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Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology

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Abstract

Major morphological and behavioral innovations in early human evolution have traditionally been viewed as responses to conditions associated with increasing aridity and the development of extensive grassland-savanna biomes in Africa during the Plio-Pleistocene. Interpretations of paleoenvironments at the Pliocene locality of Laetoli in northern Tanzania have figured prominently in these discussions, primarily because early hominins recovered from Laetoli are generally inferred to be associated with grassland, savanna or open woodland habitats. As these reconstructions effectively extend the range of habitat preferences inferred for Pliocene hominins, and contrast with interpretations of predominantly woodland and forested ecosystems at other early hominin sites, it is worth reevaluating the paleoecology at Laetoli utilizing a new approach. Isotopic analyses were conducted on the teeth of twenty-one extinct mammalian herbivore species from the Laetolil Beds (~4.3–3.5 Ma) and Upper Ndolanya Beds (~2.7–2.6 Ma) to determine their diet, as well as to investigate aspects of plant physiognomy and climate. Enamel samples were obtained from multiple localities at different stratigraphic levels in order to develop a high-resolution spatio-temporal framework for identifying and characterizing dietary and ecological change and variability within the succession. In general, dietary signals at Laetoli suggest heterogeneous ecosystems with both C_3 and C_4 dietary plants available that could support grassland, woodland, and forested communities. All large-bodied herbivores analyzed yielded dietary signatures indicating mixed grazing/browsing strategies or exclusive reliance on C_3 browse, more consistent with wooded than grassland-savanna biomes. There are no clear isotopic patterns documenting shifting ecology within the Laetolil Beds or between the Laetolil and overlying Upper Ndolanya Beds, although limited data from the U. Ndolanya Beds constrains interpretations. Comparison of the results from Laetoli with isotopic enamel profiles of other African fossil and modern communities reveals significant differences in dietary patterns. Relative to extant taxa in related lineages, carbon isotopic ranges of a number of Laetoli fossil herbivores are anomalous, indicating significantly more generalized intermediate C_3/C_4 feeding behaviors, perhaps indicative of dietary niches and habitat types with no close modern analogs. Enamel oxygen isotope ranges of fossil taxa from Laetoli are consistently more ^{18}O depleted than modern E. African herbivores, possibly indicating more humid conditions during that interval in the past. These data have important implications for reconstructing dietary trajectories of mammalian herbivore lineages, as well as the evolution of ecosystems in East Africa. Isotopic analyses of similar or related taxa at other hominin fossil sites yield signatures generally consistent with Laetoli, suggesting that

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mammalian communities in East Africa were sampling ecosystems with similar proportions of browse and grass. Collectively, the isotopic dietary signatures indicate heterogeneous habitats with significant wooded or forested components in the Laetoli area during deposition of the Laetolil and Upper Ndolanya Beds. Early hominin foraging activity in this interval may have included access to forest or woodland biomes within this ecosystem, complicating traditional interpretations linking early human evolutionary innovations with a shift to savanna habitats.

Keywords: Laetoli; Paleoecology; Isotopes; Hominin evolution; Paleodiet; Herbivore; Pliocene; Tanzania; Africa

1. Introduction

Perhaps best known for the preservation of footprint trails of early hominins and associated fauna (Leakey and Hay, 1979), the Pliocene site of Laetoli in northern Tanzania represents one of the key paleontological and paleoanthropological localities in East Africa. Volcaniclastic sediments exposed in the Laetoli region span the ca. 4–2 Ma interval and have yielded diverse faunal assemblages that include over 70 species of mammals, as well as the remains of fossil birds, reptiles, insects, gastropods, and plants (see Leakey and Harris, 1987). Hominins collected from the sequence include more than 30 specimens from the Upper Laetolil Beds (~3.8–3.5 Ma) attributed to *Australopithecus afarensis* (including the type specimen, L.H. 4) (Kohl-Larsen, 1943; Leakey et al., 1976; White, 1977; Johanson et al., 1978; Leakey, 1987b), an edentulous maxilla (EP 1500/01) assigned to *Paranthropus aethiopicus* from the Upper Ndolanya Beds (~2.7–2.6 Ma)(Harrison, 2002), and several specimens assigned to *Homo* from the overlying Pleistocene Ngaloba Beds (Leakey et al., 1976; Magori and Day, 1983). These data have contributed substantially to the establishment of a framework for understanding and interpreting the evolutionary history and paleobiology of East African faunas, including hominins, during the Plio-Pleistocene (Leakey and Harris, 1987).

Paleoecology represents an essential component of this interpretative framework, since it ultimately provides a context in which to identify potential selective pressures, interpret the adaptive significance of morphological or behavioral complexes, and link evolutionary pathways with shifts in environment and ecology. Based on initial studies of the fauna, flora and lithology of the Laetoli sequence (Leakey and Harris, 1987), the consensus of ecological reconstructions of the hominin-bearing Upper Laetolil Beds was that they represented arid to semi-arid grasslands with scattered bush and tree cover and possibly patches of acacia woodland, much like areas of the modern-day Serengeti ecosystem (Leakey and Harris, 1987 and references therein). Laetoli becomes significant in this regard in that it provides some of the earliest evidence for the establishment of modern savanna ecosystems in East Africa.

However, Andrews (1989) interpreted aspects of the fossil mammalian community structure at Laetoli to indicate more wooded ecosystems than previously considered. A subsequent assessment supported the notion that, although the composite fauna from Laetoli has a community structure consistent with the ecological diversity within the modern Serengeti ecosystem, it tends more toward the woodland end of the spectrum than toward grasslands (Andrews and Humphrey, 1999). Similarly, utilizing fauna collected at specific sites and horizons within the Upper Laetolil Beds to minimize time-averaging, community reconstructions by Reed (1997) indicate a closed to medium density woodland. Subsequent studies of the mammalian fauna from the Upper Laetolil Beds further support a more complex mosaic of habitats with greater representation of bushland and woodland (Musiba, 1999, Hicks, 1999; Kingston and Harrison, 2001, 2002; Musiba et al., 2002; Su and Harrison, 2003; Harrison and Su, 2004; Bamford and Harrison, 2004; Kingston and Harrison, 2005; Kovarovic et al., 2005; Su, 2005; Su and Harrison, 2005; Harrison, 2005; Su and Harrison, in press). Additionally, analyses of the community structure of the fossil mammals from the Upper Ndolanya Beds (Kovarovic et al., 2002) indicate a transition during the later Pliocene at Laetoli to semi-arid scrub or bushland habitats. Stable isotope investigations of paleosol carbonates (Cerling, 1992) also indicated that woodland habitats predominated during the Upper Laetolil Beds, and gave way to grassland-savanna habitats during the Upper Ndolanya Beds.

In light of emerging evidence indicating that penecontemporaneous and older hominin sites in tropical Africa are woodland or forest (Kingston et al., 1994; WoldeGabriel et al., 1994; Leakey et al., 1995; Wynn, 2000; Pickford and Senut, 2001; WoldeGabriel et al., 2001; Vignaud et al., 2002; Leakey and Harris, 2003; White et al., 2006), it is important to establish whether Laetoli is anomalous in representing grassland-savanna habitats, or whether it is closer to other early hominin sites in being more wooded and forested. The apparent inconsistencies in findings at Laetoli typify investigations at paleontological localities where numerous independent approaches have been developed to reconstruct paleoecology. In part, these problems arise from attempts to synthesize environmental proxies representing vastly different temporal and geographic scales, derived from potentially distinct habitats in dynamic, heterogeneous ecosystems. Taphonomic and representational biases intrinsic to the sedimentological context of vertebrate assemblages also complicate interpretations. Different depositional modes or regimes (e.g., fluvial, flood-plain, subaerial) sample different components of the biota, invalidating simple comparisons of fossil assemblages and their inferred ecology (Behrensmeyer and Hook, 1992). Fossils at Laetoli derive primarily from extensive volcanogenic sediments deposited on a low-relief land surface distal to major sources of water (Hay, 1981, 1987), resulting in relatively autochthonous assemblages in which the dominant taphonomic biases are related to carnivore activity and differential preservation (Su, 2005). In this respect Laetoli is unlike virtually all other early hominin sites, which are generally associated with aquatic facies, such as lake margin or fluvial deposits. Direct comparisons between Laetoli and penecontemporaneous fossil localities are compromised by this taphonomic bias, and the apparently unique paleoecological interpretations of Laetoli may be influenced by the distinctive conditions and processes leading to the preservation of this assemblage.

In addition, tropical and sub-tropical biomes in Africa have been subject to climatic and seasonal oscillations driven primarily by orbital forcing (Kutzbach and Street-Perrott, 1985; Pokras and Mix, 1987; Gasse et al., 1989; Lamb et al., 1995; Trauth et al., 2003; deMenocal, 1995; Kingston et al., in press). These short-term changes occur at periodicities ranging in duration from 20 to 400 ka or less, and would likely have precipitated a reshuffling of plant communities, providing further potential for mixing proxies of variable ecosystems in sequences spanning significant intervals of time. Although the Upper Laetolil Beds may have been deposited over a ~300 ka interval straddling a number of potential environmental shifts, evidence from different horizons and localities are typically combined to create a generalized composite ecological profile.

Paleoecological reconstructions also rely heavily on taxonomic uniformitarianism, whereby the interpretation of adaptations and modes of life of extinct organisms hinge on analogy with related modern forms. Many species, or even entire communities, may change their habitat preference through time or have sufficient behavioral flexibility to occupy a wide range of ecosystems. In recognition of these problems, taxon-free approaches, such as ecomorphology or morphologically-based community characterization have been developed (Fleming, 1973; Andrews et al., 1979; Van Couvering, 1980; Nesbit-Evans et al., 1981; Damuth, 1992; Reed, 1998). While innovative and extremely useful, these approaches require calibration in modern contexts that are assumed to have continuity in properties and composition with fossil communities, and can, therefore, ultimately involve tenuous chains of inference. In addition, interpretations of fossil assemblages as communities can be problematic due to mixing of elements from different communities through time and across space.

Given these caveats and concerns, a goal of ongoing research at the site of Laetoli is to develop additional and more refined lines of evidence for interpreting paleoecology. Reconstructing the diet of extinct species utilizing stable isotopes provides one such avenue. The underlying basis for this approach is that large-bodied mammalian herbivores can be differentiated as browsers, grazers, and intermediate or mixed feeders based on the stable carbon isotopic signature of their teeth ($\delta^{13}C_{enamel}$), independent of inferences or interpretations based on taxonomy, cranio-dental morphology or micro-/mesowear studies. Subtle carbon isotopic variations within these dietary categories, as well as stable oxygen isotopes ($\delta^{18}O_{enamel}$), provide further refinement of foraging behavior and environmental conditions. While documenting the diets of extinct taxa and evaluating evolutionary strategies is an important goal of this study, the aim is also to infer ecological characteristics of the habitats based on feeding patterns. The key assumption here is that food preferences of a species are intimately linked to physical and ecological characteristics of the habitats to which the species is adapted. This link, however, is not always direct and diet may not necessarily faithfully record standing vegetation or habitat type (Behrensmeyer and Hook, 1992; MacFadden et al., 1999). Complicating factors inherent in this approach include selectivity of animals, competitive exclusion, migration/immigration, broad habitat tolerance, social behavior, and seasonality. C_4 grasses, for example, are considered to be less nutritious than C_3 plants due to less digestible bundle sheath cells and a lower content of easily digested soluble carbohydrates (Demment and Van Soest, 1985; Caswell et al., 1973) and may be underrepresented in dietary profiles relative to their abundance in past landscapes. A strategy to limit the effect of these biases is to sample a wide range of fossil herbivores, rather than rely on a single taxon or lineage, and develop a consensus reconstruction based on the dietary patterns of the various guilds represented.

In this study, enamel from 21 species of herbivores from the Lower and Upper Laetolil Beds and the Upper Ndolanya Beds, representing 7 families, are analyzed isotopically. The overall goal is to refine our understanding of the general paleoenvironmental setting at Laetoli, examine paleoecological variability between and within the major stratigraphic units, and compare the dietary signatures with modern and fossil herbivore assemblages. Specific issues and questions to be addressed include:

(1) Is it reasonable to interpret the combined fauna from the entire Upper Laetolil Beds or are there apparent dietary shifts corresponding to ecological transitions within the sequence?

(2) Is there a significant ecological shift between the Upper Laetolil and Upper Ndolanya Beds? Recent recovery of *Paranthropus aethiopicus* from the Upper Ndolanya Beds provides an impetus to compare and contrast ecological preferences of *Australopithecus afarensis* and *P. aethiopicus* at the same sites. Further documentation of the nature of the paleoecological distinctions between these two stratigraphic units could contribute valuable evidence concerning the link between climatic change and cladogenesis among Pliocene hominins (deMenocal, 1995; Vrba et al., 1995; Potts, 1996; Bromage and Schrenk, 1999; Bobe and Behrensmeyer, 2004).

(3) How do isotopic dietary profiles from Laetoli compare to corresponding data collected at other fossil localities and from modern East African communities? Do these dietary reconstructions support an anomalous paleoecological interpretation for Laetoli relative to other early hominin sites?

(4) What is the extent of intra- and inter-site variability in the dietary signals of extinct species and what are the implications for the evolution of dietary trends within lineages. How do dietary assessments based on isotopic analyses compare to paleodiet reconstructions based on alternative approaches?

(5) Identify those taxa and lineages that are highly opportunistic, eclectic feeders that shift diet with ecological change, thereby providing the most sensitive proxies for characterizing ecosystems in the past.

2. Geologic context

Laetoli is located in the southern part of the eastern branch of the East African Rift Valley in N. Tanzania, where the central graben has splayed out into a series of tilted fault blocks with lake basins on their downthrown sides and plateaus on the upthrown sides. Sediments are exposed along the margin of the Eyasi Plateau that forms the divide between the Lake Eyasi and Olduvai Gorge drainage basins (Fig. 1). The Laetoli sediments were first described and named by Kent (1941), and their known distribution and extent was later revised by

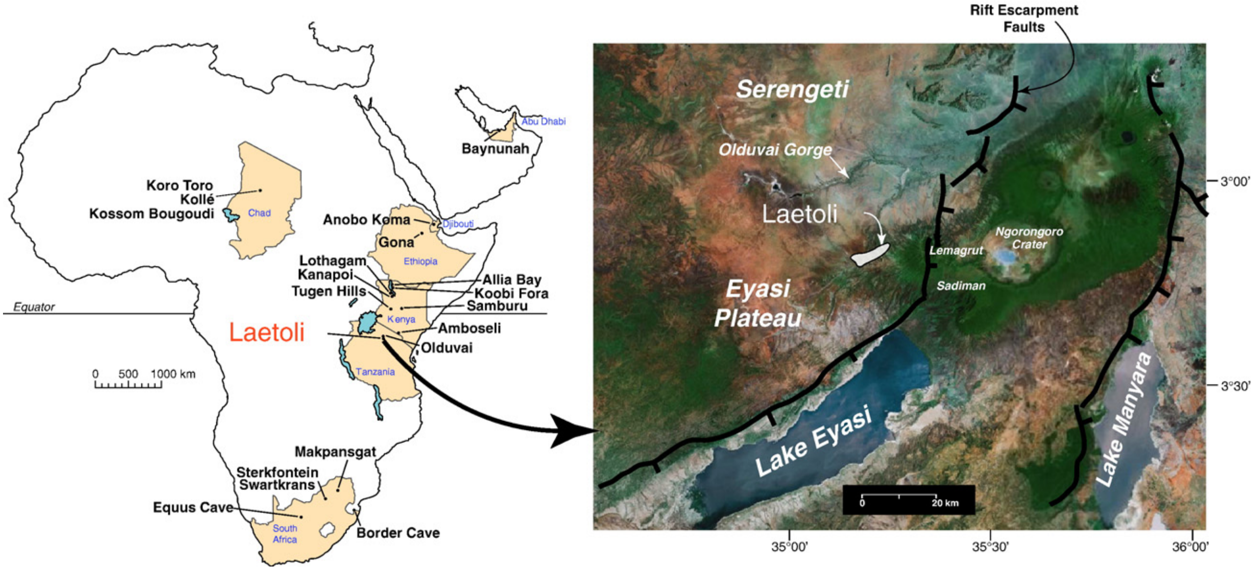

Fig. 1. Map of Africa and the Arabian Peninsula depicting location of Laetoli and other Neogene fossil vertebrate localities discussed in text or referred to in Figs. 5 and 6 where relevant herbivore enamel has been analyzed isotopically. Inset of the Laetoli region along the margin of the Eyasi Plateau, the Ngorongoro Volcanic Highlands and the Serengeti Plains.

Pickering (1964). Subsequent work established a comprehensive stratigraphic, structural and geochronologic framework for the region (Leakey et al., 1976; Hay, 1978; Drake and Curtis, 1979; Hay, 1981; Drake and Curtis, 1987; Hay, 1987; Ndessokia, 1990; Manega, 1993). The Laetoli succession is exposed over an area of >1600 km^2, although most of the paleontological collections to date have been recovered from a relatively restricted area (~100^2 km) along the upper reaches of the Garusi River (Fig. 1). These deposits overlie Precambrian basement and are bordered and overlain on the east by the Ngorongoro Volcanic Highlands (Hay, 1981). The Laetolil Beds, forming the base of the succession, are greater than 123 m thick and consist of two lithologic units (Fig. 2). The lower unit consists mainly of aeolian tuffs interbedded with airfall and water-worked tuffs. K–Ar dates indicate an age from more than 4.3 Ma to 3.8 Ma (Drake and Curtis, 1987). Fossil vertebrates have been recovered from this unit, but they are much more rare, scattered and fragmentary than in the overlying upper unit. The upper unit is comprised of a series of aeolian and airfall tuffs, including eight distinctive marker tuffs that facilitate lateral correlation between fossil localities. The diverse fauna from the upper unit, including hominins, can be reliably dated to between 3.8 Ma and 3.5 Ma (Drake and Curtis, 1987). Fossils have been recovered from more than 30 localities from throughout the Upper Laetolil Beds. Disconformably overlying the Laetolil Beds are a series of tuffs and calcretes comprising the Ndolanya Beds (15–20 m thick), also divided into an upper and lower unit based on a disconformity (Hay, 1981). Fauna from the Upper Ndolanya Beds is consistent with a radiometric date of 2.58–2.66 Ma (Gentry, 1987; Harris, 1987d; Ndessokia, 1990; Manega, 1993). This latter unit is overlain by the Olgol Lavas, which have yielded an average K–Ar date of 2.41 Ma (Drake and Curtis, 1987).

