunal list composition, and is subject, therefore, to the same biases associated with presence and absence data.

All species greater than 500 g were included in the analysis. Definition and categorization of habitat types are based on and modified from those of Lind and Morrison (1974), Pratt and Gwynne (1977), and White (1983). The modern communities are categorized into nine habitat types: forest, woodland, open woodland, riparian woodland, bushland, shrubland, grassland, floodplain grassland, and desert (Table 19.1). The ecovariables used to characterize community structure in this analysis include dietary and locomotor adaptations. There are 10 dietary and five locomotor variables (Table 19.2). For the Laetoli faunas these are assigned from published studies on inferred locomotor and dietary behaviors for fossil genera (Lewis 1995; Spencer 1995; Bishop 1999; Cerling et al. 1999; Sponheimer and Lee-Thorp 1999; Zazzo et al. 2000; papers in Leakey and Harris 2003; Werdelin and Lewis 2001; Harris and Cerling 2002; Kingston and Harrison 2007) and inferences from their extant relatives (see Su and Harrison 2007 for designations). Locomotor and dietary variables for fauna from comparative modern communities are taken from published behavioral and carbon isotopic studies (see Su and Harrison 2007 for references). In order to demonstrate which modern faunal community is most similar to that of Laetoli, Hierarchical Clustering Analysis was run on ecovariable frequencies using SPSS version 17.0 (Clustering method: furthest neighbor, chi-square between frequency). The faunas from the Upper Laetolil and Upper Ndolanya Beds are treated as two separate units in the analysis.

Indicator Species and Their Relative Abundance

Indicator species analysis is based on the assumption that closely related species are behaviorally similar from the past

Table 19.1 Modern African localities and vegetation types

Vegetation	Locality	References
Forest	Congo rainforest	Rahm (1966)
	E. of River Niger	Happold (1987)
	W. of River Niger	Happold (1987)
	E. of River Cross	Happold (1987)
	Kibale	Struhsaker (1997)
Riparian woodland (with swamps and grasslands)	Chobe National Park	Smithers (1971)
	Okavango	Smithers (1971)
	Moremi Game Reserve	Smithers (1971)
	Linyanti swamp	Smithers (1971)
Woodland	Zambia southern woodland	Ansell (1960, 1978)
	Guinea savanna woodland	Smithers (1983)
	Amboseli National Park	Behrensmeyer et al. (1979)
Open woodland	Tarangire National Park	Lamprey (1962)
	Southern savanna woodland	Smithers (1983)
	Kalahari thornveld	Rautenbach (1978a, b)
	Sudan savanna	Smithers (1983)
	Southwest arid	Smithers (1983)
Bushland	Mkomazi Game Reserve	Coe et al. (1999)
	Serengeti bush	Swynnerton (1958)
Shrubland	Sahel savanna	Smithers (1983)
	Karoo-Nama	Vernon (1999)
	Karoo-succulent	Vernon (1999)
Floodplain grassland	Kafue flats	Sheppe and Osborne (1971)
	Makgadikgadi Pan	Smithers (1971)
	Rukwa valley	Vesey-FitzGerald (1964)
Grassland	Central Kalahari	Rautenbach (1978a, b)
	Serengeti plains	Swynnerton (1958)
	Southern savanna grassland	Smithers (1983)
Desert	Namib desert	Rautenbach (1978a, b)

Table 19.2 Locomotor and dietary variable categories (following Reed 1997; Su and Harrison 2007)

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
AQ-T	Aquatic-Terrestrial	GuI	Gumnivore-Insect
F	Fossorial	TF	Total Frugivory
		TC	Total Carnivory
		I	Insectivore
		O	Omnivore
		RT	Root and Tuber

to the present, so that the habitat preferences of living members of a taxon are extended to its fossil relatives. Thus, the presence of a species with extant members that are ecologically constrained can be used to infer paleoenvironment (for examples, see Gentry 1970, 1978; Shipman and Harris 1988; Vrba 1980). This is supported by recent ecomorphological and stable carbon isotopic studies that show that certain fossil taxa generally shared similar diets with their extant relatives (Sponheimer et al. 1999; Kingston and Harrison 2007). However, species presence can be based on single or rare specimens that may have been stratigraphically or ecologically intrusive, and as such, would not be accurate indicators of paleohabitat. This bias can be ameliorated by incorporating relative abundance data, so that rare species do not take on disproportionate importance for paleoecological inferences. By combining indicator species and their relative abundance data, a more precise inference of the paleoenvironment can be obtained, as this takes into account the correlation between species abundance and habitat preferences (Su et al. 2009). It has been shown that there is differential abundance of bovid taxa in different habitats (Western 1973; Greenacre and Vrba 1984) and that habitat preferences of living species are reflected in surface bone assemblages (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980; Behrensmeyer 1993). Thus, it should be possible to make the same correlation and inferences for habitat-specific fossil taxa.

Bovids are the most common mammals at Laetoli and are the focus of this analysis. Their abundance and specificity in habitat preferences render them ideal for using relative abundances to infer habitat types. Premolars and molars were counted as identifiable specimens (NISP). Associated teeth, such as those in a mandible or maxilla, were counted only as a single NISP. Abundance data were collected at the tribal level only. Due to the uncertainty in their tribal affiliations (Gentry 2011), *Brabovus nanincisus* and *"Gazella" kohllarseni* are treated separately from other bovid tribes as "Brabovus" and "aff. Antilopini?", respectively. Bovid relative abundances are compared between localities and stratigraphic levels (ULB bovid dental NISP = 1888; UNB bovid dental NISP = 283). Locality designations follow those of Harrison and Kweka (2011). Marker tuffs are used to define the basic stratigraphic units within the Upper Laetolil Beds. However, because several horizons are exposed within a single locality (see Harrison and Kweka 2011), fossils may derive from strata that span several marker tuffs. This did not allow for the subdivision of fossils according to individual horizons separated by consecutive tuffs. However, it was possible to divide the Upper Laetolil fauna into three stratigraphic units, i.e. below Tuff 3 (BT3), between Tuff 3 and Tuff 5 (T3T5), and Above Tuff 5 (AT5) (see Table 2.2 in Harrison and Kweka (2011), for the localities associated with each unit). Most of the Upper Laetolil fossils derive from above Tuff 5. The Upper Ndolanya Beds were treated as one unit. Spatial and temporal variations in the relative abundances of the Laetoli bovids were examined through Correspondence Analysis, a multivariate analysis that can be used to examine the relationship between bovid tribal frequencies and localities/stratigraphic units. The analysis was conducted on weighted bovid dental NISP using SPSS version 17.0 (symmetrical normalization and standardization by removing row and column means).