3. Isotopic variation, dietary preferences and ecology

3.1. Isotopic overview

Analyses of stable isotopes of carbon and oxygen isolated from fossils have contributed substantially to our understanding and ability to reconstruct paleoecological and paleoclimatic parameters in Africa (e.g., Ericson et al., 1981; Tiezsen et al., 1983; Lee-Thorp, 1989; Koch et al., 1989; Morgan et al., 1994; Bocherens et al., 1996; Kohn et al., 1996; Cerling et al., 1997a,b; Kingston, 1999a,b; Sponheimer et al., 1999; Sponheimer and Lee-Thorp, 1999a,c; Zazzo et al., 2000; Schoeninger et al., 2003; Cerling et al., 2003b, van der Merwe et al., 2003). These approaches have been important in documenting ecological shifts, constraining

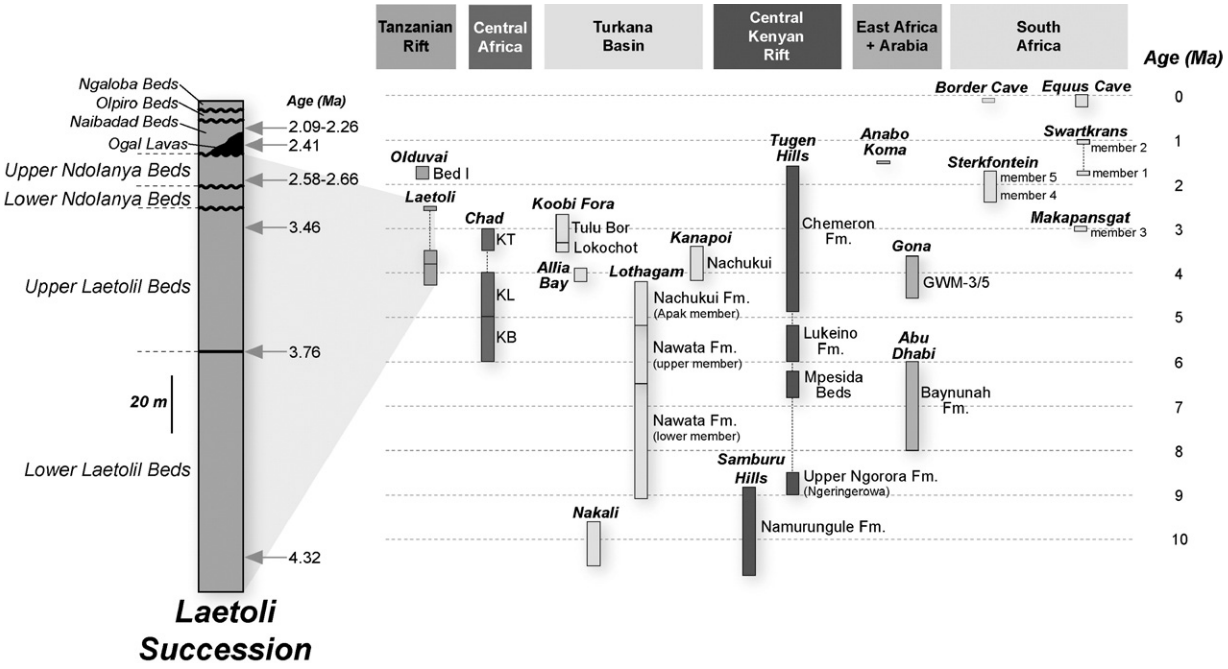

Fig. 2. Schematic stratigraphic succession exposed at Laetoli with radiometric dates and age ranges of fossil localities used for comparative purposes in this study.

Table 1
Herbivore carbonate hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ of fossil and modern samples collected at the site of Laetoli

Sample number	Formation	Taxon	$\delta^{13}C_{enamel}$	$\delta^{18}O_{enamel}$	Element	Locality	Stratigraphic level
1.1 Family Rhinocerotidae							
114	U. Laetolil Beds	*Ceratotherium praecox*	−5.9	−1	Lower cheek tooth	Loc. 9 S	Below tuff 2
115	U. Laetolil Beds	*Ceratotherium praecox*	−11.0	−1.1	Upper molar	Loc. 21	Between tuffs 5 and 8
116	U. Laetolil Beds	*Ceratotherium praecox*	−1.3	−1.8	Upper molar	Loc. 6	Between tuffs 5 and 6
117	U. Laetolil Beds	*Ceratotherium praecox*	−11.0	0.5	Lower molar	Loc. 21	Between tuffs 5 and 8
118	U. Laetolil Beds	*Ceratotherium praecox*	−11.3	−0.0	Lower cheek tooth	Loc. 9 S	Below tuff 2
119	U. Laetolil Beds	*Ceratotherium praecox*	−5.9	−0.4	Lower cheek tooth	Loc. 9 S	Below tuff 2
170	U. Laetolil Beds	Rhinocerotidae	−3.7	−0.81	Upper molar	Loc. 10	Below tuff 3
171	L. Laetolil Beds	Rhinocerotidae	−7.0	−1.0	Molar	Emboremony 1	
172	U. Laetolil Beds	Rhinocerotidae	−5.6	−1.2	Upper molar	Loc. 10	Below tuff 3
R1010-1	Modern	*Ceratotherium simum*	0.5	4.2	Upper molar	Laetoli area	
R1010-15	Modern	*Ceratotherium simum*	0.4	4.2	Upper molar	Laetoli area	
R1010-30	Modern	*Ceratotherium simum*	0.0	4.2	Upper molar	Laetoli area	
1.2 Family Giraffidae							
4	U. Laetolil Beds	*Giraffa jumae*	−10.9	2.8	Upper molar	Loc. 8	Between tuffs 5 and 7
16	U. Laetolil Beds	*Giraffa jumae*	−10.6	1.1	Upper molar	Loc. 9	Between tuffs 6 and 8
27	U. Laetolil Beds	*Giraffa jumae*	−9.98	−0.3	Upper molar	Loc. 1	Between tuffs 7 and YMT
49	U. Laetolil Beds	*Giraffa jumae*	−10.4	−1.1	Lower molar	Loc. 10E	Between tuffs 5 and 7
50	U. Laetolil Beds	*Giraffa jumae*	−10.2	1.5	Upper molar	Loc. 10E	Between tuffs 5 and 7
52	U. Laetolil Beds	*Giraffa jumae*	−8.8	8.7	Lower M2	Loc. 10W	Below tuff 3
125	U. Laetolil Beds	*Giraffa jumae*	−8.3	0.1	Upper molar	Loc. 22 E	Between tuffs 3 and 8
126	U. Laetolil Beds	*Giraffa jumae*	−9.9	0.6	Upper molar	Loc. 7	Between tuffs 5 and 7
11	U. Laetolil Beds	*Giraffa stillei*	−9.6	−0.1	Upper molar	Loc. 2	Between tuffs 5 and 7
15	U. Laetolil Beds	*Giraffa stillei*	−8.5	2.0	Upper molar	Loc. 2	Between tuffs 5 and 7
17	U. Laetolil Beds	*Giraffa stillei*	−11.2	0.1	Lower M3	Loc. 9	Between tuffs 6 and 8
24	U. Laetolil Beds	*Giraffa stillei*	−9.5	1.4	Lower premolar	Loc. 21	Between tuffs 5 and 8
25	U. Laetolil Beds	*Giraffa stillei*	−9.0	2.7	Upper molar	Loc. 16	Between tuffs 7 and just above 8
28	U. Laetolil Beds	*Giraffa stillei*	−12.4	2.2	Upper molar	Loc. 8	Below tuff 6
30	U. Laetolil Beds	*Giraffa stillei*	−9.0	8.9	Lower molar	Loc. 12 E	Between tuffs 5 and 7
51	U. Laetolil Beds	*Giraffa stillei*	−10.2	−0.1	Lower molar	Loc. 10	Below tuff 3
127	U. Laetolil Beds	*Giraffa stillei*	−10.3	3.5	Upper molar	Loc. 8	Between tuffs 5 and 7
128	U. Laetolil Beds	*Giraffa stillei*	−11.1	1.1	Lower molar	Loc. 7	Above tuff 7
129	U. Laetolil Beds	*Giraffa stillei*	−9.6	1.7	Upper molar	Loc. 9 S	Below tuff 2
130	U. Laetolil Beds	*Giraffa stillei*	−10.2	0.1	Premolar	Loc. 10 W	Below tuff 3
131	U. Laetolil Beds	*Giraffa stillei*	−10.5	0.8	Upper molar	Loc. 7	Above tuff 7
29	U. Laetolil Beds	*Sivatherium maurusium*	−12.9	1.0	Upper molar	Loc. 12/12 E	Between tuffs 5 and 7
174	U. Laetolil Beds	*Sivatherium maurusium*	−9.4	1.9	Upper molar	Loc. 21	Between tuffs 5 and 8
173	U. Ndolanya Beds	*Sivatherium maurusium*	−9.6	−0.5	Upper molar	Loc. 15	
G1	Modern	*Giraffa camelopardalis*	−12.7	4.0	Upper M1	Laetoli Area	
G2	Modern	*Giraffa camelopardalis*	−13.6	6.0	Upper M2	Laetoli Area	
G3	Modern	*Giraffa camelopardalis*	−10.6	8.0	Upper M3	Laetoli Area	
G4	Modern	*Giraffa camelopardalis*	−9.4	7.9	Upper M3	Laetoli Area	
G94 1	Modern	*Giraffa camelopardalis*	−12.4	4.9	Upper M3	Laetoli Area	
G94 12	Modern	*Giraffa camelopardalis*	−13.4	4.6	Upper M3	Laetoli Area	
GP94 1	Modern	*Giraffa camelopardalis*	−9.8	6.3	Upper P4	Laetoli Area	
GP94 20	Modern	*Giraffa camelopardalis*	−8.1	6.8	Upper P4	Laetoli Area	
1.3 Family Gomphotheriidae, Elephantidae, and Deinotheriidae							
59	L. Laetolil Beds	*Anancus kenyensis*	−2.5	−2.4	Molar	Kakesio #6	
1	U. Laetolil Beds	*Loxodonta exoptata*	−5.0	−1.9	Molar	Loc. 8	Between tuffs 5 and 7
2	U. Laetolil Beds	*Loxodonta exoptata*	−2.01	1.4	Molar	Loc. 8	Between tuffs 5 and 7
26	U. Laetolil Beds	*Loxodonta exoptata*	−0.5	−1.0	Molar	Loc. 16	Between tuffs 7 and just above 8
60	U. Laetolil Beds	*Loxodonta exoptata*	−5.6	−0.5	Molar	Loc. 10 E	Between tuffs 5 and 7

(continued on next page)

Table 1 (*continued*)

Sample number	Formation	Taxon	$\delta^{13}C_{enamel}$	$\delta^{18}O_{enamel}$	Element	Locality	Stratigraphic level
61	U. Laetolil Beds	*Loxodonta exoptata*	−4.4	−0.9	Molar	Loc. 10W	Below tuff 3
1.3 Family Gomphotheriidae, Elephantidae, and Deinotheriidae							
62	U. Laetolil Beds	*Loxodonta exoptata*	−1.2	0.4	Molar	Loc. 10W	Below tuff 3
63	U. Laetolil Beds	*Loxodonta exoptata*	−3.8	−0.6	Molar	Loc. 10	Below tuff 3
77	U. Laetolil Beds	*Loxodonta exoptata*	−4.7	−1.2	Molar	Loc. 2	Between tuffs 5 and 7
148	U. Laetolil Beds	*Loxodonta exoptata*	−3.5	−2.1	Molar	Loc. 3	Between tuffs 6 and 8
150	U. Laetolil Beds	*Loxodonta exoptata*	−4.7	−1.7	Molar	Loc. 6	Between tuffs 5 and 6
151	U. Laetolil Beds	*Loxodonta exoptata*	−3.4	−0.3	Molar	Loc. 11	Above tuff 7
152	U. Laetolil Beds	*Loxodonta exoptata*	0.9	−1.1	Molar	Loc. 10 E	Between tuffs 5 and 7
153	U. Laetolil Beds	*Loxodonta exoptata*	−2.6	−1.6	Molar	Loc. 11	Above tuff 7
23	U. Laetolil Beds	*Deinotherium bozasi*	−11.7	−0.0	Molar	Loc. 10W	Below tuff 3
71	U. Ndolanya Beds	*Loxodonta* cf. *exopatata*	−1.9	−0.3	Molar	Loc. 7E	
146	U. Ndolanya Beds	*Loxodonta* cf. *exoptata*	−4.4	0.9	Molar	Loc. 18	
147	U. Ndolanya Beds	*Loxodonta* cf. *exoptata*	0.2	0.9	Molar	Loc. 7E	
149	U. Ndolanya Beds	*Loxodonta* cf. *exoptata*	−3.1	−0.2	Molar	Loc. 18	
1.4 Family Suidae							
3	U. Laetolil Beds	*Notochoerus euilus*	−3.7	−0.4	Molar, prob. M1	Loc. 8	Between tuffs 5 and 7
5	U. Laetolil Beds	*Notochoerus euilus*	−2.2	−0.9	Molar	Loc. 8	Between tuffs 5 and 7
7	U. Laetolil Beds	*Notochoerus euilus*	−2.7	−1.5	Lower molar	Loc. 2	Between tuffs 5 and 7
8	U. Laetolil Beds	*Notochoerus euilus*	−3.5	−1.0	Premolar	Loc. 2	Between tuffs 5 and 7
10	U. Laetolil Beds	*Notochoerus euilus*	−8.2	−2.4	Molar	Loc. 2	Between tuffs 5 and 7
18	U. Laetolil Beds	*Notochoerus euilus*	−0.1	−1.3	Lower M3	Loc. 3	Between tuffs 6 and 8
22	U. Laetolil Beds	*Notochoerus euilus*	−1.1	1.4	Lower M3	Loc. 10E	Between tuffs 5 and 7
53	U. Laetolil Beds	*Notochoerus euilus*	−1.1	0.0	Molar	Loc. 10E	Between tuffs 5 and 7
54	U. Laetolil Beds	*Notochoerus euilus*	−1.0	−1.3	Molar	Loc. 10	Below tuff 3
55	U. Laetolil Beds	*Notochoerus euilus*	−2.1	−0.1	Molar	Loc. 10	Below tuff 3
154	U. Laetolil Beds	*Notochoerus euilus*	−0.5	−1.7	Molar	Loc. 9 S	Below tuff 2
155	U. Laetolil Beds	*Notochoerus euilus*	−3.4	−0.5	Molar	Loc. 8	Between tuffs 5 and 7
156	U. Laetolil Beds	*Notochoerus euilus*	−4.5	−0.5	Molar	Loc. 5 N of site	Between tuffs 6 and 8
157	U. Laetolil Beds	*Notochoerus euilus*	−0.9	−1.5	Molar	Loc. 2	Between tuffs 5 and 7
158	U. Laetolil Beds	*Notochoerus euilus*	−3.6	−0.3	Molar	Loc. 6	Between tuffs 5 and 6
159	U. Laetolil Beds	*Notochoerus euilus*	−0.5	−0.3	Molar	Loc. 11	Above tuff 7
160	L. Laetolil Beds	*Notochoerus euilus*	−0.4	−1.2	Molar	Kakesio 1–6	
162	U. Laetolil Beds	*Notochoerus euilus*	−0.3	−0.8	Molar	Loc. 10	Below tuff 3
163	U. Laetolil Beds	*Notochoerus euilus*	−5.4	−3.1	Tusk	Loc. 9 S	Below tuff 2
164	U. Laetolil Beds	*Notochoerus euilus*	0.0	0.4	Molar	Loc. 9	Between tuffs 6 and 8
165	U. Laetolil Beds	*Notochoerus euilus*	−2.1	−2.4	Molar	Loc. 5	Between tuffs 3 and 5
166	U. Laetolil Beds	*Notochoerus euilus*	−2.5	0.3	Molar	Loc. 10	Below tuff 3
167	U. Laetolil Beds	*Notochoerus euilus*	−1.3	0.0	Molar	Loc. 10	Below tuff 3
168	U. Laetolil Beds	*Notochoerus euilus*	2.0	−1.6	Molar	Loc. 10W	Below tuff 3
145	U. Ndolanya Beds	*Kolpochoerus limnetes*	−3.7	−1.8	Molar	Loc. 22 S	
P1	Modern	*Phacochoerus africanus*	−1.1	2.1	Lower M3	Laetoli Area	
P2	Modern	*Phacochoerus africanus*	−0.6	2.1	Lower M3	Laetoli Area	
WM901 1	Modern	*Phacochoerus africanus*	−0.76	4.90	Lower M3	Laetoli Area	
WM901 2	Modern	*Phacochoerus africanus*	−1.00	4.22	Lower M3	Laetoli Area	
WM901 3	Modern	*Phacochoerus africanus*	−0.55	3.44	Lower M3	Laetoli Area	
WM901 4	Modern	*Phacochoerus africanus*	−1.03	1.82	Lower M3	Laetoli Area	
WM901 5	Modern	*Phacochoerus africanus*	−0.75	2.11	Lower M3	Laetoli Area	
WM901 6	Modern	*Phacochoerus africanus*	−1.56	2.17	Lower M3	Laetoli Area	
WM901 7	Modern	*Phacochoerus africanus*	−3.11	2.70	Lower M3	Laetoli Area	
WM901 8	Modern	*Phacochoerus africanus*	−3.44	3.05	Lower M3	Laetoli Area	
WM901 9	Modern	*Phacochoerus africanus*	−1.75	3.53	Lower M3	Laetoli Area	
WM901 10	Modern	*Phacochoerus africanus*	−0.93	4.17	Lower M3	Laetoli Area	
1.5 Family Equidae							
133	U. Laetolil Beds	*Eurygnathohippus* sp.	−0.3	0.9	Molar	Loc. 9	Between tuffs 6 and 8
134	U. Laetolil Beds	*Eurygnathohippus* sp.	1.2	2.5	Upper cheek tooth	Loc. 10 W	Below tuff 3
135	L. Laetolil Beds	*Eurygnathohippus* sp.	1.9	3.0	Molar	Kakesio 1–6	

Table 1 (*continued*)

Sample number	Formation	Taxon	$\delta^{13}C_{enamel}$	$\delta^{18}O_{enamel}$	Element	Locality	Stratigraphic level
1.5 Family Equidae							
136	U. Laetolil Beds	*Eurygnathohippus* sp.	−0.4	0.3	Upper molar	Loc. 5 N of site	Between tuffs 6 and 8
137	U. Laetolil Beds	*Eurygnathohippus* sp.	−4.1	−1.3	Molar	Loc. 11	Above tuff 7
139	U. Laetolil Beds	*Eurygnathohippus* sp.	0.5	0.3	Lower cheek tooth	Loc. 10 E	Between tuffs 5 and 7
140	U. Laetolil Beds	*Eurygnathohippus* sp.	1.0	0.0	Molar	Loc. 7	Above tuff 7
56	U. Laetolil Beds	*Eurygnathohippus* sp.	−0.3	−1.5	Lower molar	Loc. 10	Below tuff 3
57	U. Laetolil Beds	*Eurygnathohippus* sp.	−3.8	−0.5	Lower molar	Loc. 10E	Between tuffs 5 and 7
58	U. Laetolil Beds	*Eurygnathohippus* sp.	−3.3	−1.8	Lower molar	Loc. 10E	Between tuffs 5 and 7
132	U. Ndolanya Beds	*Eurygnathohippus* cf. *ethiopicum*	0.4	−2.0	Lower molar	Loc. 18	
138	U. Ndolanya Beds	*Eurygnathohippus* cf. *ethiopicum*	−0.7	0.4	Molar	Loc. 7E	
69	U. Ndolanya Beds	*Eurygnathohippus* cf. *ethiopicum*	0.3	1.3	Upper molar	Loc. 18	
70	U. Ndolanya Beds	*Eurygnathohippus* cf. *ethiopicum*	0.5	−2.2	Upper molar	Loc. 15	
EQ14	Modern	*Equus burchelli*	−1.4	−2.0	Upper molar	Laetoli Area	
EQ15	Modern	*Equus burchelli*	−1.1	−1.7	Upper molar	Laetoli Area	
1.6 Family Bovidae							
14	U. Laetolil Beds	*Gazella janenschi*	−4.0	0.6	Upper M2	Loc. 13	Between tuffs 6 and 8
20	U. Laetolil Beds	*Gazella janenschi*	−8.0	−0.1	Upper M2	Loc. 10 E	Between tuffs 5 and 7
34	U. Laetolil Beds	*Gazella janenschi*	−5.5	0.3	Upper M2	Loc. 10 E	Between tuffs 6 and 7
40	U. Laetolil Beds	*Gazella janenschi*	−9.2	2.5	Lower molar	Loc. 10 W	Below tuff 3
47	U. Laetolil Beds	*Gazella janenschi*	−6.4	−1.3	Upper M3	Loc. 10	Below tuff 3
120	U. Laetolil Beds	*Gazella janenschi*	−4.6	−2.0	Upper molar	Loc. 2	Between tuffs 5 and 7
121	U. Laetolil Beds	*Gazella janenschi*	−9.8	−0.2	Lower M3	Loc. 2	Between tuffs 3 and 5
122	U. Laetolil Beds	*Gazella janenschi*	−9.4	0.0	Lower M2	Loc. 8	Between tuffs 5 and 6
123	U. Laetolil Beds	*Gazella janenschi*	−1.9	4.5	Upper molar	Loc. 15	Between tuffs 6 and 8
76	U. Ndolanya Beds	*Gazella janenschi*	−7.8	−2.0	Upper M2	Loc. 18	
13	U. Laetolil Beds	*Parmularius pandatus*	−8.6	−2.0	Upper molar	Loc. 1	Between tuffs 6 and 8
19	U. Laetolil Beds	*Parmularius pandatus*	−3.1	−0.9	Upper M1	Loc. 10 E	Between tuffs 5 and 7
33	U. Laetolil Beds	*Parmularius pandatus*	−3.8	−0.8	Lower M3	Loc. 10 E	Between tuffs 6 and 7
39	U. Laetolil Beds	*Parmularius pandatus*	−2.2	−0.4	Lower M2	Loc. 10 W	Below tuff 3
42	U. Laetolil Beds	*Parmularius pandatus*	−2.6	0.3	Upper M1	Loc.10W	Below tuff 3
43	U. Laetolil Beds	*Parmularius pandatus*	−0.4	−1.6	Lower M2	Loc. 10W	Below tuff 3
46	U. Laetolil Beds	*Parmularius pandatus*	−1.1	−0.2	Upper molar	Loc. 10	Below tuff 3
9	U. Laetolil Beds	*Parmularius pandatus*	−0.0	3.1	Lower M3	Loc. 2	Between tuffs 5 and 7
31	U. Laetolil Beds	Alcelaphini sp.	−0.1	1.5	Upper molar	Loc. 10 E	Between tuffs 6 and 7
74	U. Ndolanya Beds	Alcelaphini, medium sp.	1.1	−0.4	Lower M3	Loc. 18	
73	U. Ndolanya Beds	Alcelaphini, large sp.	0.6	1.0	Lower M2	Loc. 18	
12	U. Laetolil Beds	Hippotragini sp.	−9.1	1.7	Upper molar	Loc. 1	Between tuffs 6 and 8
21	U. Laetolil Beds	Hippotragini sp.	−5.0	0.7	Lower molar	Loc. 10E	Between tuffs 5 and 7
35	U. Laetolil Beds	Hippotragini sp.	−4.0	2.3	Upper molar	Loc. 10 E	Between tuffs 6 and 7
36	U. Laetolil Beds	Hippotragini sp.	−7.5	2.8	Upper M1	Loc. 10 E	Between tuffs 6 and 7
45	U. Laetolil Beds	Hippotragini sp.	−2.3	2.7	Upper M3	Loc. 10 W	Below tuff 3
141	U. Laetolil Beds	Hippotragini sp.	−4.9	1.3	Upper molar	Loc. 21	Between tuffs 5 and 8
142	U. Laetolil Beds	Hippotragini sp.	−7.7	1.5	Upper molar	Loc. 21	Between tuffs 5 and 8
143	U. Laetolil Beds	Hippotragini sp.	−6.2	1.9	Upper molar	Loc. 8	Between tuffs 5 and 8
38	U. Laetolil Beds	*Madoqua avifluminis*	−6.4	−2.7	Upper molar	Loc. 10	Below tuff 3
41	U. Laetolil Beds	*Madoqua avifluminis*	−10.6	1.6	Upper M3	Loc 10 W	Below tuff 3
48	U. Laetolil Beds	*Madoqua avifluminis*	−7.3	−1.8	Lower molar	Loc. 10 E	Between tuffs 5 and 7
32	U. Laetolil Beds	*Tragelaphus sp.*	−8.1	−2.5	Upper M2	Loc. 10 E	Between tuffs 6 and 7
37	U. Laetolil Beds	*Tragelaphus sp.*	−7.9	−2.1	Upper M3	Loc. 10	Below tuff 3
44	U. Laetolil Beds	*Tragelaphus sp.*	−8.2	2.9	Upper M1	Loc. 10 W	Below tuff 3
177	U. Laetolil Beds	*Tragelaphus sp.*	−11.8	−2.2	Upper molar	Loc. 21	Between tuffs 5 and 8
Md64	Modern	*Madoqua kirkii*	−11.1	−2.2	Lower M3	Laetoli Area	

vegetation types in past ecosystems, characterizing habitat heterogeneity in space and time, revealing dietary niche partitioning in fossil terrestrial communities, and correlating climatic perturbations and oscillations in terrestrial ecosystems. Much of this research has focused on analyses of the carbonate fraction of bioapatite in tooth enamel that reflects overall dietary patterns and prevailing climatic conditions. Empirical data, as well as theoretical models, indicate that enamel apatite retains the original *in vivo* biogenic signal, unaffected by the fossilization processes (Wang and Cerling, 1994; Koch et al., 1997; Kohn et al., 1999; Sponheimer and Lee-Thorp, 1999b; Lee-Thorp, 2000; Lee-Thorp and Sponheimer, 2003). As yet, no clear criteria have been developed to assess the extent of diagenetic alteration in fossil enamel. Perhaps the most convincing evidence for minimal alteration is that the distinct isotopic offset between grazers and browsers documented in modern ecosystems is maintained in the fossil assemblages. For example, in the Laetoli fossil data, the giraffid and deinothere enamel yielded distinct browsing isotopic signatures while the equids and alcelaphines have carbon isotopic values more consistent with grazing. These differences range up to 12–13‰ for enamel fragments collected from the same sedimentary horizons, similar to modern ranges. The dietary signal is incorporated into bioapatite as the enamel is forming and there is no subsequent physiological turnover. It therefore provides a proxy for diet during the interval in which teeth are mineralizing.

3.2. Carbon

The stable carbon isotopic composition ($\delta^{13}C$) of modern and fossil herbivore tooth enamel is directly related to the isotopic composition of primary plants in the food chain (DeNiro and Epstein, 1978; Tiezsen et al., 1983; Ambrose and DeNiro, 1986; Cerling and Harris, 1999). Terrestrial plants using different photosynthetic pathways under varying environmental conditions can be differentiated on the basis of the relative abundance of two naturally occurring stable isotopes of carbon, ^{12}C and ^{13}C. These isotopic distinctions in plant physiology are transferred to herbivore tissue that can then be analyzed to reveal dominant dietary sources.

In African ecosystems the C_3 photosynthetic pathway is characteristic of most trees and shrubs, as well as high altitude grasses that prefer wet, cool growing seasons. The tissues of C_3 plants have $\delta^{13}C$ values that range from about −22‰ to 36‰ with a mean of −27.1‰ ± 2.0‰ (Deines, 1980; O'Leary, 1981; Farquhar et al., 1989; Cerling et al., 2003a). Isotopic variability in C_3 plants reflects genetic and environmental factors, such as water stress, nutrient availability, light intensity, CO_2 partial pressure, and temperature (Farquhar et al., 1982; Tieszen, 1991; Heaton, 1999). Overall, there tends to be an increase in the amount of ^{13}C in C_3 plants from wet to mesic and xeric habitats and the $\delta^{13}C$ value of C_3 plants tends to be least negative in open, arid, and hot habitats and most negative in cool, moist, forested environments. In closed canopy understories where free exchange with atmospheric CO_2 is restricted and light conditions are low, $\delta^{13}C$ values can be very negative (<30‰)(Medina and Minchin, 1980; Sternberg et al., 1989; van der Merwe and Medina, 1989). As altitude increases, leaf carbon isotope discrimination (Δ) decreases, resulting in more positive $\delta^{13}C$ values for C_3 plants at higher elevations (Tieszen et al., 1979b; Korner et al., 1991; Sparks and Ehleringer, 1997).

C_4 physiology is linked almost exclusively to monocotyledons, especially grasses and sedges growing in hot, arid habitats. A mean $\delta^{13}C$ value of −13.1‰ ± 1.2‰ has been calculated for C_4 plants with a range of about −14 to −11‰ (O'Leary, 1988; Heaton, 1999; Cerling et al., 2003a). There are several C_4 subtypes distinguished on the basis of biochemical pathways and anatomy that contribute to the variability. Three subpathways are dominant in East African grasses — arid adapted C_4 species that utilize the NAD-me and PEP-ck subpathways (Hattersley, 1992; Chapman, 1996) with an average $\delta^{13}C$ value of about −13.0 ± 0.7‰ (Cerling et al., 2003a), and classical-NADP subpathway grasses that are found in more mesic environments, such as riparian or lake margin settings, with an average $\delta^{13}C$ of −11.8 ± 0.2‰ (Cerling et al., 2003a).

This general distinction between grasses and other plants based on isotopic analyses is ideal for differentiating broad dietary strategies, such as browser, grazers or mixed feeders, based on semi-quantitative assessments of relative proportions of dietary C_4 and C_3 plants. While this rather coarse-grained approach cannot resolve specific aspects of the type of browse, such as leaves, fruit, or seeds, its strength lies in the unambiguous distinction between gross feeding strategies. Plants that fix CO_2 by the CAM (Crassulacian acid metabolism) pathway, C_3–C_4 intermediates, and C_4 dicots potentially complicate this dichotomy, but it is unlikely that these plants comprised a significant component of the equatorial African biomass during the Pliocene.

3.3. Oxygen

The oxygen isotopic composition ($\delta^{18}O$) of vertebrate tooth enamel has also been used to reconstruct different aspects of diet and climate. The $\delta^{18}O$ of oxygen in enamel apatite is directly related to that of the body water, which is a complex function of climate, diet, and physiology (Longinelli, 1984; Luz and Kolodny, 1985; Koch et al., 1989; Kohn, 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999a). The $\delta^{18}O$ of the body water is chiefly determined by the $\delta^{18}O$ of drinking water (which is linked to local temperature of precipitation, latitude, altitude, aridity, and evaporative processes), the $\delta^{18}O$ of water in ingested foods, behavioral and physiological water conservation mechanisms, and the $\delta^{18}O$ of metabolic and atmospheric oxygen. Despite the complexity of oxygen flux in terrestrial herbivores, some general patterns and principles are beginning to emerge: (1) drinking behavior has a dominant effect on $\delta^{18}O$ values of mammals; (2) obligate-drinking herbivores track $\delta^{18}O$ of meteoric water most faithfully, whereas $\delta^{18}O$ values of drought-tolerant animals that obtain most of their water from food track humidity (Kohn et al., 1996); (3) aquatic taxa, such as hippopotamuses, are significantly depleted in ^{18}O relative to other herbivores; (4) in some habitats there is a positive correlation between oxygen and carbon isotopic compositions (Koch et al., 1991; Kohn et al., 1996) reflecting ^{18}O enrichment in C_4 plants relative to C_3 vegetation, (5) although obligate browsers, such as giraffes, tend to be relatively ^{18}O-enriched in some ecosystems (Kohn et al., 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999a,b,c), the opposite trend has also been documented (Bocherens et al., 1996: Schoeninger et al., 2001), and (6) carnivores are depleted in ^{18}O relative to herbivores (Sponheimer and

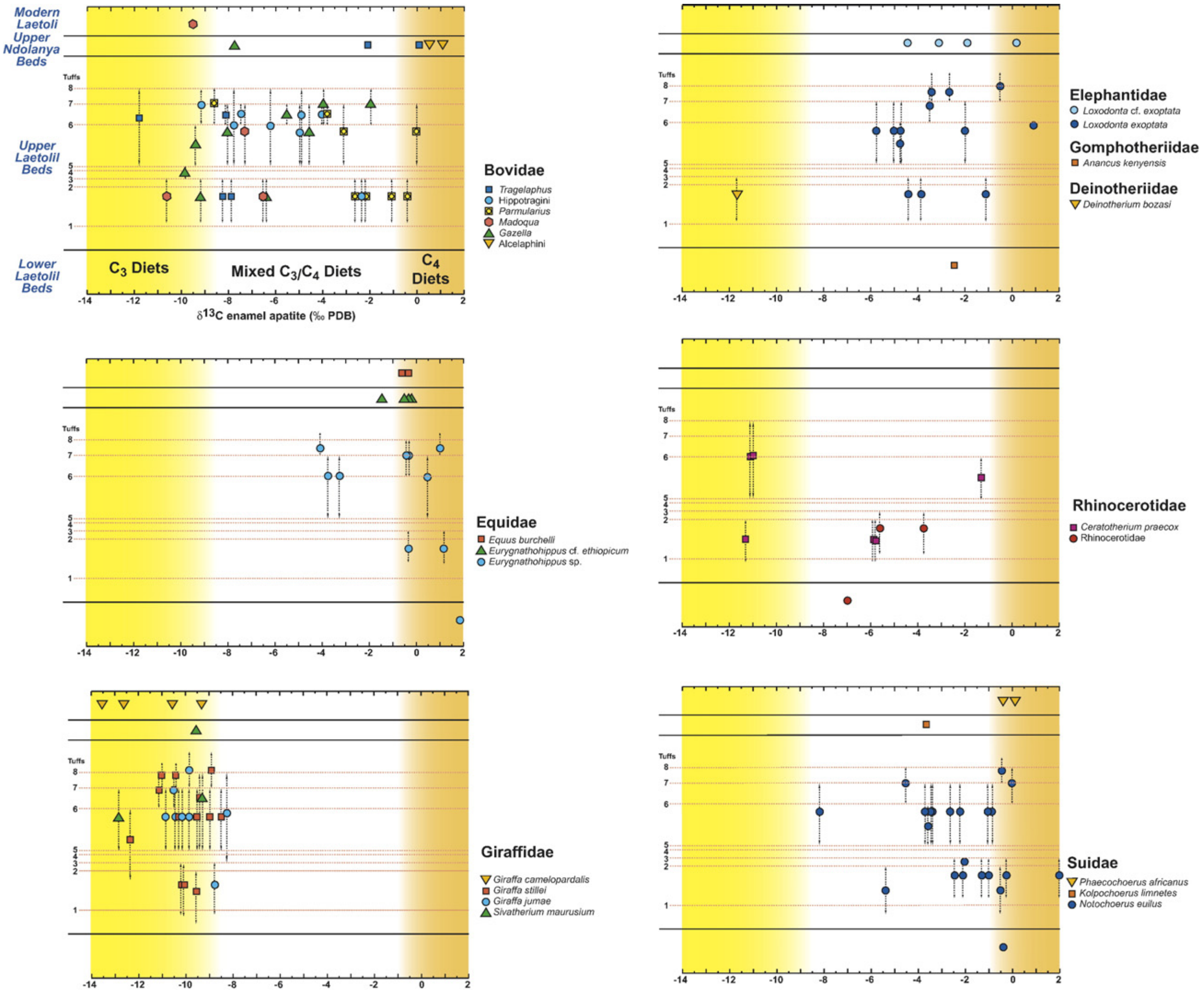

Fig. 3. Stable carbon isotopic composition ($\delta^{13}C_{enamel}$) of herbivore enamel from Laetoli relative to stratigraphy. Vertical arrows depict the stratigraphic range to which each sample can be constrained.

Lee-Thorp, 1999a,b,c). δ^{18}O values of different teeth in a single jaw and of different chronologic positions within a single tooth have been shown to vary systematically in modern herbivores, reflecting source variability related to seasonal shifts in the isotopic composition of precipitation and vegetation, seasonal shifts in diet, seasonal migrations, and humidity recorded during the lifetime of the animal (Koch et al., 1989; Kohn et al., 1996; Bryant et al., 1996; Fricke et al., 1998; Sharp and Cerling, 1998; Gadbury et al., 2000).