Table 19.3 Comparative hominin-bearing Plio-Pleistocene sites used in the bovid relative abundance analysis

Locality	Age (Ma)	References
Lothagam, Kenya		Leakey and Harris (2001)
Apak Member	~5.0–4.2	
Kaiyumung Member	<3.9	
Hadar, Ethiopia		Reed (2008)
Basal member	3.8–3.4	
Sidi Hakoma	3.42–3.26	
Denen Dora	3.26–3.18	
Kada Hadar	3.2	
Omo, Ethiopia		Bobe (1997); Alemesged (2003)
Shungura Member B	3.36–2.95	
Shungura Member C	2.95–2.6	
Middle Awash, Ethiopia		
Aramis	4.4	White et al. (2009)

Relative abundances of bovid tribes from the Upper Laetolil Beds and Upper Ndolanya Beds are compared to those from other Plio-Pleistocene sites using Correspondence Analysis (Table 19.3). The count data for the comparative Plio-Pleistocene sites were derived from the published literature (see Table 19.3 for references). While the data from different sites are not directly comparable due to different collecting methodologies and taphonomic factors, the use of only dental material minimizes the effects of these factors as these elements tend to be more systematically collected.

Results and Discussion

Community Structure

Relative frequencies of the locomotor and dietary variables indicate that terrestrial, carnivorous, and mixed-feeding species dominate the faunal list for the Upper Laetolil Beds (86%, 30%, and 22%, respectively) and that terrestrial, mixed-feeding, and grazing species dominate the faunal list for the Upper Ndolanya Beds (87%, 32%, and 21%, respectively) (Table 19.4). The high proportion of mixed-feeders among the herbivorous species indicates the availability of not only wooded habitats, but also of grasslands. It is unclear, however, what the proportion of these two major types of habitats is in relation to each other. To examine the locomotor and dietary

Table 19.4 Frequencies of species locomotor and dietary variables of the Upper Laetolil Beds (*ULB*) and the Upper Ndolanya Beds (*UNB*). See Table 19.2 for Locomotor and Trophic codes

	ULB (%)	UNB (%)
Locomotor		
T	86	87
T-A	6	8
F	5	3
A	3	3
Aq	0	0
Trophic		
G	8	21
FG	0	0
B	16	18
MF	22	32
TF	10	8
TC	30	18
RT	5	3
I	3	0
O	6	0

variable frequencies further, and to put them in relation to the faunal communities of known habitats, they are compared to those of modern communities using Hierarchical Clustering. In the results of the Hierarchical Clustering analysis, the modern faunal communities are found to be divided into three distinct clusters: (1) those found in wet and/or wooded habitats (i.e., floodplain grassland, open woodland, riparian woodland, and woodland), (2) those found in more arid and less wooded habitats (i.e., desert, shrubland, grassland), and (3) those found in forests (Fig. 19.1). The faunal community of the Serengeti Plains does not fall into any of these three groups, but instead clusters with the faunas of Upper Laetolil Beds and Upper Ndolanya Beds, which group most closely with each other (Fig. 19.1). This suggests that the Laetoli fossil communities may share similar ecological parameters with that of the Serengeti and that the types of habitat in which they were found may have been comparable. It is possible that the similarity between the faunal communities of Pliocene Laetoli and

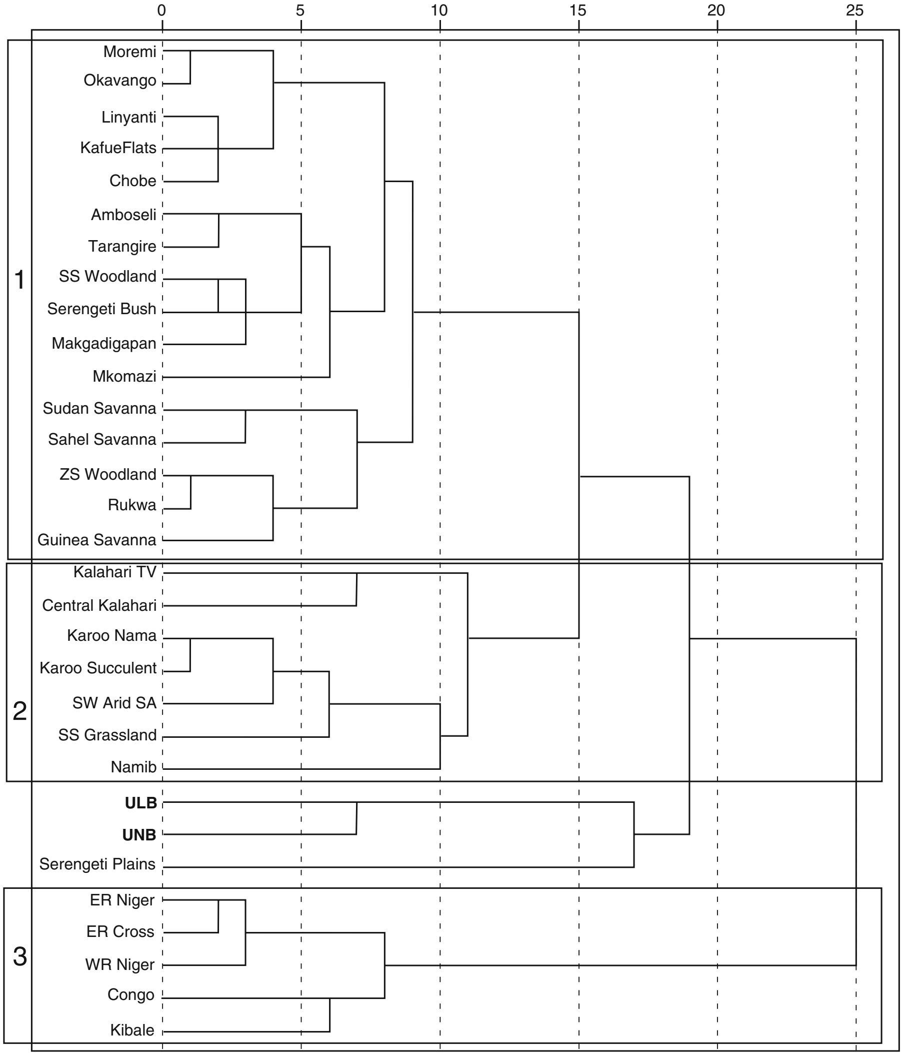

Fig. 19.1 Dendrogram from the hierarchical clustering analysis of the Laetoli and modern faunal communities. Upper Laetolil Beds (*ULB*) and Upper Ndolanya Beds (*UNB*) are in bold. There are three distinct clusters: (*1*) faunal communities of wet and/or wooded habitats (i.e., floodplain grassland, open woodland, riparian woodland, and woodland), (*2*) faunal communities of more arid and less wooded habitats (i.e., desert, shrubland, grassland), and (*3*) faunal communities of forests. Note that ULB and UNB are clustered with Serengeti Plains, and grouped with cluster 2 (i.e., faunal communities of more arid and less wooded habitats)

that of modern Serengeti is due to geographic proximity, rather than strictly ecological similarity. If geographic proximity is the driving factor behind the distinct grouping of the faunal communities of Laetoli and Serengeti Plains, then the faunal community of the Serengeti Bush might be reasonably expected to also be found within the ULB-UNB-Serengeti Plains cluster. However, it appears to be distinct from that of the Serengeti Plains, and is instead found in Cluster 1 (Fig. 19.1). This suggests that the distinctiveness of the faunal communities of ULB-UNB-Serengeti Plains cluster may indeed be reflective of shared ecological parameters. The clustering of forest communities apart from all other modern communities indicate that the faunal communities that inhabit forests are distinctive and may be more easily detectable in the fossil record than those of other habitat types (Su et al. 2009).