4. Methods

Fossil enamel fragments were collected in the course of field prospecting during the 2000 and 2001 field seasons with an effort to provide taxonomic identification coupled with specific stratigraphic provenance. As most of the fossil material was surface collected rather than excavated directly from the sediments, each enamel fragment is associated with a narrow stratigraphic range based on the relationship of the fossil find to specific site stratigraphy and

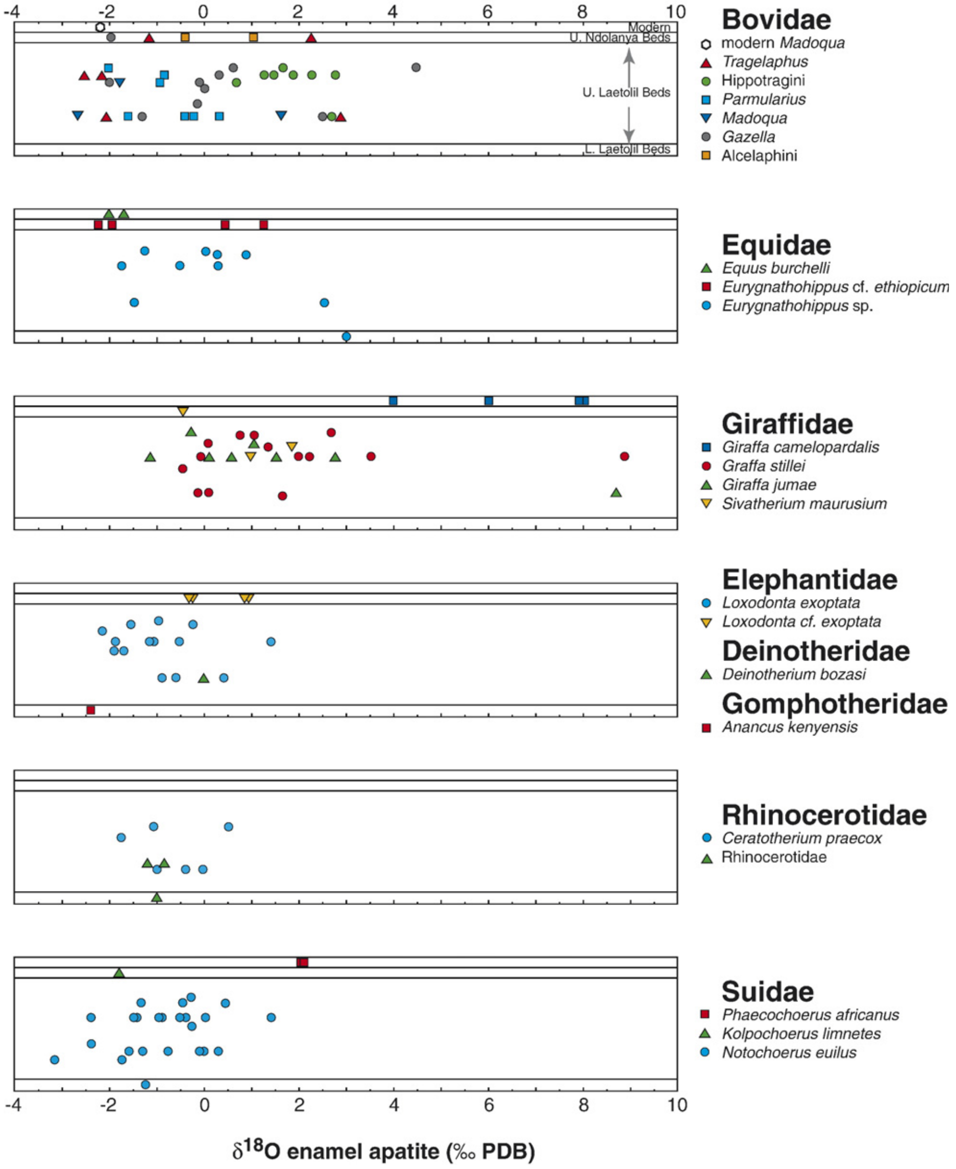

Fig. 4. Stable oxygen isotopic composition ($\delta^{18}O_{enamel}$) of herbivore enamel from the Laetoli Succession. Vertical placement of data points reflects relative stratigraphic position as shown.

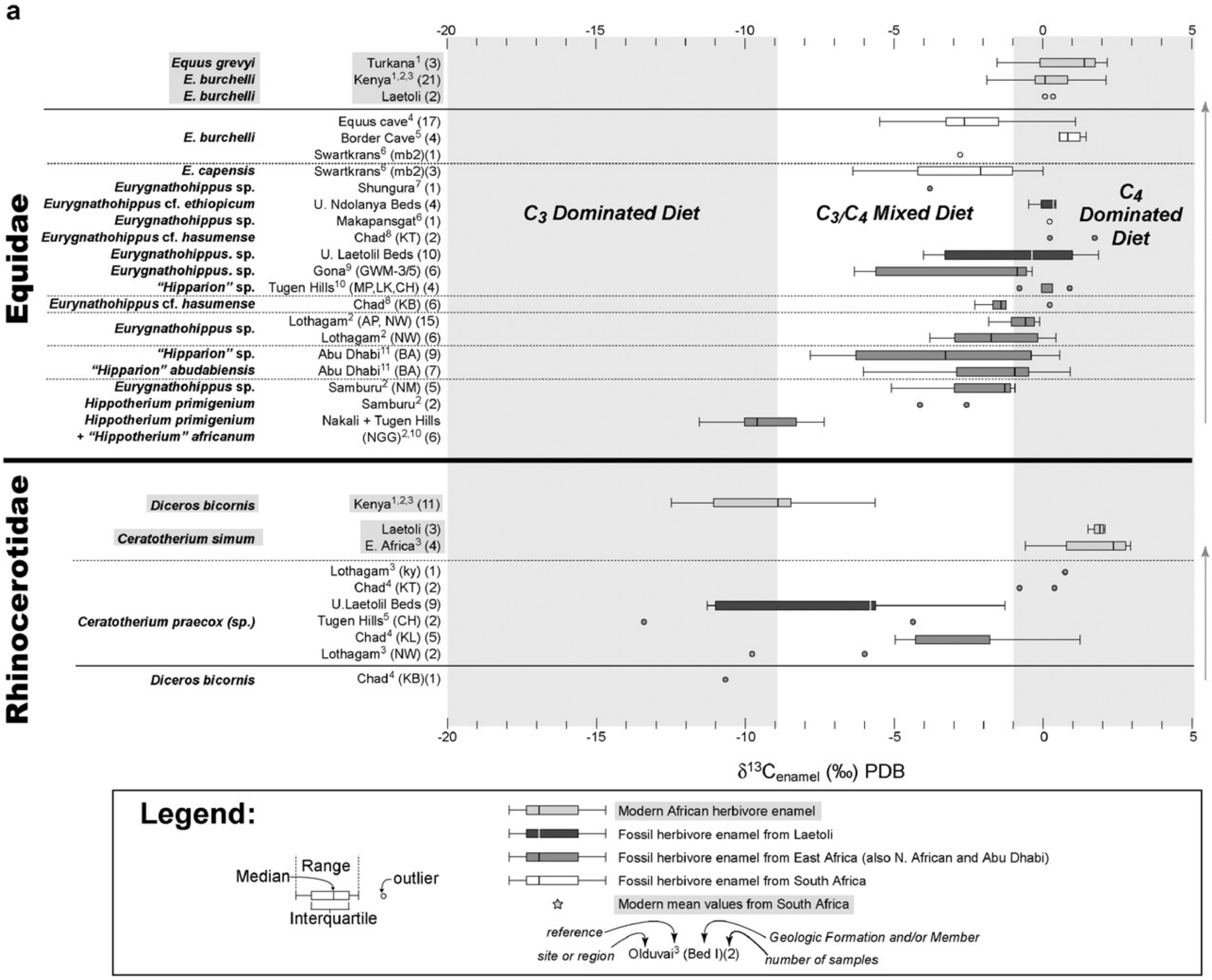

Fig. 5. a–c. Box and whiskers plots of $\delta^{13}C_{enamel}$ of Laetoli material and relevant fossil and modern enamel samples. Each box encloses 50% of the data with the median value of the variable indicated by a vertical line in the box. The sides of the box mark the limits of ±25% of the variable population. The lines extending from the sides of each box mark the minimum and maximum values within the data set that fall within an acceptable range. Outliers are displayed as individual points. Modern African samples, fossil Laetoli material, South African fossil, and other fossil data are differentiated as indicated in the key. Where appropriate, taxa within family groups are arranged temporally, with younger samples above. Numbers in parenthesis after site location represent number of samples analyzed. All modern samples are shifted +1.5‰ as discussed in the text. Abbreviations: *Turkana Basin* (*Lothagam, Samburu, Kanapoi, Koobi Fora*) [NC = Nachukui Fm.; NW = Nawata Fm.; NM = Namurungule Fm.; KF = Koobi Fora Fm.; ok = Okote Member, Koobi Fora Fm.; kbs = KBS Member, Koobi Fora Fm.; ub = Upper Burgi Member, Koobi Fora Fm.; tb = Tulu Bor Member, Koobi Fora Fm.; l = Lokochot Member, Koobi Fora Fm.; ky = Kaiymung Member, Nachukui Fm.] *Chad* [KB = Kossom Bougoudi unit; KL = Kollé unit; KT = Koro Toro unit] *Tugen Hills* [CH = Chemeron Fm.; LU = Lukeino Fm.; MP = Mpesida Fm.; NGG = Ngeringerowa Beds, Ngorora Fm.] *Gona* [GWM-3/5 = Gona Western Margin block 3 and 5 sites] *Abu Dhabi* [BA = Baynunah Fm.] *Sterkfontein and Swartkrans* [mb1–6 = members 1–6]. References: *Proboscidea* [[1](Cerling et al., 1999), [2](Bocherens et al., 1996), [3](Zazzo et al., 2000), [4](Semaw et al., 2005), [5](Schoeninger et al., 2003)] *Rhinocerotidae* [[1](Cerling and Harris, 1999), [2](Bocherens et al., 1996), [3](Cerling et al., 2003a,b), [4](Zazzo et al., 2000), [5](Kingston, 1992)] *Suidae* [[1](Harris and Cerling, 2002), [2](Bocherens et al., 1996), [3](Plummer et al., 1999), [4](Zazzo et al., 2000), [5](Lee-Thorp, 1989)] *Giraffidae* [[1](Cerling and Harris, 1999), [2](Lee-Thorp, 1989), [3](Semaw et al., 2005), [4](Zazzo et al., 2000)] *Equidae* [[1](Cerling et al., 2003a), [2](Cerling et al., 2003b), [3](Bocherens et al., 1996), [4](Sponheimer and Lee-Thorp, 1999a,b,c), [5](Lee-Thorp, 1989), [6](Lee-Thorp et al., 1994), [7](Ericson et al., 1981), [8](Zazzo et al., 2000), [9](Semaw et al., 2005), [10](Kingston, 1992), [11](Kingston, 1999b)] *Bovidae* [[1](Cerling et al., 2003c), [2](Lee-Thorp et al., 2000), [3](van der Merwe et al., 2003), [4](Sponheimer et al., 1999), [5](Zazzo et al., 2000), [6](Semaw et al., 2005), [7](Cerling et al., 2003b), [8](Lee-Thorp, 1989), [9](Lee-Thorp et al., 1994), [10](van der Merwe and Thackeray, 1997), [11](Plummer et al., 1999), [12](Lee-Thorp and van der Merwe, 1993), [13](Sponheimer et al., 2003)].

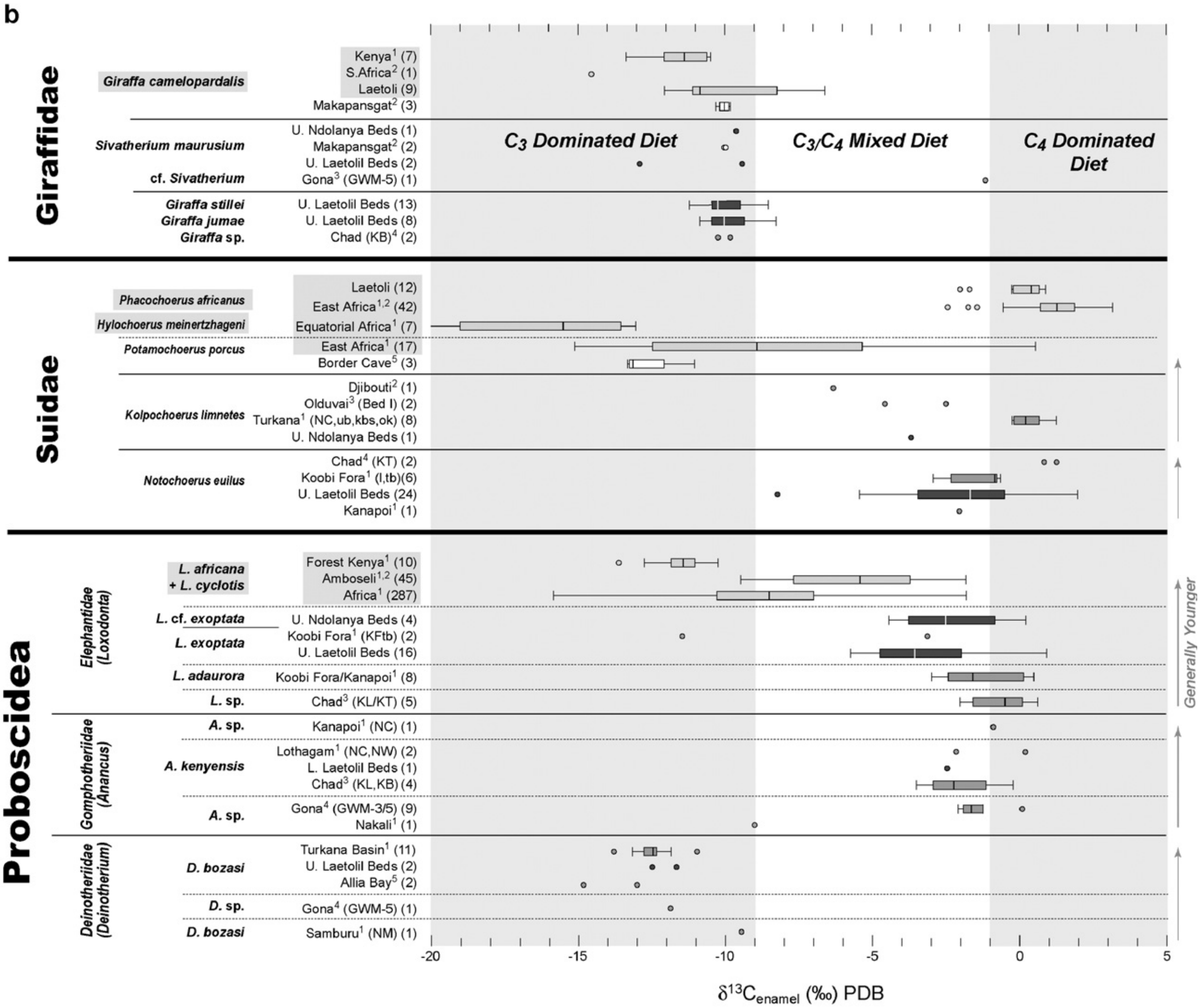

Fig. 5 (*continued*).

topography rather than a discrete horizon (Table 1). In almost all cases, molar enamel (especially third molars) was analyzed, limiting the potentially confounding effects of weaning or juvenile dietary signals present in teeth forming during this developmental stage. Although small amounts of enamel (3–20 mg) were ultimately analyzed for each tooth, large sections of the fragments (50–100 mg) were homogenized during preparation to average out intra-tooth isotopic variability. Isotopic analyses in this study focused on the carbonate in enamel bioapatite.

Enamel was carefully cleaned of adhering sediment, dentine, and weathering rinds with a high speed Dremel drilling tool with tungsten–carbide bits, and then ground in an agate mortar. Powdered enamel was reacted for 24 h with ∼2% NaOHCl in 15 ml plastic centrifuge tubes to digest any organic material and then rinsed to a pH of 7 by centrifugation with double distilled water. Residue was treated with 0.1 M CH_3COOH for 16 h under a weak vacuum to remove any secondary carbonate, rinsed to neutrality by centrifugation with double distilled water, and freeze dried. 30–20 mg of the dried samples were reacted with 100‰ phosphoric acid (H_3PO_4) at 90 °C in sealed borosilicate reaction y-tubes for 48 h. The liberated carbon dioxide was cleaned, separated cryogenically into 6 mm sealed tubes with silver wire, and sealed. The sealed tubes with the CO_2 and silver were heated to 50 °C to remove impurities, such as SO_2 or H_2S, that could contribute interfering masses. Mass spectrometry was performed at Yale Stable Isotope Laboratory using a MAT-Finnegan 251 mass spectrometer interfaced with a tubecracker and

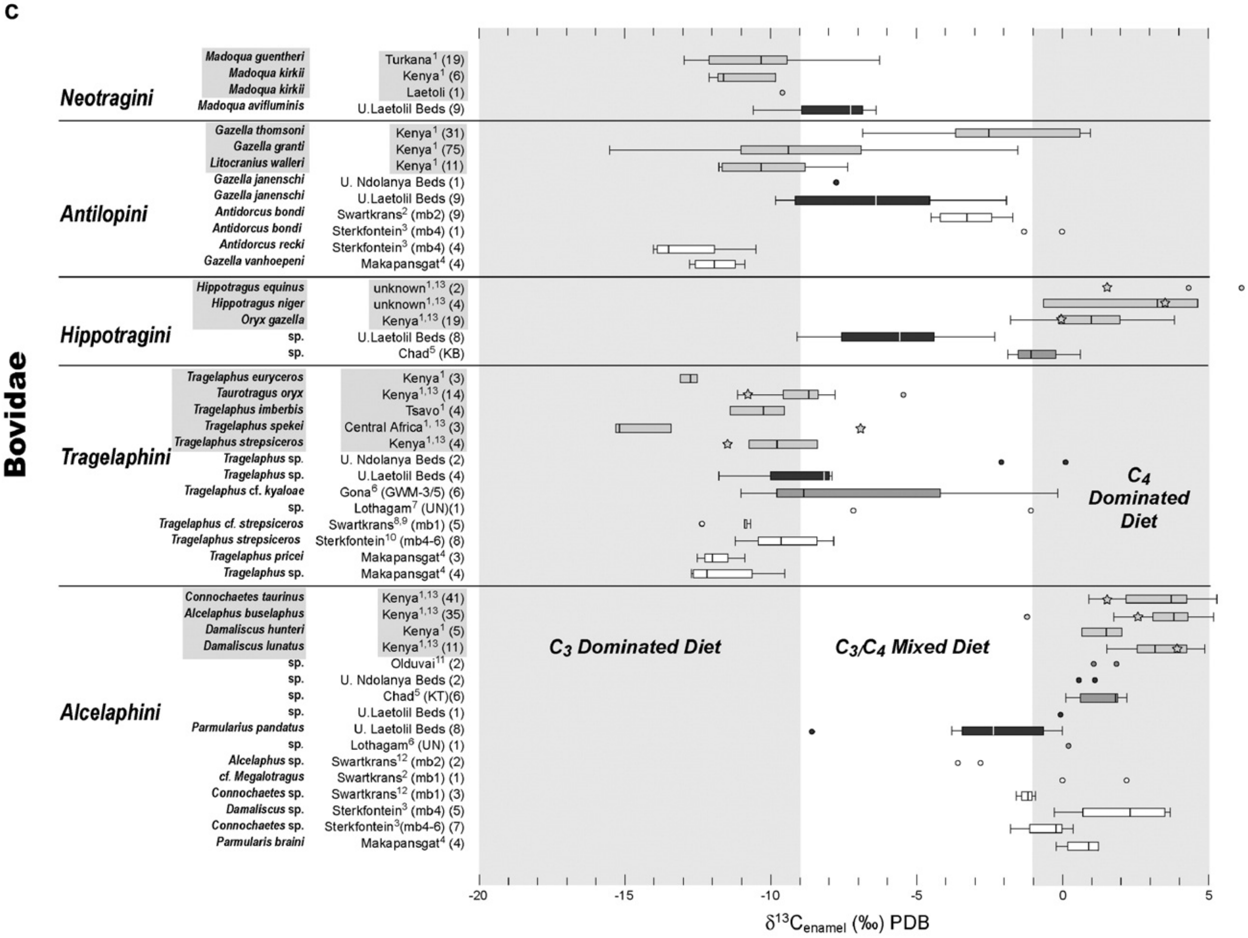

Fig. 5 (*continued*).

at the University of Florida, Department of Geoscience Stable Isotope Lab using a VG Prism 602 also interfaced with a tubecracker. Once it was established that SO_2 or H_2S was not being generated during digestion in the phosphoric acid, samples were analyzed online using a Mountain Mass multi-prep system interfaced with the VG Prism. Results are reported using the standard ‰ notation where:

$$\delta^{13}C = (^{18}\mathrm{O}) = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000$$
$$R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C} \text{ or } {}^{18}\mathrm{O}/{}^{16}\mathrm{O}$$

Carbon and oxygen values are reported relative to PDB (Pee Dee Belemnite). Precision was ±0.09‰ for δ^{13}C ratios and ±0.17‰ for δ^{18}O ratios for eight replicate pairs of fossil enamel. International and in-house laboratory standards analyzed with the enamel samples at both facilities utilizing the two techniques yielded a standard deviation of ±0.05‰ ($n=36$) for C and ±0.11 for O ($n=36$). Based on these data, overall analytical precision was better than 0.10‰ for C and 0.22‰ for O.

5. Results and interpretation

5.1. General

Over 160 representative enamel samples of 21 herbivore taxa, almost all identified to species, were analyzed isotopically from multiple stratigraphic horizons within the Laetoli succession (Table 1, Figs. 3–5). Feeding guilds are differentiated primarily on the basis of ™^{13}C variation in the enamel. Specific assessments of the relative dietary intake of C_3 or C_4 biomass rely on boundary conditions contingent on variation in C_3 and C_4 plants due to environmental factors, physiological fractionation as dietary carbon incorporated into the enamel crystals (estimates range from +9.5‰ to +15‰ relative to diet), and changes in atmospheric $p\mathrm{CO}_2$ and δ^{13}C values. These variables are not necessarily constant across habitats,

Table 2
Dietary classification with $\delta^{13}C$ ranges based on mixing model

Dietary classification	General foraging strategy[a]	Approximate modern $\delta^{13}C$ range	+1.5‰ adjusted pre-industrial fossil $\delta^{13}C$ range[b]
Obligate grazer	Almost exclusively monocots (>95%)	>0.5‰	>2‰
Variable grazer	Predominance of monocots (75–95%) but with seasonal, geographic, or ecological variability in C_3 dicot consumption	0.5 to −2.5‰	2 to −1‰
Browser–grazer intermediate	Mixed diets characterized by intermediate proportions of dicots and monocots	−2.5 to −9.5‰	−1 to −8‰
Variable browser	Predominance of dicots (75–95%) with seasonal, geographic or ecological variability in C_4 monocot consumption	−9.5 to −12.3‰	−8 to −10.8‰
Obligate browser	Almost exclusively dicots (>95% C_3 dicots)	<−12.3‰	<−10.8‰

[a] Categories based on discussions of East African herbivore foraging strategies in Tieszen et al. (1979a,b), McNaughton and Georgiadis (1986), and Gagnon and Chew (2000).

[b] All modern enamel data is converted to this range to facilitate comparisons in Fig. 5.

across taxa with different digestive physiology, or through evolutionary time. As a result it is difficult to attribute specific proportions of C_3/C_4 dietary input based on carbon isotopic values of herbivore enamel. Despite these caveats, isotopic analyses of modern large-bodied herbivores in Africa consistently indicate that browsers have $\delta^{13}C_{enamel}$ values less than about −8‰ to −10‰ and grazers typically greater than −2‰ to 1‰ (Bocherens et al., 1996; Harris and Cerling, 2002; Cerling et al., 2003a; Sponheimer et al., 2003). Assuming an isotopic enrichment factor of 14.1‰ for tooth enamel relative to diet and C_3 and C_4 endmembers of −25.6±2.0‰ and −13.1±1.2‰ respectively (incorporating +1.5‰ correction for post-industrial ^{13}C depletion), a mixing model for C_3–C_4 biomass estimates is used to distinguish general herbivore foraging strategies (Table 2). Where dietary signals of modern and fossil enamel samples are compared (e.g., Figs. 3 and 5), +1.5‰ is added to modern enamel values to correct for depletion of ambient atmospheric $\delta^{13}C$ relative to pre-industrial value (Marino and McElroy, 1991).

In general, $\delta^{13}C_{\text{ enamel}}$ results from Laetoli indicate significant variation in diet between and within some of the fossil taxa (Fig. 3). Giraffids yield signals indicating essentially obligate browsing and the equids are variable to obligate grazers, but all other taxa indicate varying degrees of mixed C_3/C_4 feeding strategies. In the context of this variability, there are no clear dietary trends or patterns within the Laetolil Beds reflecting differential availability of browse or grass through time. Instead, these data indicate long-term, relative ecological stability locally and possibly regionally. The documented ranges of feeding strategies indicate a heterogeneous vegetation, that probably included grasslands, open woodlands, more closed woodlands, and possibly forest. This general interpretation is supported by recent preliminary reassessments of the fauna and flora from the succession (Su and Harrison, 2003; Bamford and Harrison, 2004; Harrison and Su, 2004; Su, 2005).

Oxygen isotope signatures of fossil mammals from Laetoli also show no apparent patterns through the succession (Fig. 4). The general range of inter- and intra-specific $\delta^{18}O_{enamel}$ variability in the Laetoli assemblage is consistent with that documented in other African fossil assemblages as well as modern herbivore populations (Fig. 6) (Lee-Thorp, 1989; Bocherens et al., 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999a; Clementz and Koch, 2001; Harris and Cerling, 2002; Cerling et al., 2003a,b,c, 2004; this study). The Laetoli oxygen data further support the notion of relative long-term environmental stability through the sequence, although the data do not necessarily preclude the possibility of short-term ecological shifts. Comparison of the Laetoli fossil data with relevant East and Central African fossil reveal a pattern of ^{18}O depletion in the fossil material relative to potential descendent extant taxa in several of the lineages (Fig. 6). Fossil suids, giraffids, rhinocerotids, and to an extent equids from the Laetoli sequence are all significantly more depleted in ^{18}O compared to modern equatorial assemblages, possibly indicating more humid conditions at Laetoli during deposition of the sequence. Simple comparisons of $\delta^{18}O_{enamel}$ values between geographically and temporally distinct assemblages, however, are complicated by the great diversity in behaviors and local conditions controlling $\delta^{18}O$ (summarized in Fig. 6).

An additional goal of this study was to compare and contrast isotopic herbivore signatures from the Upper Laetolil and Upper Ndolanya Beds. The transition between these units is represented by a sedimentary hiatus spanning about 1 Ma. During this interval there was a taxonomic turnover in the mammalian fauna, in which more than one third of the species make their initial appearance, including *Paranthropus aethiopicus*

(Harrison, 2002). Assessments of mammalian fauna (Leakey and Harris, 1987; Kovarovic et al., 2002; Harrison and Su, 2004) suggest more arid and open conditions during Upper Ndolanya times relative to earlier intervals. Within the range of variability, isotopic data do not unequivocally document such a transition to more arid, seasonal, and open habitats. However, the comparison is compromised by relatively few data from limited taxa sampled within the Upper Ndolanya Beds. The foraging strategies of taxa recovered from both formations, such as loxodont elephants (mixed feeding with emphasis on grazing), hipparionine equids (grazing), and sivatheres (browsing), remain consistent across this transition, but it is conceivable that these taxa would not shift diets as long as components of their preferred microhabitats persisted. Evidence for dietary and ecological change is possibly provided by data from the bovids, which suggest a transition from mixed C_3/C_4 diets and exclusive browsing to grazing in the tragelaphines. In addition, alcelaphines from the Upper Ndolanya Beds yielded the most positive $\delta^{13}C_{enamel}$ signatures for the bovids, indicating a diet of pure C_4 graze.

A key aspect of interpreting the Laetoli isotopic data is an evaluation of isotopic enamel signals derived from other modern and fossil herbivore assemblages (Figs. 5a,b,c, 6). Studies utilized in this comparison were limited to published tooth enamel isotopic data sets that included the same species or closely related forms to those found at Laetoli. These included all Pliocene or Late Miocene assemblages from Afro-Arabia. Some sites where fossil herbivores have been analyzed isotopically, such as Langebaanweg (Franz-Odendaal et al., 2002) and Elandsfontein (Luyt et al., 2000) in

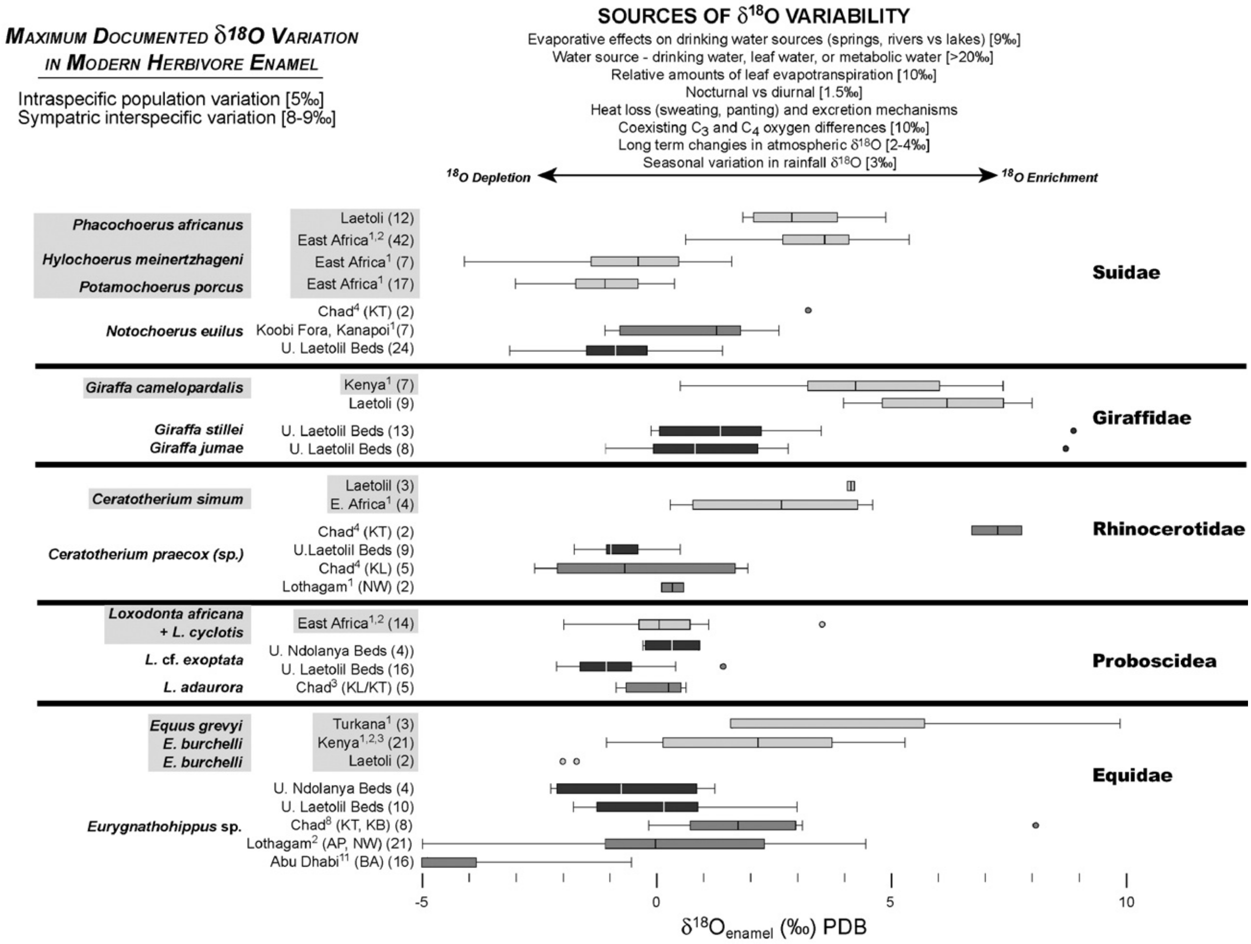

Fig. 6. Box and whiskers plots of $\delta^{18}O_{enamel}$ of Laetoli material and relevant fossil and modern enamel samples. Legend and references as in Fig. 5. Where appropriate, taxa within family groups are arranged temporally, with younger samples above. Included above are a number of factors that influence the oxygen isotopic composition of herbivore enamel. Permil (‰) values in brackets following the sources of $\delta^{18}O$ variability indicate some of the maximum ranges currently documented for these variables in modern African ecosystems (where known).

Table 3
Statistical analyses of isotopic data of Laetoli fossil and modern African herbivores

Fossil and modern taxa/populations compared		$\delta^{13}C$			$\delta^{18}O$
		Sampled randomization test[a]	Two-sample Kolmogorov–Smirnov test	Mann–Whitney test	Mann–Whitney test
Eurygnathohippus (Upper Laetolil Beds) *N*=10, range=6‰	*Equus burchelli* (modern) 6 sites, Kenya, *N*=22, range=4.5‰	0.065	0.019	0.002	0.056
	Amboseli, Kenya (modern) N=7, Range=3.5‰	0.204	0.089	0.025	0.315
Ceratotherium praecox (Upper Laetolil Beds) *N*=9, range=10‰	*Ceratotherium simum* (modern) 4 sites, Kenya, Tanzania+Sudan, *N*=7, range=3.5‰	0.140	0.001	0.001	0.001
	Laetoli, Tanzania (modern) *N*=3, range=0.5‰	0.102	0.022	0.009	0.009
Notochoerus euilus (Upper Laetolil Beds) *N*=24, range=10.3‰	*Phacochoerus africanus* (modern) 13 Sites, 5 eq. Africa countries, *N*=52, range=5.6‰	0.004	<0.001	<0.001	<0.001
	Nakuru, Kenya, *N*=10, range=2.5‰	0.000	<0.001	<0.001	<0.001
	Laetoli, TZ, *N*=12, range=2.9‰	0.001	0.001	0.001	<0.001
Giraffa stillei (Upper Laetolil Beds) *N*=13, range=3.9‰	*Giraffa camelopardalis* (modern) 8 sites, East Africa, *N*=15, range=6.2‰	0.169	0.059	0.170	<0.001
	Laetoli, *N*=9, range=5.5‰	0.340	0.489	0.804	<0.001

[a] Numbers here represent the probability that the difference in isotopic enamel is due to chance alone. These data were generated utilizing a Visual Basic program in Excel written by Robert Edgar (Farlow Herbarium, Harvard University) using principles of two-sample randomization tests described in Manly (1997). In general, the program generates random populations using the isotopic values of the populations being compared (maintaining the sample size for each population) and calculates the difference in the magnitude of the ranges of each population generated. The program then locates where in that distribution the observed range difference falls. The more the observed difference falls into the tail(s) of the distribution, the less likely it is that the observed difference in range is due to chance. The sampling simulation runs 10,000 times.

South Africa or Tighenif in Algeria (Bocherens et al., 1996), were excluded, as the paleohabitats at the time appear to be C_3 dominated with limited evidence of C_4 grasses. Studies based on isotopic analyses of collagen and/or bone apatite were also generally excluded due to many factors involved in accurately converting these isotopic proxies into equivalent enamel values. Isotopic analyses of fossil enamel in which data were presented as averages (e.g., Luyt and Lee-Thorp, 2003), in figures without lists of specific values (e.g., Leakey et al., 1996; Cerling et al., 1997b; Schoeninger et al., 2003), or without specific taxonomic identification (e.g., Levin et al., 2004), were not considered, unless the implications of the data altered our interpretations significantly. Available relevant oxygen isotopic values were more limited than carbon data as a number of key studies reported only $\delta^{13}C_{enamel}$. Data on modern mammals were gleaned from a number of sources, with a focus on East and South African assemblages (e.g., Lee-Thorp, 1989; Bocherens et al., 1996; Cerling et al., 1999; Cerling and Harris, 1999; Harris and Cerling, 2002; Cerling et al., 2003a,c; Sponheimer et al., 2003).

Following is an interpretation of isotopic data for each of the herbivore families sampled at Laetoli compared with data collected elsewhere and an assessment of paleodietary reconstructions based on various alternate lines of evidence.

5.2. Rhinocerotidae

Diceros and *Ceratotherium* are represented at Laetoli (Guerin, 1987), with *Ceratotherium praecox* and *Diceros bicornis* from the Upper Laetolil Beds and *Ceratotherium simum* from the Upper Ndolanya Beds. The association of *C. praecox* and *D. bicornis* in the Upper Laetolil Beds has been interpreted to denote dry thorn bush and savanna (Guerin, 1987). In a recent revision of Pliocene rhinocerotids, Geraads (2005) transferred specimens from Laetoli attributed to *C. praecox* and *D. bicornis* by Guerin (1987) to *Ceratotherium mauritanicum* and *Diceros* cf. *praecox* respectively. However, until the rhinocerotids from Laetoli have been fully analyzed and their taxonomic affinities reassessed (Fortelius, in preparation), we provisionally refer to these two taxa as *Ceratotherium praecox* and *Diceros bicornis*.

Ceratotherium is thought to have diverged from *Diceros* stock during the late Miocene (Thenius, 1955; Harris and Leakey, 2003; Geraads, 2005). The fossil record of *Ceratotherium* is interpreted to document a progressive adaptation to grazing, initially by increased hypsodonty and later by modification of the orientation of the lophs of the upper molars, a progressive elongation of the cranium, and development of a wide mouth for grazing (Harris, 1983a). The emergence of *Ceratotherium* in the late Miocene and Pliocene has been linked to the spread of grasslands (Harris, 1983a; Carroll, 1988). *Diceros bicornis* can be traced back to the early Pliocene (Hooijer, 1978; Guerin, 1987; Geraads, 2005). Based on analogy with the modern form, the *Diceros* lineage has been viewed as an obligate browser.