Indicator Species and Their Relative Abundances

The Upper Laetolil Beds (ULB) is dominated by alcelaphines (28%) and neotragines (29%) (Table 19.5). Extant alcelaphines are committed grazers found mostly in open habitats, with many species requiring regular access to water (Kingdon 1982, 1997; Smithers 1983; Sponheimer et al. 2003). The high proportion of neotragine is atypical, as they are usually one of the rarest elements of the bovid fauna in East African Plio-Pleistocene sites. Laetoli neotragines are made up overwhelmingly of *Madoqua*. As a group, extant neotragines, particularly *Madoqua*, are mostly arid-adapated and dependent on low-level thickets and succulents (Kingdon 1982, 1997). The classification of *Madoqua* habitat preferences can be problematic. Because *Madoqua* inhabits dense thickets and bushes and they browse almost exclusively, they are often classified as heavy cover animals (for example see Kovarovic and Andrews 2007). However, the dense thickets and bushes that modern dik-diks inhabit are often situated in open habitats, since they prefer an unobstructed view of predators (Kingdon 1982). Thus, while *Madoqua* is a heavy cover animal in relation to its immediate surroundings, it is often situated within a greater ecological context of more open habitats. This distinction is important since the interpretation of ecological preferences of modern relatives can dramatically affect inferences of the paleoenvironment based on the fossil taxa, especially in the case of Laetoli where *Madoqua* is particularly abundant. The prevalence of *Madoqua* may be indicative of relatively open habitats with an abundance of thickets, shrubs, and bush.

Table 19.5 Percentage (%) of bovid tribes in the Upper Laetolil Beds (*ULB*) and Upper Ndolanya Beds (*UNB*). NISP = number in parentheses

	ULB	UNB
	(1888)	(283)
Aepycerotini	7	0
Aff. antilopini?	5	0
Alcelaphini	28	54
Antilopini	11	24
Bovini	0.5	2
Cephalophini	0.7	0
Hippotragini	16	2
Brabovus	3	0
Neotragini	29	12
Tragelaphini	0.4	6
?Reduncini	0.1	0

Hippotragines (16%) also make up a significant proportion of the Upper Laetolil bovid fauna. All species of the modern hippotragine tribe are arid-adapted animals; however, some are better adapted to desert conditions than others (Kingdon 1982, 1997). Modern *Hippotragus*, the genus to which most of the Laetoli hippotragines are identified (Gentry 2011), requires regular water and prefers grassland-woodland ecotones or open woodland habitats, while avoiding closed woodland and forest habitats (Joubert 1976; Kingdon 1982, 1997; Smithers 1983). Antilopines comprise 11% of the bovid fauna in ULB. As a group, modern gazelles prefer open habitats, such as short- to medium-grasslands and open bushlands, and have significant browse in their diet, so that they range from mixed-feeders to browsers in their dietary preferences (Kingdon 1982, 1997; Estes 1991). The dominance of these tribes, particularly alcelaphines and neotragines, signals the abundance of their preferred habitats, which may consist of open grasslands, dense thickets and bushes, open woodlands, and grassland-woodland ecotones. While there is no geological evidence for permanent sources of large bodies of water at Laetoli, there were ephemeral streams and permanent springs present (Su and Harrison 2008) and these would have supplied those animals that required regular access to water.

Bovid tribes associated with wet and/or wooded conditions, i.e., Tragelaphini, Cephalophini, Aepycerotini, Reduncini (Kingdon 1982, 1997; Smithers 1983), are rare in the Upper Laetolil Beds. Tragelaphines and cephalophines together comprise less than 1% of the ULB bovid fauna, and aepycerotines are 7% of the ULB bovid fauna (Table 19.5). It is worth noting here that the presence of cephalophines is unusual. They are rarely found in African fossil localities (Gentry 2011), with only two other recorded instances at Lukeino (Thomas 1980) and Koobi Fora (Harris 1991). Most species of extant cephalophines are found in woodland and forest habitats, except for *Sylvicapra*, the bush duiker (Kingdon 1982; Newing 2001). *Sylvicapra* is not found in forests, but in savannas and open woodland habitats, where there are bush, thickets, and dense underbrush (Kingdon 1982). It has also been hypothesized that forest cephalophines are secondarily adapted to forest habitats (Kingdon 1982; Heckner-Bisping 2001), suggesting that *Sylvicapra* may exhibit the habitat preferences of ancestral cephalophines. It is conceivable that the Laetoli cephalophine (gen. et sp. indet.) may have been ecologically more similar to *Sylvicapra* than to the forest forms. Two possible reduncine teeth were recovered, but their precise taxonomic attribution is uncertain (Gentry 2011). Regardless, they comprise only 0.1% of the bovid fauna (Table 19.5). The low abundance of these taxa suggest that while densely wooded and/or wet habitats were present, they were probably not the dominant habitats on the Upper Laetoli paleolandscape. Of course, taphonomic factors may have impacted the abundance of the bovids that are often associated with densely wooded habitats. Previous taphonomic analysis showed that medium-sized bovids in the range of 25–100 kg are probably under-represented in the Laetoli fauna, due to a combination of carnivore activity and lower probability for immediate burial (Su and Harrison 2008). Specimens of tragelaphines, cephalophines, and aepycerotines from the Upper Laetolil Beds fall within this under-represented weight category (Su and Harrison 2008). It is likely that the original proportions of these bovids were higher than what is preserved and collected. However, antilopines, which also fall within this weight class and are likely similarly under-represented, are more abundant than tragelaphines, cephalophines, and aepycerotines combined (Table 19.5). This suggests that tragelaphines, cephalophines, and aepycerotines may indeed have been relatively rare in the original Upper Laetolil bovid fauna.