Isotopic analyses of modern rhinocerotid teeth clearly reflects this dietary partitioning (Lee-Thorp, 1989; Koch et al., 1991; Bocherens et al., 1996; Cerling and Harris, 1999; Cerling et al., 2003b; this study) with *Ceratotherium simum* yielding $\delta^{13}C_{enamel}$ values consistent with a variable to obligate C_4 grazing diet averaging about 0.0‰ and *Diceros bicornis* with a C_3 browsing diet with a mean of about −10.5‰ (Fig. 5a). Cerling and Harris (1999) suggest that more positive $\delta^{13}C_{enamel}$ values (ca. −10 to −7‰) of *D. bicornis* from arid habitats, such as Amboseli (Bocherens et al., 1996), Koobi Fora, or Ngureman in Kenya may indicate C_4 dicots or CAM plants in the diet. An enamel fragment of *D. bicornis* from the KB unit in Chad (~6–5 Ma) represents the only fossil of this species analyzed and has yielded a $\delta^{13}C_{enamel}$ value within the range of modern *Diceros* (Zazzo et al., 2000). More isotopic data exist for *Ceratotherium*, and these suggest a more complicated dietary trajectory than traditionally considered. At Lothagam, Cerling et al. (2003b) note that of the identified rhino enamel fragments, a tooth of *C. praecox* (*Ceratotherium* sp.? of Geraads, 2005) from the Lower Nawata Fm. (7.4–6.5 Ma) indicates a C_3 dietary preference, even though contemporaneous equids exhibit a significant C_4 component in their diet. *Ceratotherium* higher in the sequence (Upper Nawata Fm. and Kaiyumung Member of the Nachukui Fm.; ~6.5–3.0 Ma) indicate a variable grazing diet. Harris and Leakey (2003) hypothesize that changes in the diet of white rhinos between the Lower and Upper members of the Nawata Formation reflect an ecological change during the late Miocene. Analyses of *Ceratotherium* enamel from the early Pliocene of Chad also indicate a shift from more mixed diets early in the sequence to variable C_4 grazing, but several million years later (~4–3.5 Ma) (Zazzo et al., 2000). Isotopic signatures of *Ceratotherium* from the Laetolil Beds reveal no apparent dietary shifts through the sequence and reflect a wide spectrum of dietary preferences ranging from variable browsing to intermediate browsing–grazing. A specimen from the Upper Laetolil Beds indicates an almost exclusive C_4 diet, while several samples, some potentially contemporaneous, reflect a diet consisting of essentially pure C_3 browse. The distribution of $\delta^{13}C_{enamel}$ for *Ceratotherium* from the Upper Laetolil Beds is statistically more negative (more browsing) than the range documented for early Pliocene *C. praecox* from Chad (Mann–Whitney, $p<0.01$).

Relative to modern populations of white rhino in equatorial Africa, *C. praecox* from the Laetolil Beds are statistically more ^{13}C depleted (Table 3)(not significant relative to modern Laetoli specimens but sample size was small), indicating more of a browsing niche. Based on a Sampled Randomization Test (Table 3), there is a 86% probability that the dietary breadth of the fossil *Ceratotherium* is significantly greater than that of extant *Ceratotherium*. Cumulatively the $\delta^{13}C_{enamel}$ values suggest that *Ceratotherium* was more of an opportunistic feeder, rather than an obligate or variable grazer, and that tracking the diet of this lineage through the Pliocene may provide a useful means of documenting environmental and habitat change. If this is the case, browsing *Ceratotherium* in the Upper Laetolil Beds indicate more wooded habitats than those sampled in broadly contemporary sites in Chad (5–3.5 Ma) and Lothagam in northern Kenya (~6.5–3.0 Ma).

The range of oxygen data for Laetolil Beds specimens are statistically more depleted in ^{18}O (Mann–Whitney, $p<0.01$) than modern *Ceratotherium*, with the median of Laetoli fossil $\delta^{18}O_{enamel}$ values over 5‰ more negative relative to modern local *Ceratotherium.* These data suggest greater humidity in the past in the Laetoli region although it is important to acknowledge other variables that could contribute to this offset (summarized in Fig. 6).

5.3. Proboscidea

Proboscidean material from the Laetolil Beds has been attributed to three species (Beden, 1987; Harris, 1987a): *Anancus kenyensis* from the Lower Laetolil Beds, and

Deinotherium bozasi and *Loxodonta exoptata* from the Upper Laetolil Beds. Proboscideans from the Upper Ndolanya Beds include *Deinotherium bozasi* and *Loxodonta* cf. *exoptata* (Beden, 1987; Harris, 1987a). The latter apparently represents a slightly more advanced form with a greater number of plates on M_2 and slightly thinner enamel than that from the Laetolil Beds. The isotopic signatures for these taxa indicate diverse foraging strategies that reflect niche partitioning (Fig. 5b). Deinothere molar $\delta^{13}C_{enamel}$ values are consistent with an exclusive C_3 browsing signal and are similar to isotopic signals of *D. bozasi* from the Turkana Basin and Samburu Hills (Cerling et al., 1997b; Cerling et al., 1999; Schoeninger et al., 2003). Carbon isotopic evidence indicates mixed C_3/C_4 to variable C_4 grazing dietary strategies for *Anancus* and *Loxodonta* at Laetoli with $\delta^{13}C_{enamel}$ values ranging from ca. −6‰ to 0‰. There are no apparent trends or statistically significant shifts in proboscidean dietary signals through the sequence (Fig. 3).

The low-crowned, thick enameled bunodont teeth of *A. kenyensis* indicate adaptations for crushing and grinding rather than shearing, suggesting a foraging strategy dominated by browsing (Tassy, 1994). The $\delta^{13}C_{enamel}$ of a molar fragment of *A. kenyensis* collected from Lower Laetolil Beds is −2.5‰, reflecting a predominantly C_4 grass diet. This result lies within the range established for *A. kenyensis* from Chad (KB and KL units) (6–4 Ma) (Zazzo et al., 2000), and is similar to enamel analyzed from the Nachukui Formation at Lothagam (Apak Member) (5.5–4.2 Ma) and Kanapoi (Lonyumum Member) (4.5–4.0 Ma)(Cerling et al., 1999, 2003b). These data provide evidence for an almost exclusive grazing strategy for *A. kenyensis* over a wide geographic region during the late Miocene and early Pliocene. A fragment of enamel identified as *Anancus* sp. at Nakali (10.4–9.6 Ma)(Cerling et al., 1999) yielded a dietary signature consistent with the average $\delta^{13}C$ value of C_3 vegetation, suggesting that perhaps earlier forms were variable browsers. This sample, however, derives from prior to the Late Miocene expansion of C_4 grasslands when C_3 grasses and grasslands may have been more widespread in Equatorial Africa (Jacobs et al., 1999).

Relative to contemporaneous gomphotheres, the teeth of *Loxodonta* are distinguished by an increase in shearing index, thinner and more folded enamel, and an increase in molar crown height (Maglio, 1973; Beden, 1987). Aspects of these general trends and accompanying changes in mandible and cranial architecture have been linked to functional shifts in masticatory function as Elephantidae expanded its geographic and ecological range (Todd and Roth, 1996). Although the inference is that these changes relate to progressive modifications for a primarily grazing diet, specific dietary interpretations appear to be based more on contextual data rather than on functional or biomechanical interpretations. Beden (1987) suggests that the origin of *Loxodonta exoptata* relates to vegetational changes driven by climatic shifts that resulted in the reduction of humid forest and their replacement by wooded savannas. More specifically, the Laetoli environment is reconstructed as a ‘wet’ wooded savanna based on the absence of the more arid-adapted *Elephas recki* (Beden, 1987). Ecological and dietary interpretations of proboscidean evolution, such as these, are based in part on the association of *L. exoptata* and reconstructed savanna habitats at Laetoli. However, accumulating isotopic analyses of Equatorial African proboscidean fossil material (Kingston, 1992; Morgan et al., 1994; Cerling et al., 1997a,b, 1999; Zazzo et al., 2000; Schoeninger et al., 2003; Cerling et al., 2003b) demonstrate a transition from C_3 to C_4 dominated diets in proboscideans at about 8 Ma. $\delta^{13}C$ values indicate that gomphotheriids and elephantids were grazers or mixed feeders more than browsers at least 4 Ma preceding the occurrence of the Laetoli proboscideans. These data do not support the notion that the Laetoli *Loxodonta* reflect a novel foraging niche.

The range of $\delta^{13}C_{enamel}$ values for Laetoli *Loxodonta* specimens is consistent with material from other fossil localities (Fig. 5b), suggesting similar C_4 dominated diets and possibly similar ecosystems. The Laetoli values, especially those of the Upper Laetoli Beds, are in general more ^{13}C-depleted than the enamel of *Loxodonta* from Chad (Zazzo et al., 2000), as well as *L. adaurora* from the Turkana Basin (Cerling et al., 2003b), indicating that Laetoli *Loxodonta* were more mixed feeders than grazers. If *L. adaurora* is ancestral to *L.exoptata*, these data suggest that the lineage is not characterized by a simple trend of progressively increasing graminivory. Also, if dietary preference is linked to habitat type, the greater browsing component of Laetoli *Loxodonta* relative to Chad and Turkana possibly suggests that Laetoli was at least as wooded, if not more so, than these other Pliocene sites.

Variable grazing to intermediate foraging isotopic signatures of late Miocene and Pliocene fossil elephantids contrast with the $\delta^{13}C_{enamel}$ of extant African *Loxodonta*, which indicate a diet generally dominated by C_3 biomass (Cerling et al., 1999). Hypotheses to explain this discrepancy include reduction of C_4 grasslands at the terminal Pliocene resulting in increased competition from other grazing taxa or incorrect phylogenetic assumptions linking fossil grazing lineages with modern browsing elephants (Cerling et al., 1999). Alternatively, this change in foraging strategy may reflect an adaptive shift to browsing niches left vacant by the extinction or regional extirpation of other large-bodied herbivores, such as deinotheres, chalicotheres, sivatheres, camelids and large bovines.

Oxygen isotopic values of *Loxodonta* enamel from the Upper Laetolil Beds are the most ^{18}O-depleted relative to reported $\delta^{18}O_{enamel}$ values at other East African fossil sites, including the Upper Ndolanya Beds, and modern elephants (Fig. 6). These differences are statistically significant (Mann–Whitney, $p<0.01$ for modern *Loxodonta* and $p<.05$ for Chad and the Ndolanya Beds *Loxodonta*). These data may also indicate less arid conditions 3.8–3.5 Ma in the Laetoli region relative to these other sites.

5.4. Bovidae

5.4.1. Overview

Bovids represent a speciose and ubiquitous group, adapted to diverse diets and habitats. Evolutionary patterns of this family have been linked specifically to environmental change and faunal turnover during the Miocene and Plio-Pleistocene of Africa (Vrba, 1985, 1995; Bobe and Eck, 2001; Alemseged, 2003). Analyses of fossil bovids have been central to paleoecological reconstructions of habitats associated with early hominins (WoldeGabriel et al., 1994; Sponheimer et al., 1999; Pickford and Senut, 2001; WoldeGabriel et al., 2001; Vignaud et al., 2002; Sponheimer and Lee-Thorp, 2003). Approaches to habitat and diet reconstruction of extinct bovids in Africa include taxonomic uniformitarianism (using modern related forms as analogs) (Shipman and Harris, 1988), relative representation of bovid tribes (Vrba, 1980, 1985; Shipman and Harris, 1988), ecomorphology based on postcranial indices (Plummer and Bishop, 1994; Kappelman et al., 1997; DeGusta and Vrba, 2003; Kovarovic, 2004; White et al., 2006), and cranio-dental feeding adaptations (Spencer, 1997; Sponheimer et al., 1999). Although a number of isotopic studies have provided critical data relevant to these reconstructions (Lee-Thorp, 1989; Sponheimer et al., 1999; Luyt and Lee-Thorp, 2003), isotopic contributions have in part been constrained by the difficulty of taxonomic identification beyond the tribe level using fossil enamel fragments and to a limited understanding of isotopic variability among modern taxa. Recent compilations of isotopic profiles of modern bovid taxa in conjunction with foraging and habitat preferences (Cerling et al., 2003c; Sponheimer et al., 2003; Gagnon and Chew, 2000) provide a valuable quantitative framework for assessing the diet of fossil bovids. In general, there is correspondence in dietary estimates based on isotopic analyses of similar taxa in East and South Africa, with less than 10% differences in 17 of 18 taxa that co-occur in these regions (Cerling et al., 2003c).

Bovids are the most abundant mammalian taxa in the Laetoli faunal assemblage, comprising 35% of the Laetolil Bed specimens and 81% of the Upper Ndolanya Bed material (Leakey, 1987a). Eight bovid tribes are represented in the collections, although several taxa are not adequately known to be able to resolve their taxonomic status below the tribal or family levels. Here we focus isotopic analyses on taxa from five of the bovid tribes that are relatively well represented in the Laetoli collections — Tragelaphini, Hippotragini, Alcelaphini, Neotragini, and Antilopini (Fig. 5c).

5.4.2. Tragelaphini

Modern tragelaphines (i.e., nyala, kudu, eland, and bushbuck) are generally browsers with low-crowned teeth and digestive tracts adapted for nutritious vegetation and fruit (Kingdon, 1982, 1997). A mixed diet including a monocot grazing component has been reported for several taxa (reviewed in Gagnon and Chew, 2000). They currently inhabit a wide diversity of ecosystems ranging from forests to arid, seasonal bushland, although Kingdon (1982) suggests that ancestral representatives may have preferred moister woodlands and forests. Postcranial morphology of fossil tragelaphines reflects light to heavy cover environments (Kappelman et al., 1997). Isotopic analyses of enamel and horn keratin of extant tragelaphines from South and East Africa indicate diets dominated by browsing, although there is evidence for mixed C_3/C_4 feeding within the tribe (e.g., eland, *Taurotragus oryx*) (Lee-Thorp, 1989; Cerling et al., 2003a; Sponheimer et al., 2003). $\delta^{13}C_{enamel}$ values of enamel of *Tragelaphus* cf. *kyaloae* from Gona (Semaw et al., 2005) (−0.1 to 11.0‰), however, indicate that the foraging strategy of specific taxa within this lineage can span the entire browsing/grazing spectrum. Tragelaphines sampled from the Upper Laetolil Beds yielded isotopic signatures ranging from −7.8 to −11.8‰, values consistent with modern taxa, as well as fossil tragelaphines from Makapansgat (i.e., *Tragelaphus* sp. aff. *T. angasi* and *Tragelaphus pricei*) (Sponheimer et al., 1999), Lothagam (Upper Nawata Fm.) (Cerling et al., 2003b) and Sterkfontein (Luyt and Lee-Thorp, 2003). The only described tragelaphine from the Upper Ndolanya Beds is *Tragelaphus* sp. cf. *buxtoni*, which is larger and morphologically distinct from *Tragelaphus* sp. from the Upper Laetolil Beds (Gentry, 1987). The modern-day mountain nyala (*T. buxtoni*), from the Bale Massif of

Ethiopia is a specialist browser that prefers mosaic woodland, bushland, grassland habitats (Kingdon, 1997). Unfortunately, no specimens of this taxon were included in the isotopic analysis. However, two specimens from the Upper Ndolanya Beds tentatively identified as tragelaphines of similar size to those from the Upper Laetoli Beds were included in the study. Interestingly, they are ^{13}C-enriched, indicating variable grazing behavior, unlike any other tragelaphine analyzed other than an unprovenanced sample from Lothagam (Cerling et al., 2003b) and ^{13}C-enriched samples from Gona (Semaw et al., 2005).

5.4.3. Alcelaphini

The tribe Alcelaphini includes wildebeest, impala, topi, hirola and kongoni, all variable to obligate grazers (Gagnon and Chew, 2000), inhabiting open woodland or edaphic/secondary grasslands (Estes, 1991; Scott, 1979), with postcranial adaptations for specialized cursoriality (Kappelman et al., 1997). Isotopic profiles of extant alcelaphines consistently reflect diets dominated by C_4 grass (Cerling et al., 2003c; Sponheimer et al., 2003). In the Laetolil Beds, alcelaphines are represented by *Parmularius pandatus* and a larger species, Alcelaphini sp. indet. Four species of alcelaphines are known from the Upper Ndolanya Beds: *? Aepyceros melampus*, *Parestigorgon gadjingeri*, Alcelaphini medium sp., and Alcelaphini small sp. (Gentry, 1987). With the exception of *P. pandatus*, representative specimens from several of these taxa yielded grazing signals greater than 0‰. *Parmularius pandatus* values, however, ranged from −8.6‰ to 0.6‰ with a median of about −2‰, indicating significant browsing in three specimens. Other than two specimens of *Alcelaphus* sp. from Swartkrans with similar $\delta^{13}C_{enamel}$ signals, these values are more negative than any extant or fossil alcelaphines and on average are 3‰ more negative relative to *Parmularius braini* from Makapansgat (Sponheimer et al., 1999) to which *P. pandatus* has been compared morphologically (Gentry, 1987). This may signify that some early lineages or individual taxa of small-sized alcelaphines may not have been as committed to specialized grazing niches as their modern-day counterparts.

5.4.4. Hippotragini

Ecological, dietary and social patterns of hippotragines have been interpreted as adaptations to an ancestral ‘desert ordeal’ during the early Pliocene (Kingdon, 1997). The modern oryxes and roan and sable antelopes dominate the larger-scale desert bovid niches, with well developed adaptive strategies to deal with heat, drought, and unpredictable desert pastures. All modern species are primarily obligate grazers, associated with habitats ranging from desert grasslands to open woodlands (Estes, 1991; Gagnon and Chew, 2000). Fossil Hippotragini from Laetoli include *Praedamalis deturi* and ? Hippotragini sp. nov. from the Laetolil Beds, and Hippotragini gen. et sp. indet. from the Upper Ndolanya Beds. Isotopic signals of eight enamel fragments of hippotragines from the Upper Laetolil Beds ranged from about −2‰ to −9‰ reflecting a mixed C_3/C_4 diet, but with an emphasis on browse. Analyses of hippotragines from other fossil localities is limited to three specimens from the Kossom Bougoudi Unit in Chad (~6–5 Ma) which ranged from −1.9‰ to 0.6‰ and seven specimens from Sterkfontein Members 4 and 5 West (2.4–1.7 Ma) (*Hippotragus* cf. *gigas*, *Hippotragus* cf. *gigas* (?), *Hippotragus equinus*, and *Hippotragus* sp. af. *gigas*) with means ranging from −1.1‰ ± 1.6‰ to −10.2‰ ± 0.04‰ (Luyt and Lee-Thorp, 2003). The relatively negative values from Laetoli and Sterkfontein contrast with all modern Hippotragini isotopic data from East and South Africa that cumulatively yield a mean of 0.8‰ (±1.1‰) for 62 specimens (Sponheimer and Lee-Thorp, 2003). The distribution and occurrence of hippotragines at Pliocene sites in Africa serves to highlight the fact that the group was formerly more common and widespread, and more ecologically diverse than their modern-day representatives. It suggests that hippotragine diversity declined during the Plio-Pleistocene, probably as a consequence of being forced into increasingly more marginal environments by the radiation of alcelaphines. If this scenario is correct, some Pliocene hippotragines, such as those at Laetoli, may well have been mixed feeders relying more heavily on browsing, especially given that the range of niches available to browsers at this time would have accommodated a greater taxonomic diversity, and there would have been less competition for access to grasses from obligate specialist grazers.