The Upper Ndolanya Beds is dominated by alcelaphines (54%), followed by antilopines (24%) (Table 19.5). The overwhelming abundance of alcelaphines in the Upper Ndolanya Beds suggest that it was drier and more open than the Upper Laetolil Beds. However, tragelaphines are much more common in the Upper Ndolanya Beds (6%) compared to the Upper Laetolil Beds (0.4%). This apparent contradiction is reinforced by evidence from ostrich eggshell stable isotopic data and gastropods that suggest that the Upper Ndolanya Beds was cooler, wetter, and more wooded than the Upper Laetolil Beds (Kingston 2011; Tattersfield 2011). Furthermore, studies of enamel carbon isotopic signatures and mesowear of Upper Ndolanya Beds tragelaphines indicate that they were mixed feeders with significant graze in their diet (Kaiser 2011; Kingston 2011), while studies of phytoliths suggest the prevalence of arid C_4 grasses in the Upper Ndolanya Beds (Rossouw and Scott 2011). There does not appear to be any way to reconcile these contradictory lines of evidence at this time.

The association of bovid tribes with localities and stratigraphic units is examined through the use of Correspondence Analysis. Frequencies of bovid tribes in each locality and stratigraphic unit is presented in Tables 19.6 and 19.7, respectively. The results of the locality analysis show that the first dimension explains 34.4% of the inertia and the second dimension explains 20% of the inertia. There is no clear association of any bovid taxon to any particular Upper Laetolil locality. However, when bovid abundances are analyzed based on stratigraphic position, clear associations of bovid tribes to stratigraphic units (as described in Materials and Methods) are seen. The results of the stratigraphic analysis show that the first dimension explains 69.4% of the inertia and Dimension 2 explains 25.4% of the inertia. The first dimension separated UNB from the ULB stratigraphic units, such that UNB is distinct from all ULB stratigraphic units (Fig. 19.2). Although alcelaphines represent more than half of the UNB bovids, tragelaphines and bovines are most closely associated with UNB (Fig. 19.2), probably due to the fact that tragelaphines and bovines are relatively more common in UNB compared to ULB. While tragelaphines are most closely associated with UNB compared to ULB stratigraphic units, they are actually distinct from any stratigraphic unit. This is probably a reflection of their overall rarity in the bovid fauna. Overall, Upper Ndolanya Beds is most closely associated with alcelaphines, antilopines, bovines, and tragelaphines, a mix of taxa that have habitat preferences that range from grassland to woodland. Alcelaphines, antilopines, aff. antilopines, hippotragines, and ?reduncines associate most closely with AT5, while neotragines, aepycerotines, *Brabovus*, and cephalophines associate most closely with BT3 (Fig. 19.2). The bovids associated with AT5 can generally be classified as those that are commonly found in habitats with less woody vegetation, such as grassland, shrubland, and wooded grassland. The bovids associated with BT3 can generally be classified as those that are most commonly found in habitats with more woody vegetation, such as bushland, open woodland, closed woodland, and forest. T3T5 is distinct from the other ULB stratigraphic units, but more closely associates with the “open” habitat bovids (Fig. 19.2). While this analysis is relatively coarse-grained in resolution, it does suggest that there was a shift in ecology from the lower part (below Tuff 3) to the upper part (above Tuff 5) of the Upper Laetolil Beds, as has been suggested by other studies (Kingston 2011; Kovarovic and Andrews 2011; Rossouw and Scott 2011; Tattersfield 2011). The bovid relative abundance suggests that there was a greater proportion of woody vegetation (including trees, shrubs, and bushes) in the lower part of the Upper Laetolil sequence (below Tuff 3) and decreased over time.

In order to place the relative abundances of the ULB and UNB bovids into context, they are compared to those from other Plio-Pleistocene sites using Correspondence Analysis (see Table 19.3 for a list of sites). The first and second dimensions account for 58.8% and 27.3% of the inertia, respectively. Three distinct clusters can be seen in the plot of Dimensions 1 and 2: (1) Laetoli and its associated bovids, (2) Aramis and its associated bovids, and (3) all other Plio-Pleistocene sites and their associated bovids (Fig. 19.3). The Upper Laetolil Beds are considered as one unit in this analysis and, along with the Upper Ndolanya Beds, they are most closely associated with bovid tribes that are usually found in drier habitats with less woody vegetation cover,

Table 19.6 Percentage (%) of bovid tribes in the Upper Laetolil Beds by locality. NISP = number in parentheses

	Loc. 1	Loc. 1NW	Loc. 2	Loc. 3	Loc. 4	Loc. 5	Loc. 6
	(86)	(6)	(188)	(44)	(19)	(75)	(98)
Aepycerotini	8	33	8	7	11	23	2
aff. antilopini?	3	0	4	7	0	3	2
Alcelaphini	10	0	34	18	21	8	35
Antilopini	0	17	10	14	5	7	12
Bovini	2	0	0.5	0	0	0	0
Celphalophini	0	0	1	5	0	1	0
Hippotragini	14	33	18	14	26	3	22
Brabovus	2	0	1	9	0	9	1
Neotragini	59	17	24	25	32	47	23
Tragelaphini	0	0	0	2	5	0	2
?Reduncini	0	0	0	0	0	0	0
	Loc. 7	Loc. 8	Loc. 9	Loc. 9 S	Loc. 10	Loc. 10E	Loc. 10 W
	(128)	(121)	(108)	(108)	(109)	(196)	(174)
Aepycerotini	2	7	6	10	12	4	8
aff. antilopini?	5	7	7	10	8	2	3
Alcelaphini	32	32	30	26	20	18	36
Antilopini	9	9	20	6	15	17	5
Bovini	0	1	0	0	1	0.5	0
Celphalophini	0	1	0	0	1	0	1
Hippotragini	21	18	24	2	8	20	7
Brabovus	2	2	2	0	3	0.5	4
Neotragini	29	21	10	45	32	37	36
Tragelaphini	0	1	1	1	0	0	0
?Reduncini	0	0	0	0	0	0.5	0
	Loc. 11	Loc. 12	Loc. 12E	Loc. 13	Loc. 13SG	Loc. 13E	Loc. 15
	(56)	(15)	(32)	(52)	(32)	(13)	(28)
Aepycerotini	4	0	3	6	3	0	0
aff. antilopini?	2	0	3	4	9	0	7
Alcelaphini	29	33	13	71	50	62	36
Antilopini	13	7	9	2	13	15	21
Bovini	0	7	0	0	0	0	0
Celphalophini	0	0	0	0	0	0	0
Hippotragini	25	27	13	6	9	15	21
Brabovus	2	7	16	0	3	0	0
Neotragini	27	20	44	12	13	8	14
Tragelaphini	0	0	0	0	0	0	0
?Reduncini	0	0	0	0	0	0	0
	Loc. 16	Loc. 17	Loc. 19	Loc. 20	Loc. 21	Loc. 22	Loc. 22E
	(71)	(11)	(6)	(11)	(47)	(45)	(9)
Aepycerotini	8	9	0	9	4	11	0
aff. antilopini?	4	0	0	0	4	2	0
Alcelaphini	24	9	50	18	38	29	11
Antilopini	14	18	0	9	17	11	0
Bovini	4	0	0	0	2	2	11
Celphalophini	1	0	0	0	0	0	11
Hippotragini	27	18	17	36	21	20	56
Brabovus	3	18	0	0	0	7	0
Neotragini	13	27	33	27	13	18	11
Tragelaphini	0	0	0	0	0	0	0
?Reduncini	1	0	0	0	0	0	0

such as alcelaphines, antilopines, and hippotragines. Since Laetoli is the only site in the comparative sample to have recorded occurrences of cephalophines, it is not surprising that this bovid tribe associates most closely with ULB.

The results of this analysis show that the pattern of bovid tribal frequencies at Laetoli (ULB and UNB) differs from those found at other Plio-Pleistocene sites. This signifies important ecological differences. Hadar paleoenvironments

Table 19.7 Percentages (%) of bovid tribes in the Upper Laetolil Beds by stratigraphic units. See text for discussion of stratigraphic units. NISP = number in parentheses

	below T3	T3–T5	above T5
	(391)	(75)	(1422)
Aepycerotini	10	23	6
aff. antilopini?	7	3	4
Alcelaphini	29	8	29
Antilopini	8	7	12
Bovini	0.3	0	0.8
Celphalophini	0.5	1	0.5
Hippotragini	6	3	20
Brabovus	3	9	2
Neotragini	38	47	26
Tragelaphini	0.3	0	0.4
?Reduncini	0	0	0.1

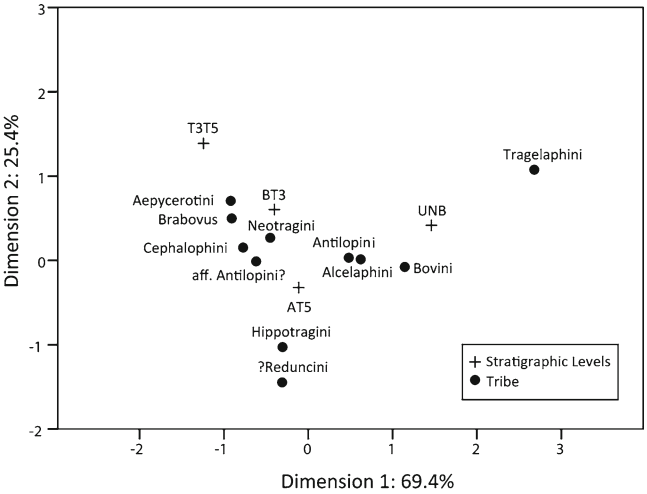

Fig. 19.2 Results of a correspondence analysis of bovid tribes from the Upper Laetolil Beds (*ULB*) and Upper Ndolanya Beds (*UNB*). The Upper Laetolil Beds are divided into three stratigraphic units: below Tuff 3 (*BT3*), between Tuff 3 and Tuff 5 (*T3T5*), and above Tuff 5 (*AT5*). See text for discussion

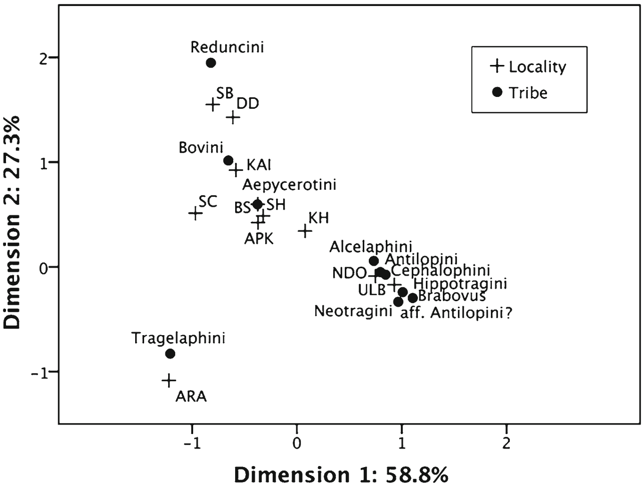

Fig. 19.3 Results of a correspondence analysis of bovid tribes from Laetoli in comparison with other Plio-Pleistocene fossil sites. Abbreviations: *ULB*, Upper Laetolil Beds; *UNB*, Upper Ndolanya Beds; *ARA*, Aramis; *APK*, Apak Member, Lothagam; *KAI*, Kaiyumung Member, Lothagam; *SH*, Sidi Hakoma Member, Hadar; *DD*, Denen Dora Member, Hadar; *SB*, Shungura Member B; *SC*, Shungura Member C. See Table 19.3 for the age and references for each site. See text for discussion

appear to have varied through time, but were generally wooded, with varying proportions of floodplain grassland (Bonnefille et al. 2004; Reed 2008). It is not until the upper part of the Denen Dora Member that there was a shift to more open woodland and wooded grassland (Reed 2008). Omo, during the deposition of Shungura Members B and C, was likely to have been a wooded and wet environment with closed woodland, riverine forest, and edaphic grassland (Bonnefille and DeChamps 1983; Wesselman 1985; Reed 1997; Bobe and Eck 2001; Bobe et al. 2002), which changed to one that was more open and arid after 2.5 Ma (Bobe et al. 2002; Alemseged 2003). The Lothagam fauna indicates that the paleoecological setting in the Apak Member was predominantly woodland with abundant grassland nearby, which transitioned into a more open habitat with a relative increase in grassland and bushland in the Kaiyumung Member (Leakey and Harris 2003). Aramis is distinct from other Plio-Pleistocene sites in its pattern of bovid relative abundance (Fig. 19.3), mostly due to the overwhelming dominance of tragelaphines (White et al. 2009). Geological, isotopic, and faunal data indicate that Aramis was most likely densely wooded during the Pliocene (White et al. 2009; WoldeGabriel et al. 2009). Given the results of the Correspondence Analysis and the pattern of bovid frequencies at each site, it is likely that Laetoli was less wooded than the other fossil sites included in this study. The difference in vegetation cover may have been due to the differential presence of permanent bodies of water. While all of the comparative sites had either a river or a lake (Bobe et al. 2002; Feibel 2003; Campisano and Feibel 2007; WoldeGabriel et al. 2009), there is no evidence to indicate that either was present at Laetoli during the Pliocene. Instead, water sources were apparently limited to small springs and seasonal watercourses (Harris 1987; Hay 1987; Ditchfield and Harrison 2011).