5.4.5. Antilopini

High percentages of antilopines (in combination with alcelphines) in fossil bovid assemblages have been interpreted to indicate relative arid grassland habitats (Vrba, 1980; Greenacre and Vrba, 1984). This is primarily because modern antilopines have limbs specialized for cursoriality, and physiological and dietary adaptations to drought (Kingdon, 1982; Plummer and Bishop, 1994). Modern gazelles, dibatag, and gerenuk inhabit desert, grassland, savanna and open woodland biomes (Gentry, 1992), and have diets ranging from variable grazers in Grant’s or Thomson’s gazelles

(*Gazella granti* and *G. thomsoni*) to the variable browsing gerenuk (*Litocranius walleri*) (Gagnon and Chew, 2000). A compilation of $\delta^{13}C_{enamel}$ values of modern antilopine data from South and East Africa ($n=78$) yields an average dietary signal of −9.2‰ (±1.5‰) (Sponheimer and Lee-Thorp, 2003) for the tribe. This reflects mixed feeding strategies, but with an emphasis on browsing. Enamel analyses of extant antilopines from Kenya suggest that while the diet of Grant's gazelle is highly variable isotopically, it is primarily a browser (Cerling et al., 2003c). Thomson's gazelle also had a variable isotopic signature, but one dominated by C_4 grass, while the gerenuk had $\delta^{13}C_{enamel}$ values corresponding to a diet of essentially pure C_3 browse (Cerling et al., 2003c). Antilopines from Laetoli include *Gazella janenschi* from the Laetolil Beds, and *G. janenschi*, *Antidorcus* sp., and Antilopini sp. 1 from the Upper Ndolanya Beds. Gentry (1987) notes that the teeth of *G. janenschi* are rather generalized and fairly hypsodont and Gentry and Gentry (1978a,b) suggest that *G. janenschi* is ancestral to *G. thomsoni* and *G. rufifrons*. As with the modern gazelles, analyses of *G. janenschi* from the sequence indicate a variable diet (−2‰ to −10‰), but with a median of −7‰, indicating a foraging strategy focused more on browsing than modern antilopines. Although these represent the only fossil antilopines analyzed from East Africa, isotopic data on fossil antilopines from South Africa indicate that they had diets ranging from exclusive browsing, to mixed feeding and grazing (Lee-Thorp, 1989; Lee-Thorp et al., 1994; Sponheimer et al., 1999; Lee-Thorp et al., 2000; Luyt and Lee-Thorp, 2003; van der Merwe et al., 2003).

5.4.6. Neotragini

Fossil neotragines, referred to *Madoqua avifluminis* and ?*Raphicerus* sp., have been recovered from the Laetolil and Upper Ndolanya Beds (Gentry, 1987). *Madoqua avifluminis* is similar in body size and overall dental morphology to Kirk's dikdik (*M. kirkii*), which is common in the Laetoli region today. The latter are small, long-legged antelopes that exhibit specialized thermoregulatory adaptations for heat and aridity. They typically inhabit dense, low dry thickets dominated by evergreen scrub, although they occur in a wide range of arid woodland to bushland habitats (Kingdon, 1982). Although dikdiks have been known to eat grass during the wet season, they prefer dicot browse (Kingdon, 1982). $\delta^{13}C_{enamel}$ signatures of modern Kirk's and Guenther's (*M. guentheri*) dikdiks suggest essentially exclusive C_3 browsing (Cerling et al., 2003c; this study). Analysis of *M. avifluminis* from the Upper Laetolil Beds yielded values ranging from −6.5‰ to −10.6‰ with a median over 3‰ more positive than the modern taxa (using 1.5‰ correction), suggesting that the extinct forms incorporated 15–20% more grass into their diets.

5.4.7. Summary

Collectively, carbon isotopic analyses of Laetoli bovids indicate a tendency towards mixed C_3/C_4 foraging strategies with no taxa engaged in exclusive obligate browsing or obligate grazing, other than some of the large alcelaphines from the Upper Ndolanya Beds. In contrast, isotopic data of modern taxa show that the vast majority of African bovids are C_3 or C_4 specialists that maintain their specialized diets despite forage heterogeneity in home ranges (Sponheimer et al., 2003). The $\delta^{13}C_{enamel}$ ranges for the fossil taxa from the bovid tribes considered here, with perhaps the exception of the tragelaphines, are unique with respect to modern representatives, suggesting that ancestral lineages were perhaps more generalized or occupied different niches. While this finding may limit the utility of applying modern bovid dietary patterns as analogs for paleoecological reconstruction, the data do suggest that, as predominantly mixed feeders, the diet of extinct bovids may vary depending on the specific ecology of local habitats, and therefore be a much better guide to tracking ecological variability. During Upper Laetolil times, bovid diets indicate that C_4 grasses were available, but they did not dominate the diets as might be expected in more open habitats, including those that currently characterize the Laetoli landscape. A further consideration in linking dietary patterns to ecology is the extent to which various taxa may engage in short- or long-range movements. Migratory behavior represents an adaptive strategy to buffer against annual or bi-annual seasonal fluctuations in resources in modern African rangelands (McNaughton et al., 1988) and is utilized by a number of large-bodied ungulates. 'Transient' taxa interact with habitats through which they range in complex ways, having major effects on ecosystem processes as well as community structure. These activities would significantly affect analyses of fossil 'communities' and it will ultimately be important to differentiate elements of resident communities from migratory components when utilizing aspects of the fauna to reconstruct paleoecology. The faunas of the Upper Ndolanya Beds, dominated by medium-to large-sized bovids, may represent such a mix of resident and migratory communities, and account in part for its distinctiveness from the fossil assemblage from the Laetolil Beds. Nevertheless, large-scale migration may imply that environmental conditions during Ndolanya times may have been more arid and seasonal.

5.5. Equidae

Two hipparonine equids were recognized at Laetoli by Hooijer (1987a,b)— *Hipparion* sp. from the Upper Laetolil Beds and *Hipparion* cf. *ethiopicum* from the Upper Ndolanya Beds (Leakey, 1987a). Following Bernor and Armour-Chelu (1999) and Bernor and Harris (2003) these species are provisionally included in *Eurygnathohippus*, pending detailed description and further systematic studies of the Laetoli collections.

In conjunction with a global expansion of C_4 biomass during the late Miocene, equid diets transitioned from C_3 dominated to C_4 dominated in tropical and subtropical Africa (Cerling et al., 1997b). This transition is documented in fossil equid material from sites in northern and central Kenyan Rift. Analyses of equid enamel from Nakali (~10 Ma) (Cerling et al., 2003b) and Tugen Hills (Ngeringerowa Beds of the uppermost Ngorora Fm., ~8.5–9.0 Ma) (Kingston, 1992; Morgan et al., 1994) yielded dietary signals indicating variable browsing or C_3 grazing (Fig. 5a). A number of craniodental characters associated with late Miocene equids in Africa (*Hippotherium primigenium* and *Hipparion africanum*) suggests that they were primitively mixed feeders, incorporating both graze and browse in their diets (Bernor and Armour-Chelu, 1999; Cerling et al., 2003b). While Forsten (1972) interprets early hipparionines as forest dwellers, Churcher and Richardson (1978) instead suggest that the earliest hipparionines in Africa inhabited relatively dry grasslands. The latter interpretation, along with paleofloral evidence (Jacobs et al., 1999), suggests that C_3 grasslands may have been a component of East African ecosystems prior to the Late Miocene isotopic transition. Mixed C_3/C_4 equid diets, allocated to the transition, have been documented at Samburu (Namarungule Fm. ~9 Ma), Abu Dhabi (Baynunnah Fm. ~8–6 Ma), and Lothagam (lowest Lower Nawata ~7.5 Ma). Except at Langebaanweg (South Africa), where C_4 grasses were not established by ~5 Ma (Franz-Odendaal et al., 2002), equid enamel younger than about 7 Ma in tropical and sub-tropical Africa, including all modern samples, have previously yielded $\delta^{13}C_{enamel}$ values in the range of −2‰ to 3‰, indicating C_4 dominated to exclusive C_4 grass diets (Morgan et al., 1994; Bocherens et al., 1996; Cerling et al., 1997b; Kingston, 1999a; Zazzo et al., 2000; Cerling et al., 2003a,b).

Collectively, these data suggest a gradual replacement of C_3 grass and browse by a diet of C_4 grasses between 9 and 6 Ma (Cerling et al., 1997b). The shift in vegetational physiognomy associated with this transition remains unclear, since it could involve the replacement of C_3 grasslands by C_4 grasslands, more wooded or forested C_3 habitats by C_4 grasslands or patches, or some combination of these. Regardless, the transition had a significant impact on the evolution of East African ecosystems and coincided with or resulted in the establishment of many of the modern East African mammalian lineages. However, the Laetoli equid data indicate a possibly more complex scenario as the $\delta^{13}C_{enamel}$ values of ~−4‰ for two specimens of *Eurygnathohippus* from the Upper Laetolil Beds indicate a mixed C_3/C_4 diet at 3.8–3.4 Ma, well after the transitional interval. Laetolil equids were either C_4 grazers supplementing their diet with C_3 browse or C_3 grasses or they were more eclectic feeders. These strategies possibly reflect behaviors or adaptations associated with more wooded habitats. Additionally, recent analyses of enamel attributed to *Eurygnathohippus* sp. from the GWM-5 block (~4.3–3.7 Ma) at Gona (Semaw et al., 2005) yielded some intermediate dietary signals of −6.3‰ and −5.6‰. Accumulating equid isotopic data from East Africa suggest that the expansion of C_4 grasses in East African ecosystems resulted in a dietary switch from C_3 vegetation to a more mixed C_3/C_4 diet as well as the exclusive grazing niche occupied by modern equids, with dietary proportions of dietary C_3 and C_4 biomass presumably reflecting local availability. Similarly, South African equid enamel analyzed from Swartkrans (Member 2, ~1.5 Ma) and Equus Cave (ca. 30 ka) also yield isotopic signatures consistent with mixed foraging strategies. In contrast, the overall isotopic range for *Eurygnathohippus* sp. from the Upper Laetolil Beds is more positive than other fossil assemblages (except for KT unit in Chad) and more similar to the adjusted extant equid values. This difference indicates either less C_3 biomass in the diet than equids at other sites or that local C_4 grasses were ^{13}C-enriched because they were dominantly classical-NADP subtypes associated with more mesic environments than the arid adapted Nad-me or PEP-ck C_4 grasses (Chapman, 1996). Supporting this later interpretation, $\delta^{18}O_{enamel}$ values for Laetoli *Eurygnathohippus* are similar to or more negative than those of other fossil localites and generally more negative than all sampled modern *Equus burchelli* from East Africa (not statistically significant, Mann–Whitney, $p=0.06$).

5.6. Suidae

Pigs are frequently utilized as paleoecological indicators in paleoanthropology. Like early hominins, they are large-bodied omnivores that are thought to represent a potentially useful proxy for generating hypotheses about hominin paleobiology (Bishop, 1999). In addition, the taxonomic diversity and ubiquity of suids in the East African fossil record has led to their importance in biostratigraphy. Assessments of dietary patterns and habitat preferences of extinct suids based on dental morphology, isotopic analyses, and ecomorphology have revealed complex adaptive strategies and behaviors in the various lineages (Bishop et al., 1999; Kullmer, 1999; Harris and Cerling, 2002). Of the two suid species from the Laetolil Beds, the large *Notochoerus euilus* is much more common than the bush pig, *Potamochoerus porcus*. The absence of suid taxa commonly found at contemporary sites in East Africa (such as *Nyanzachoerus kanamensis*) may be attributed to the lack of standing water and greater aridity at Laetoli (Harris, 1987b; White, 1995).

Isotopic analyses of suid specimens from the Laetolil Beds is focused here exclusively on *N. euilus*, which is characterized by relatively enlarged third and fourth premolars, elongate molars, and an increase in the both area and hyposodonty (although see Kullmer, 1999) of the third molars (Cooke and Wilkinson, 1978; Harris, 1983b; Pickford, 1986). As these dental features are interpreted as adaptations to an abrasive grazing diet, their preferred habitat has been interpreted as savanna or grasslands biomes (Cooke and Wilkinson, 1978; Harris, 1983b). Harris (1987b) also notes that the high frequency of *N. euilus* relative to *Potamochoerus* (which today prefers woodland and forested habitats), as well as the large tusk and body size, which are viewed as antipredator adaptations, indicate savanna and grassland habitats (Harris, 1987b). Ecomorphological analysis of the postcrania of *N. euilus*, however, indicate morphological characters associated with woodland habitat preferences (Bishop et al., 1999). Based on a report of similarity in tooth abrasion patterns with *Hylochoerus* (Cooke, 1985), Kullmer (1999) also suggests that *Notochoerus euilus* might have shared a more similar mode of life to the forest-dwelling modern giant forest hog (*Hylochoerus meinhertzhageni*) rather than to that of the more commonly associated modern analog—warthogs (*Phacochoerus*) (Harris, 1987b). Carbon isotopic signatures of 24 enamel fragments of *N. euilus* from the Laetolil Beds indicate predominantly C_4 to mixed C_3/C_4 diets (−8.2‰ to 2‰) throughout the sequence, with no apparent trend within the stratigraphic sequence (Fig. 3). These values support morphologically-based interpretations of grazing, but also are consistent with the notion that these suids were eclectic feeders, incorporating significant amounts of C_3 biomass into their diet. One specimen, from between Tuffs 7 and 5 in the Upper Laetolil Beds, yielded a $\delta^{13}C_{\text{enamel}}$ signal of −8.2‰, indicative of almost exclusive C_3 browsing. In general, these data are consistent with isotopic analyses of penecontemporaneous specimens of *N. euilus* from the Turkana Basin which also indicate mixed feeding (Harris and Cerling, 2002), but extend the overall range of dietary preferences, especially toward the C_3 endmember (Fig. 5b). Zazzo et al. (2000) report values of 0.9‰ and 1.3‰ for two samples of *N. euilus* collected from the Koro Toro unit in Chad (~3.5–3 Ma), which, if representative of the population, indicate dedicated grazing. If the foraging behavior of suids, such as *N. euilus*, is eclectic and flexible, and is directly contingent on the floral composition of local and regional ecosystems, the isotopic data from Laetoli shows that suid habitats were similar in C_3/C_4 proportions to contemporaneous localities in the Turkana Basin and Chad with perhaps more wooded components. Bishop (1999) and Bishop et al. (1999) note that the apparent discrepancy between hypsodonty and postcranial adaptations in *N. euilus* can be accommodated by inferring paleohabitats in which tropical grasses are more sparsely distributed in the substratum of open woodlands or in the disturbed portions of closed woodland habitats, rather than as grasslands. It is interesting that the range of isotopic signatures for *N. euilus* at Laetoli and Turkana is intermediate between modern bush pigs and warthogs, suggesting that neither extant taxon is an appropriate behavioral analog. The range of $\delta^{13}C_{\text{enamel}}$ values for *Notochoerus euilus* is over 10‰ (+2‰ to <−8‰) (n=24), statistically greater than the range of modern warthogs collected from 16 variable biomes in five tropical African countries (N=52) (Table 3). These data indicate that *N. euilus* was more of an eclectic feeder than modern *Phacochoerus* with a range similar to the bushpig but incorporating more C_4 grass. Oxygen isotopic values for *N. euilus* are statistically more ^{18}O-depleted relative to modern warthogs (Table 3) and more similar to modern bushpigs and giant forest hogs, possibly indicating more closed conditions with reduced evaporative effects.

A third suid species at Laetoli, *Kolpochoerus limnetes*, is represented by specimens from the Upper Ndolanya Beds. An immigrant from Eurasia, the *Kolpochoerus* lineage first appears in Africa during the middle Pliocene and provides a potential ancestor for the extant giant forest hog (*Hylochoerus meinertzhageni*) (White and Harris, 1977). *K. limnetes* is a long-lived species (~4–1 Ma), becoming progressively larger with more complex molars through time (Harris, 1983b), but never approaching the highly hypsodont condition of *Notochoerus*, suggesting that early *Kolpochoerus* were primarily browsers during the middle to late Pliocene. Increase in the height of the molars, in conjunction with broadening of the premaxilla, during the early Pleistocene suggest that the later *Kolpochoerus* may have added grazing to its feeding habits and exploited savanna habitats (Harris, 1983b). Postcranial adaptations in *K. limnetes* indicate a gradual change in habitat preference over time from woodland to habitats with a mix of woodland and grassland (Bishop, 1999). Kullmer (1999) notes strong dental affinities with *Potamochoerus* and interprets *Kolpochoerus* as an omnivore inhabiting forests, woodland, and dense bush. Increase in the occlusal area of M^3 during the early Pleistocene suggests that *Kolpochoerus* might have lived in ecotonal areas and fed at least partially on grass (Kullmer, 1999). However, isotopic analyses of *K. limnetes* enamel from the Turkana Basin (Nachukui Fm.) indicate that the earliest kolpocheres were exclusive grazers (Harris and Cerling, 2002; Cerling et al., 2005). However, Harris and Cerling (2002) note that the $\delta^{18}O$ values are more consistent with bush pigs or forest hogs that are more water dependent. The single sample of *K. limnetes* analyzed from the Upper Ndolanya Beds yielded a value of −3.7‰, indicative of a mixed diet. This signal is outside the range of the Turkana sample (−0.1 to 1.4‰) and more similar to isotopic signatures of *K. limnetes* from Olduvai Bed I (Plummer et al., 1999). At Anabo Koma, a ~1.6 Ma site in Djibouti, the $\delta^{13}C_{enamel}$ of a specimen of *K. limnetes* was −6.3‰ suggesting an even greater intake of C_3 browse. Although there may be a long-term trend towards increasing graminivory in the *K. limnetes* lineage, the isotopic data currently available suggests a more eclectic and opportunistic foraging strategy for the lineage during its evolutionary history. During the late Pliocene in East Africa, *K. limnetes* populations in different geographic regions, perhaps different ecosystems, were either grazing exclusively or browsing heavily according to the local conditions.