Paleoenvironmental Implications

The cumulative evidence from the analyses presented here indicates that while densely wooded habitats were present and more prevalent at Laetoli in the Pliocene than today, they were unlikely to have been the dominant vegetation type. Pliocene Laetoli (ULB and UNB) is most similar in ecovariable structure to modern-day shrubland and grassland habitats, dominated by bovid species that are associated with more arid and less wooded habitats. This is corroborated by the rodent fauna, which is dominated by taxa whose extant relatives are found in arid, open habitats, such as *Pedetes*, *Saccostomus*, and *Heterocephalus* in the Upper Laetolil Beds and *Xerus* and

Gerbilliscus in the Upper Ndolanya Beds (Denys 2011). While it is impossible to say with certainty that these fossil rodents share similar ecological preferences as their extant relatives, it has been shown that there is a strong correlation between rodent taxa and vegetation beginning as early as 6 Ma (Denys 1985, 1999). Thus, it is not unreasonable to infer that fossil relatives of modern arid, open habitat rodents may have had similar ecological preferences and that their dominance may indicate the prevalence of such habitats during the Pliocene at Laetoli. This is not to say, however, that Laetoli was a grassland or savanna. Other lines of evidence for the Upper Laetolil Beds indicate that the paleoenvironment was much more complex. Terrestrial gastropod composition in the Upper Laetolil Beds suggests that the paleoenvironment was heavily vegetated, with woodlands and forests (Tattersfield 2011). Analyses of phytoliths indicate that while grasses were ubiquitous and common (grass=54% of total phytoliths), they were never dominant in the ULB sequence (Rossouw and Scott 2011). This inference is supported by enamel carbon isotopic (Kingston and Harrison 2007; Kingston 2011) and mesowear (Kaiser 2011) analyses that reveal that the ULB bovids were much more generalized in their dietary preferences than their extant relatives. Even alcelaphines, which are commonly classified as dedicated C_4 grazers, were consuming significant portions of C_3 vegetation (Kingston and Harrison 2007; Kingston 2011) and this suggests that woody vegetation was abundant during the deposition of the Upper Laetolil Beds at Laetoli. However, evidence from phytoliths indicate that C_3 grasses were present and may have contributed to the C_3/C_4 signal seen in many bovid taxa (Rossouw and Scott 2011), so they might have been more dedicated to grazing than it seems based on carbon isotopic data. Thus, the balance of evidence suggests that while there were significant proportions of dense woodland, and perhaps even riverine forest habitats along ephemeral watercourses, the Upper Laetolil paleohabitat was likely dominated by a mosaic of grassland, shrubland, and open woodland.

By examining bovid abundances in different stratigraphic units (below Tuff 3, between Tuffs 3 and 5, above Tuff 5) separately, it is possible to see a shift in ecological conditions from the lower part (below Tuff 3) to the upper part (above Tuff 5) of the Upper Laetolil Beds. The lower part of ULB appeared to have had a greater proportion of woody vegetation compared to the upper part of ULB. Similar ecological shifts from wetter and more wooded to drier and less wooded conditions are suggested by the stable oxygen isotopic signature of ostrich eggshell fragments, phytoliths, and gastropod composition (Kingston 2011; Rossouw and Scott 2011; Tattersfield 2011). Interestingly, phytolith analysis indicates that mesic C_4 grass was the dominant grass phytolith above Tuff 7; the two possible reduncine specimens (?Reduncini) are also from above Tuff 7, suggesting that there might have been limited areas of wet grasslands during the latest part of the Upper Laetolil Beds. However, this is directly contradicted by the paleoecological inference based on the gastropod fauna. Tattersfield (2011) indicates that there was a slight shift to drier conditions above Tuff 5, which intensified above Tuff 7. It is difficult to reconcile these contradictory lines of evidence, but there is general agreement that there was an ecological shift to drier and more open habitats in the upper part of the Upper Laetolil Beds.

There is no clear inference that can be drawn about the paleoenvironment of Upper Ndolanya Beds based on the bovid abundance data. While alcelaphines are the dominant bovid taxon in the Upper Ndolanya Beds, suggesting an open, arid habitat, tragelaphines are relatively more abundant in the Upper Ndolanya Beds compared to the Upper Laetolil Beds. However, Upper Ndolanya tragelaphines were apparently variable grazers (Kingston 2011), which may indicate the dominance of arid grassland habitats that necessitated animals that emphasized browse in their diet to consume large amounts of graze. Studies of ecomorphology, mesowear, enamel carbon isotopes, and phytoliths all indicate that the Upper Ndolanya Beds was more arid and open than the Upper Laetolil Beds (Kovarovic et al. 2002; Kingston and Harrison 2007; Kingston 2011; Kaiser 2011; Rossouw and Scott 2011). Contradictory evidence is derived from ostrich eggshell oxygen isotope and gastropods, which indicate that the Upper Ndolanya paleoenvironment was cooler, more humid, and more wooded than that of the Upper Laetolil Beds (Kingston 2011; Tattersfield 2011). Furthermore, the Upper Ndolanya woodland/forest gastropod community is found at all UNB localities, suggesting that these habitats were relatively widespread, rather than constrained to microhabitats (Tattersfield 2011). Taphonomic factors may be at play here, because the preservation of large mammals differs in the Upper Ndolanya Beds and Upper Laetolil Beds. Until detailed taphonomic analyses are conducted for the Upper Ndolanya Beds, it is difficult to determine the role it played in influencing the paleoecological inferences drawn from different lines of evidence. Other considerations include the possibility that the large bovid fauna (e.g., alcelaphines) in the Upper Ndolanya Beds may have been migratory forms that were non-residents in the Laetoli area, thus inflating their proportions.

Summary

The results of the analyses highlight the complexity of the Laetoli paleohabitat and the reasons why there has been so much debate. The ecology of the Upper Laetolil Beds was most likely a mosaic environment dominated by grassland, shrubland, and open woodland, with dense woodland and possible riverine forest along ephemeral watercourses. However, the paleoenvironment was not static, and there was a transition between the lower part and the upper part of the sequence in which ecological conditions became generally drier and less wooded. The mammalian community of the Upper Ndolanya Beds is most similar to those of modern-day shrubland and grassland habitats. When combined with the dominance of alcelaphine bovids and evidence from community structure, mesowear, enamel carbon isotopes, and phytoliths, the Upper Ndolanya Beds was likely dominated by semi-arid to arid grasslands. However, contradictory evidence from stable oxygen isotopes and gastropods implies that the ecology of the Upper Ndolanya Beds was cooler, wetter, and more wooded than that of the Upper Laetolil Beds. Unfortunately, it is not possible at this time to reconcile the conflicting evidence. It is evident that much of the ongoing debate that surrounds paleoenvironmental reconstructions of Laetoli is due to the ecological complexity and to the difficulties in reconciling contradictory evidence. This study highlights the importance of using different lines of evidence to reconstruct the paleoenvironment so that a more nuanced and finer-grained interpretation can be made.

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References

Alemseged, Z. (2003). An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. *Journal of Human Evolution, 44*, 451–478.

Andrews, P., Lord, J. M., & Nesbit Evans, E. M. (1979). Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society, 11*, 177–205.

Ansell, W. F. H. (1960). *Mammals of northern Rhodesia*. Lukasa: Government Printer.

Ansell, W. F. H. (1978). *The mammals of Zambia*. Chilanga, Zambia: National Park and Wildlife Service.

Behrensmeyer, A. K. (1993). The bones of Amboseli. *National Geographic Research and Exploration, 9*, 402–421.

Behrensmeyer, A. K., & Dechant-Boaz, D. E. (1980). The recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology. In A. K. Behrensmeyer & A. P. Hill (Eds.), *Fossils in the making: Vertebrate taphonomy and paleoecology* (pp. 72–92). Chicago: University of Chicago Press.

Behrensmeyer, A. K., Western, D., & Dechant Boaz, D. E. (1979). New perspectives in vertebrate paleoecology from a recent bone assemblage. *Paleobiology, 5*, 12–21.

Bishop, L. (1999). Suid paleoecology and habitat preferences at African Pliocene and Pleistocene hominid localities. In T. G. Bromage & F. Schrenk (Eds.), *African biogeography, climate change, and human evolution* (pp. 216–225). Oxford: Oxford University Press.

Bobe, R. (1997). Hominid environments in the Pliocene: An analysis of fossil mammals from the Omo Valley, Ethiopia. Ph.D. dissertation, University of Washington, Seattle.

Bobe, R., & Eck, G. G. (2001). Responses of African bovids to Pliocene climatic change. *Paleobiology, 27*, 1–47.

Bobe, R., Behrensmeyer, A. K., & Chapman, R. (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution, 42*, 475–497.

Bonnefille, R., & DeChamps, R. (1983). Data on fossil flora. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the International Omo Research Expedition*, Annales, S. 8, Sciences Geologiques, Musée de l'Afrique Centrale, Tervuren, pp. 191–207.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., & Peyron, O. (2004). High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 12125–12129.

Campisano, C. J., & Feibel, C. S. (2007). Connecting local environmental sequences to global climate patterns: Evidence from the hominin-bearing Hadar Formation, Ethiopia. *Journal of Human Evolution, 53*, 515–527.

Cerling, T. E., Harris, J. M., & Leakey, M. G. (1999). Browsing and grazing in elephants: The isotope record of modern and fossil proboscideans. *Oecologia, 120*, 364–374.

Coe, M., McWilliam, N., Stone, G., & Packer, M. (1999). *Mkomazi: The ecology, biodiversity and conservation of a Tanzanian savanna*. London: Royal Geographical Society (with The Institute of British Geographers).

Denys, C. (1985). Paleoenvironmental and paleobiogeographical significance of the fossil rodent assemblages of Laetoli (Pliocene, Tanzania). *Palaeogeography, Palaeoclimatology, Palaeoecology, 52*, 77–97.

Denys, C. (1999). Of mice and men. Evolution in East and South Africa during Plio-Pleistocene times. In T. Bromage & F. Schrenk (Eds.), *African biogeography, climate change and human evolution* (pp. 226–252). Oxford: Oxford University Press.

Denys, C. (2011). Rodents. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Fossil hominins and the associated fauna, vol. 2, pp. 15–53). Dordrecht: Springer.

Estes, R. D. (1991). *The behavior guide to African mammals*. Berkeley: University of California Press.

Ditchfield, P., & Harrison, T. (2011). Sedimentology, lithostratigraphy and depositional history of the Laetoli area. In: T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology, and paleoenvironment, vol. 1, pp. 47–76). Dordrecht: Springer.

Feibel, C. S. (2003). Stratigraphic and depositional history of the Lothagam sequence. In M. G. Leakey & J. M. Harris (Eds.), *Lothagam: The dawn of humanity in eastern Africa* (pp. 17–30). New York: Columbia University Press.

Gentry, A. W. (1970). Revised classification for *Makapania broomi* Wells and Cooke (Bovidae, Mammalia) from South Africa. *Palaeontologia Africana, 13*, 63–67.

Gentry, A. W. (1978). Bovidae. In V. Maglio & H. S. B. Cooke (Eds.), *Evolution of African mammals* (pp. 540–572). Cambridge: Harvard University Press.

Gentry, A. W. (2011). Bovidae. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Fossil hominins and the associated fauna, vol. 2, pp. 363–465). Dordrecht: Springer.

Greenacre, M. J., & Vrba, E. S. (1984). Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology, 65*, 984–997.

Happold, D. C. D. (1987). *The mammals of Nigeria*. Oxford: Clarendon.

Harris, J. M. (1987). Summary. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 524–531). Oxford: Clarendon.

Harris, J. M. (1991). *Koobi Fora research project* (Vol. 3). Oxford: Clarendon.

Harris, J. M., & Cerling, T. E. (2002). Dietary adaptations of extant and Neogene african suids. *Journal of Zoology, London, 256*, 45–54.

Harrison, T., & Kweka, A. (2011). Paleontological localities on the Eyasi Plateau, including Laetoli. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology, and paleoenvironment, vol. 1, pp. 17–45). Dordrecht: Springer.

Hay, R. L. (1987). Geology of the Laetoli area. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 23–47). Oxford: Clarendon.

Heckner-Bisping, U. (2001). Appendix E – The walking patterns of duikers in respect to their origin in evolution. In V. J. Wilson (Ed.), *Duikers of Africa* (pp. 743–752). Bulawayo: Chipangali Wildlife Trust.

Joubert, S. C. J. (1976). The population ecology of the roan antelope, *Hippotragus equinus equinus* (Desmarest, 1804) in the Kruger National Park. Ph.D. dissertation, University of Pretoria, Pretoria.

Kaiser, T. M. (2011). Feeding ecology and niche partitioning of the Laetoli ungulate faunas. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, vol. 1, pp. 329–354). Dordrecht: Springer.

Kingdon, J. (1982). *East African mammals Volume IIIC: Bovidae*. Chicago: University of Chicago Press.

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. San Diego: Academic.

Kingston, J. (2011). Stable isotopic analyses of Laetoli fossil herbivores. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, vol. 1, pp. 293–328). Dordrecht: Springer.

Kingston, J., & Harrison, T. (2007). Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology, 243*, 272–306.

Kovarovic, K., & Andrews, P. (2007). Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *Journal of Human Evolution, 52*, 663–680.

Kovarovic, K., & Andrews, P. (2011). Environmental change within the Laetoli fossiliferous sequence: Vegetation catenas and bovid ecomorphology. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, vol. 1, pp. 367–380). Dordrecht: Springer.

Kovarovic, K., Andrews, P., & Aiello, L. (2002). An ecological diversity analysis of the Upper Ndolanya Beds, Laetoli, Tanzania. *Journal of Human Evolution, 43*, 395–418.

Lamprey, H. F. (1962). The Tarangire Game Reserve. *Tanganyika Notes and Records, 60*, 10–22.

Leakey, M. D., & Harris, J. M. (Eds.). (1987). *Laetoli: A Pliocene site in northern Tanzania*. Oxford: Clarendon.

Leakey, M. G., & Harris, J. M. (Eds.). (2001). *Lothagam: The dawn of humanity in eastern Africa*. New York: Columbia University Press.

Leakey, M. G., & Harris, J. M. (2003). Lothagam: Its significance and contributions. In M. G. Leakey & J. M. Harris (Eds.), *Lothagam: The dawn of humanity in eastern Africa* (pp. 625–660). New York: Columbia University Press.

Lewis, M. E. (1995). Plio-Pleistocene carnivoran guilds: Implications for hominid paleoecology. Ph.D. dissertation, State University of New York, Stony Brook.

Lind, E. M., & Morrison, M. E. S. (1974). *East African vegetation*. Bristol: Longman.

Newing, H. (2001). Bushmeat hunting and management: Implications of duiker ecology and interspecific competition. *Biodiversity and Conservation, 10*, 99–118.

Pratt, D. J., & Gwynne, M. D. (1977). *Rangeland management and ecology in East Africa*. London: Hodder and Stoughton.

Rahm, U. (1966). Les mammifères de la forêt équatoriale de l'est du Congo. *Musée Royal de l'Afrique Centrale Annales, Serie 8, 149*, 9–121.

Rautenbach, I. L. (1978a). A numerical re-appraisal of southern African biotic zones. *Bulletin of the Carnegie Museum of Natural History, 6*, 175–187.

Rautenbach, I. L. (1978b). Ecological distribution of the mammals of the Transvaal (Vertebrata: Mammalia). *Annals of the Transvaal Museum, 31*, 131–153.

Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution, 32*, 289–322.

Reed, K. E. (2008). Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. *Journal of Human Evolution, 54*, 743–768.

Rossouw, L., & Scott, L. (2011). Phytoliths and pollen, the microscopic plant remains in Pliocene volcanic sediments around Laetoli, Tanzania. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, vol. 1, pp. 201–215). Dordrecht: Springer.

Sheppe, W., & Osborne, T. (1971). Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs, 41*, 179–205.

Shipman, P., & Harris, J. M. (1988). Habitat preference and paleoecology of *Australopithecus boisei* in eastern Africa. In F. E. Grine (Ed.), *Evolutionary history of the "robust" australopithecines* (pp. 343–382). New York: Aldine de Gruyter.

Smithers, R. H. N. (1971). The mammals of Botswana. *Museum Memoirs of the National Museums and Monuments of Rhodesia, 4*, 1–340.

Smithers, R. H. N. (1983). *The mammals of the southern African subregion*. Pretoria: University of Pretoria.

Spencer, L. M. (1995). Antelopes and grasslands: Reconstructing African hominid environments. Ph.D. dissertation, State University of New York, Stony Brook.

Sponheimer, M., & Lee-Thorp, J. A. (1999). Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science, 283*, 368–370.

Sponheimer, M., Reed, K. E., & Lee-Thorp, J. A. (1999). Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: A case study from the Makapansgat Limeworks hominin locality. *Journal of Human Evolution, 36*, 705–718.

Sponheimer, M., Lee-Thorp, J. A., DeRuiter, D. J., Smith, J. M., van der Merwe, N. J., Reed, K., Grant, C. C., Ayliffe, L. K., Robinson, T. F., Heidelberg, C., & Marcus, W. (2003). Diets of southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy, 84*, 471–479.

Struhsaker, T. T. (1997). *Ecology of an African rain forest*. Gainesville: University Press of Florida.

Su, D. F., & Harrison, T. (2007). The paleoecology of the Upper Laetolil Beds at Laetoli: A reconsideration of the large mammal evidence. In R. Bobe, Z. Alemseged, & A. K. Behrensmeyer (Eds.), *Hominin environments in the East African Pliocene: An assessment of the faunal evidence* (pp. 279–313). Dordrecht: Springer.

Su, D. F., & Harrison, T. (2008). Ecological implications of the relative rarity of fossil hominins at Laetoli. *Journal of Human Evolution, 55*, 672–681.

Su, D. F., Ambrose, S. H., DeGusta, D., & Haile-Selassie, Y. (2009). Paleoenvironment. In Y. Haile-Selassie & G. WoldeGabriel (Eds.), *Ardipithecus kadabba: Late Miocene evidence from the Middle Awash* (pp. 521–547). Berkeley: University of California Press.

Swynnerton, G. H. (1958). Fauna of the Serengeti National Park. *Mammalia, 22*, 435–450.

Tattersfield, P. (2011). Gastropoda. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Fossil hominins and the associated fauna, vol. 2, pp. 567–587). Dordrecht: Springer.

Thomas, H. (1980). Les bovidés du Miocène supérieur des couches de Mpesida et de la Formation de Lukeino (District de Baringo, Kenya). In: R. E. F. Leakey, & B. A. Ogot (Eds.), *Proceedings of the 8th Pan-African Congress of Prehistory*, Nairobi, 1977 (pp. 82–91).

Vernon, C. J. (1999). Biogeography, endemism and diversity of animals in the Karoo. In W. R. J. Dean & S. J. Milton (Eds.), *The Karoo: Ecological patterns and processes* (pp. 57–85). Cambridge: Cambridge University Press.

Vesey-Fitzgerald, D. F. (1964). Mammals of the Rukwa Valley. *Tanganyika Notes and Records, 62*, 61–72.

Vrba, E. S. (1980). The significance of bovid remains as indicators of environment and prediction patterns. In A. K. Behrensmeyer & A. P. Hill (Eds.), *Fossils in the making* (pp. 247–271). Chicago: University of Chicago Press.

Werdelin, L., & Lewis, M. E. (2001). A revision of the genus *Dinofelis* (Mammalia, Felidae). *Zoological Journal of the Linnean Society, 132*, 47–258.

Wesselman, H. B. (1985). Fossil micromammals as indicators of climatic change about 2.4 Myr ago in the Omo Valley, Ethiopia. *South African Journal of Science, 81*, 260–261.

Western, D. (1973). The structure, dynamics and changes of the Amboseli ecosystem. Ph.D. dissertation, University of Nairobi, Nairobi.

White, F. (1983). *The vegetation of Africa: A descriptive memoir to accompany UNESCO/AETFAT/UNSO vegetation maps of Africa*. Paris: UNESCO.

White, T. D., Ambrose, S. H., Suwa, G., Su, D. F., DeGusta, D., Bernor, R. L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I. X., Haile-Selassie, Y., Howell, F. C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M., &Vrba, E. (2009). Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science, 326*, 87–93.

WoldeGabriel, G., Ambrose, S. H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A. M., Renne, P. R., Jolly-Saad, M. C., Stewart, K. M., &White, T. D. (2009). The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. *Science, 326*, 65–70.

Zazzo, A., Bocherens, H., Brunet, M., Beauvilain, A., Biliou, D., Mackaye, H. T., Vignaud, I., & Mariotti, A. (2000). Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate. *Paleobiology, 26*, 294–309.