5.7. Giraffidae

At Laetoli, giraffid material has been attributed to three species from both the Upper Laetolil and Ndolanya Beds — a medium-sized and large giraffine (*Giraffa stillei* and *G. jumae* respectively) and a sivathere (*Sivatherium* cf. *maurusium*). While these taxa co-occur at other East African Plio-Pleistocene localities, Laetoli is unusual in that giraffids comprise a significant proportion of the mammalian specimens (8.7%) and that *G. stillei*, is numerically the most abundant species (comprising 65% of *Giraffa* specimens) (Leakey, 1987a; Harris, 1987c). It is likely that there was ecological partitioning to accommodate a relatively high abundance of three sympatric giraffids, presumably based on different optimum feeding heights, differential selectivity in browse, or foraging in different microhabitats. Harris (1987c) notes that there are few functional differences between the two giraffines and suggests that competition for dietary resources was mitigated by differences in size, resulting in specialization to vegetation of different heights. Based on a study of the feeding ecology of the Masai giraffe, *G. camelopardalis tippelskirchi*, in the Serengeti National Park (Pellow, 1983), Harris (1991) proposed that the larger *G. jumae* may have specialized in foraging in a habitat equivalent to mid-slope open *Acacia–Commiphora* woodland and *G. stillei* in shorter ridge-top or riverine woodlands. Sivatheres have been associated with habitats ranging from forest to open woodland (Churcher, 1978; Geraads, 1985). Features of sivatheres, including a relatively short neck, have suggested to some a grazing or mixed low-browsing/grazing strategy (Meladze, 1964; Hamilton, 1973; Churcher, 1978; Geraads, 1985). Based on premaxillary shape and tooth microwear, Solounias et al. (1988) suggested that the Miocene sivathere *Samotherium boissieri* (another potential ancestor of *Sivatherium*) had dietary adaptations most similar to committed grazers, and could have occupied a grazing niche. Application of three dietary reconstruction tools, hypsodonty, microwear, and mesowear, indicate a mixed feeding strategy for *Sivatherium hendeyi* from the early Pliocene of South Africa (Franz-Odendall and Solounias, 2004).

Carbon and oxygen isotopic analyses of enamel carbonate potentially provide a means of differentiating these feeding niches within wooded or forested habitats. In addition to carbon isotopic variability associated with the C_3/C_4 bimodality, $\delta^{13}C$ patterns observed in forests and forest ecotones indicate significant enrichment in ^{13}C in C_3 plant tissue (and browsers foraging on them) upwards in forest canopies and laterally into well-lit, less dense forest clearings or across ecotones from forest to woodland settings (van der Merwe and Medina, 1991; Schoeninger et al., 1997; 1998; Cerling et al., 2004). These trends relate to depletion of ^{13}C in closed canopy habitats due primarily to soil-respired ^{13}C-depleted CO_2 trapping under forest canopies (i.e., the “canopy effect”) (Medina and Minchin, 1980) and irradiance intensity (Farquhar et al., 1989). The $\delta^{18}O$ signal of herbivore enamel, as outlined earlier, is mediated by multiple factors including drinking behavior, diet, physiology, and climate, and the utilization of oxygen isotopes to differentiate microhabitats and specific feeding niches is considerably more complicated.

Overall, carbon isotopic analyses did not differentiate feeding niches in the Laetoli giraffids (Fig. 3). This may reflect the complexity of the browsing strategies of these taxa or the limited resolution in differentiating aspects of C_3 vegetation and microhabitat by isotopic analyses. It remains unclear as to how much intra-populational isotopic variation and conflation of samples from different time periods in the sequence may obscure guild signatures. Characterization of intra- and inter-tooth variation in several modern East African herbivores revealed that teeth of modern giraffes from Laetoli exhibited the greatest $\delta^{13}C_{enamel}$ variability (Kingston, 2003), exceeding differences between fossil conspecifics and between giraffid species in the Laetoli sequence. Microsampling of a P^4 and M^3 from an individual *G. camelopardalis* documents almost 2‰ variation in $\delta^{13}C_{enamel}$ within each tooth and over 6‰ between microsamples from the two teeth. This variability may relate to shifts in the isotopic signature of browse due to seasonal changes in local environmental conditions, seasonal dietary shifts well documented for extant giraffes, size related changes in browse available during growth, and ranging and migratory patterns [ranges up to 650 km^2 have been recorded (Kingdon, 1979)]. In this study, the confounding effects of intra- and inter-tooth variability were in part controlled for by bulk sampling and analyzing third molars respectively. However, additional analyses of modern giraffes are needed before developing criteria for interpreting fossil samples.

Sivatherium in the Laetoli sequence could not be differentiated isotopically from *Giraffa* spp. The isotopic signature of enamel fragments of a giraffid from the Baynunah succession, Abu Dhabi, *?Bramatherium* sp. (a potential ancestor of *Sivatherium*), yielded $\delta^{13}C_{enamel}$ values of −1.6‰ and −2.6‰, indicating a dietary intake of essentially C_4 plants (Kingston, 1999b). Of nine late Miocene herbivore species analyzed from Samos, Greece, *Samotherium boissieri* displayed the least negative values in $\delta^{13}C$ (−5.4‰), which was interpreted to indicate that it preferred moisture-stressed C_3 plants, possibly C_3 grasses, or had a C_4 component in its diet (Quade et al., 1994). Harris and Cerling (1998) report that late Miocene and early Pliocene sivatheres from East Africa have exclusive browsing isotopic signatures, but they become grazers in the late Pliocene. An isotopic carbon signature of −1.2‰ was reported for an enamel fragment attributed to cf. *Sivatherium* recovered from the GWM-5 block (~4.3–3.7 Ma) at Gona (Semaw et al., 2005) (Fig. 5b), indicating a foraging strategy dominated by C_4 grazing in early to middle Pliocene. Analyses of *S. maurusium* enamel from the Upper Laetolil and Upper Ndolanya Beds reveal no evidence of a grazing component in the diet. In fact, the $\delta^{13}C_{enamel}$ signature of one specimen yielded the most negative carbon isotopic value of all herbivores sampled, potentially indicative of browsing in more wooded or forested portions of the habitat where water stress and/or irradiance were reduced.

Within the Laetoli assemblage, giraffids (and hippotragine bovids) tend to have the most ^{18}O-enriched oxygen values, with statistically significant more positive $\delta^{18}O_{enamel}$ means and averages than the other herbivore taxa (Mann–Whitney, $p<0.05$)(Fig. 4). In other fossil faunas and modern assemblages, giraffids and other obligate browsers that derive much of their water from vegetation rather than from drinking meteoric water have a higher $\delta^{18}O_{enamel}$ than grazers (Cerling et al., 1997a; Quade et al., 1995; Kingston, 2003). This trend has been attributed to less drinking coupled with canopy-feeding or foraging in relatively open and arid biomes where leaf water is enriched in the isotopically heavy water $H_2^{18}O$ relative to local source water. Differences in $\delta^{18}O_{enamel}$ between the Laetoli giraffid species are not significant. Although both extinct and modern giraffids at Laetoli exhibit the most positive $\delta^{18}O_{enamel}$ herbivore signatures, there is significant variation, with some extinct giraffids exhibiting values similar to those of other fossil herbivores and others with enamel 4–5‰ more positive relative to other taxa. In contrast to these findings, modern *Giraffa camelopardalis* at Morea Estate, South Africa yielded the most ^{18}O-depleted herbivore enamel (Sponheimer and Lee-Thorp, 2001), which the authors interpret as reflecting a higher incidence of drinking in the well-watered lowveld or due to the analysis of dP_4s rather than adult molars. Analyses of inter-tooth variation in a maxilla of extant *G. camelopardalis* from Laetoli revealed that earlier formed P^4 enamel was over 2‰ more positive relative to bulk $\delta^{18}O_{enamel}$ of the M^3 (Kingston, 2003). Overall, these data suggest diverse behaviors during growth, between individuals, and in different ecosystems, with perhaps the more negative values in giraffes reflecting greater access to standing water or juvenile browsing on lower vegetation in the canopy where rates of evapotranspiration are reduced. Despite these complexities, it is interesting to note that giraffids from the Laetolil beds are statistically ^{18}O-depleted relative to modern giraffes (Table 3), suggesting reduced evapotranspiration in more closed canopies in the past at Laetoli or perhaps more drinking by the extinct giraffids.

6. Discussion

The Laetoli isotopic data indicate a wide range of foraging strategies, characterized in general by mixed C_3/C_4 feeding and highly variable diets. Although C_4

grasses evidently represented a significant component of herbivore forage at Laetoli during the Pliocene, only equids (representing about 3% of the mammalian taxa) reflect a predominantly C_4 grazing niche. Relatively negative $\delta^{13}C_{enamel}$ values of a number of specimens of *Eurygnathohippus* from the Upper Laetolil Beds indicate, however, that even some equids consumed significant amounts of browse (assuming C_3 grass was not available or extremely limited). Other extinct herbivores, such as the suid *Notochoerus euilus* and the rhinocerotid *Ceratotherium*, generally interpreted as grazers, yielded $\delta^{13}C_{enamel}$ values reflecting eclectic diets ranging from mostly grass to essentially exclusive browse. Fossil representatives of Hippotragini and Alcelaphini at Laetoli have isotopic signatures indicating mixed C_3/C_4 diets, contrasting with their modern counterparts, which are primarily obligate grazers. Studies of extinct herbivores suggests that morphological adaptations, including hypsodonty, generally interpreted as specialization into a grazing niche, may in fact reflect a widening of the niche breadth that allowed grazing as well as browsing (Perez-Barberia et al., 2001; Feranec, 2003). Earliest representatives of lineages with grazing adaptations may have been intermediate feeders with a preference for browse.

The Laetoli data also highlight a significant difference between overall dietary patterns in modern and fossil herbivores in Africa, specifically that foraging patterns of fossil herbivore lineages appear more eclectic than extant African taxa. Cerling et al. (2003b) observe that mixed C_3/C_4 diets with $\delta^{13}C_{enamel}$ values between ca. $-7‰$ to $-3‰$ are rare in modern East African herbivores, yet this intermediate browser–grazer range is typical of many if not most fossil herbivores taxa at Laetoli, as well as some of the other fossil sites. Despite interpretations of dietary specialization based on craniodental morphology, the isotopic signals suggest that many of these extinct herbivores were primitively generalists relative to modern taxa and may have occupied fundamentally different feeding niches or inhabited ecosystems in the past for which there are no modern analogs. However, it may be significant to recognize that most modern herbivore enamel utilized for comparison has been retrieved from game parks or regions with significant anthropogenic disturbance. It is conceivable that the apparent modern dietary specialization represents a strategy within the generalized foraging spectrum of these herbivore lineages in diversity impoverished and low productivity ecosystems. Alternatively, the apparent dietary diversity of fossil species may reflect shifting niche partitioning as competing taxa became extinct or experienced adaptive radiations. The shift of *Loxodonta* from C_4 grazing to a predominantly browsing niche, for example, may reflect the extinction of competing large browsers during the Plio-Pleistocene rather than a change in available habitats.

Assessment of the isotopic data within a detailed stratigraphic context did not reveal significant changes or trends in foraging strategy in any of the lineages within the Laetolil Beds or between the Upper Laetolil and Upper Ndolanya Beds. Limited sampling from the Upper Ndolanya Beds, however, compromised the latter result and ongoing isotopic research is examining the isotopic nature of significant changes in taxonomic representation documented between these two stratigraphic units. The faunal transition between the Upper Laetolil and Upper Ndolanya Beds, straddling a ~1 Ma interval, and reflecting quite different taphonomic biases, is interpreted to reflect a shift towards drier and more open habitats (Leakey, 1987a; Harris, 1987d; Kovarovic et al., 2002). This culminates in Upper Ndolanya Beds faunas in which large bovids (especially alcelaphines) comprise more than 80% of the mammalian taxa. Isotopic analyses of these alcelaphine bovids ($n=2$) yielded among the most positive $\delta^{13}C_{enamel}$ values, and ongoing isotopic research has targeted this group to assess the extent to which this taxon represents a dominant obligate grazing guild, not otherwise documented in the sequence. Although not statistically significant, it is interesting to note that several taxa analyzed across this transition, at the genus or family level, reflected slightly more ^{13}C-enriched median carbon isotopic values in the younger Upper Ndolanya Beds, indicating either a greater grazing component, an increase in aridity, shifts in the $\delta^{13}C$ of atmospheric CO_2, or some combination of these. While the isotopic data are preliminary for the Upper Ndolanya Beds, they are consistent with a scenario in which representation of resident taxa during Ndolanya times, foraging in habitats perhaps locally or regionally more grassy than Laetolil Bed biomes, is swamped by migratory, grazing bovids. These data suggest that although the ecology of *A. afarensis* and *P. aethiopicus* had many elements in common, they may have differed significantly in the specific niches that were available to them at the different times.

Although consistent carbon isotopic variability for the various taxa throughout the Upper Laetolil Beds does not unequivocally rule out the possibility of subtle shifts in ecology or community composition through the ~300 ka represented, isotopic profiles suggest that it may be reasonable to analyze the assemblage as a composite. The intra-specific carbon isotopic variability of the three Laetolil Beds taxa traditionally interpreted as grazers (the suid *N. euilus*, the rhinocerotid *C. praecox*, and the equid *Eurygnathohippus*), appears greater than that documented for extant populations of related herbivore species sampled from varied East African ecosystems. The small sample sizes currently complicate attempts to statistically support this claim. Sampled Randomization Tests were used to generate probabilities that differences in intra-specific ranges could be due to chance alone (Table 3). These probabilities ranged from 0.065, 0.140, to 0.004 for the equids, rhinocerotids, and suids respectively, tentatively supporting the significance of these differences. Significantly greater intra-population isotopic variability within the Lateoli sequence relative to modern taxa could indicate either greater dietary diversity of foraging niches for these taxa in the past or foraging flexibility related to instability in the resource base due to short-term eruptive events or Milankovitch scale climatic change. Ongoing work is examining this issue at Laetoli.

An additional objective of this research was to identify a mammalian taxon or lineage whose diet would possibly serve as a reliable paleoecological proxy, in effect an isotopic ecological indicator. Based on the diverse and shifting dietary patterns documented isotopically in Africa during the Neogene, including modern representatives, it is clear that developing a composite profile of dietary patterns of many representative taxa is ultimately essential. Foraging patterns of mammalian lineages appear more flexible and variable than suspected based on related extant taxa and are contingent on dietary strategies of sympatric taxa. Faced with incremental or subtle environmental shifts, many taxa are able to maintain foraging niches, and ecological change may only be revealed by combining isotopic analyses of many herbivore lineages with other dietary or ecological proxies such as ecomorphology and micro-/mesowear analysis. Alternatively, dietary shifts may reflect niche jostling within the community independent of any environmental or large-scale ecological changes.

The almost complete absence of specialized grazing guilds and the heavy reliance on browse by most fossil herbivores do not support the inference that Laetoli was dominated by extensive grassland habitats. Evidence of a variable C_4 grazing component in all lineages, other than giraffids, however, does indicate that grasses were ubiquitous, although the proportions and distribution of grass with respect to woody shrubs and trees remains unknown. The Laetoli herbivore dietary spectrum and taxonomic representation indicates the occurrence of habitats dominated by closed woodlands with a substratum of C_4 grasses or open woodland interspersed with grassy patches. Relative to other fossil localities where enamel has been extensively analyzed, Laetoli isotopic values generally indicate similar dietary patterns, although there is a consistent bias towards a greater C_3 dietary component among Laetoli herbivores. Compared to modern African herbivore isotopic profiles, the Laetoli cumulative dietary spectrum is heavily weighted towards C_3 biomass. It is difficult to reconcile these data with earlier interpretations that Laetoli represents a grassland-savanna habitat.

Oxygen isotopic values of fossil herbivore teeth from Laetoli are consistent with the ranges documented at other fossil localities although they appear to tend more toward the negative end of the range. Relative to modern representatives of the various lineages, the Laetoli fossils have statistically significantly more ^{18}O-depleted isotopic signatures. While these differences may relate to a number of factors including global or regional shifts in atmospheric $\delta^{18}O$, regional variation in the $\delta^{18}O$ of available water, and behavioral/physiological changes, it is also possible that these trends reflect greater evaporative regimes or aridity in modern East African ecosystems relative to those inhabited by the Laetoli fossil faunal communities. The latter interpretation corroborates environmental interpretations based on the carbon isotopic data from the sequence.

The Laetoli isotopic data also indicate that modern African ecologies may not provide appropriate analogs, specifically in the foraging behavior of the herbivore community, but perhaps also in the overall physiognomy and composition of the vegetation. Previous studies of the fauna and flora at Laetoli have clearly identified a suite of proxies indicating aridity, seasonality, and grass dominated habitats (Hay, 1981, 1987; Bonnefille and Riollet, 1987; Meylan, 1987; Meylan and Auffenberg, 1987; Denys, 1987; Petter, 1987; Bonnefille, 1995). These reconstructions are compatible with ecological conditions favorable to support the C_4 dietary biomass recorded in the teeth. The different data sets together indicate heterogeneity in the types of habitats present in the past. During the Pliocene, as now, Laetoli was adjacent to volcanic highlands and while locally the land surface was of low-relief (Hay, 1981), it was topographically diverse regionally and fauna presumably had access to variable habitats associated with differential drainage, altitude, bedrock, and localized microclimates. Laetoli does represent a unique habitat for early hominins in that it is not proximate to a lake margin or major river system, and the juxtaposition of grassland and woodland indicators in the fossil assemblage cannot simply be attributed to riverine or lake-fringing gallery forests that give way distally to grassland. In addition, the local environment was significantly influenced by volcanic activity, presumably resulting in an indeterminate number of vegetational successions due to the numerous volcanic eruptive events documented in the sedimentary succession.

7. Conclusions

Isotopic analyses of a suite of mammalian herbivore taxa from the Pliocene site of Laetoli, including multiple samples of 21 herbivore taxa representing 8 families, were used to develop a consensus reconstruction of available forage and by inference habitat types. Dietary patterns of the various herbivore guilds represented in the Laetolil and Upper Ndolanya Beds indicate eclectic, mixed C_3/C_4 diets for all herbivore families other than the browsing giraffids. These patterns, along with considerable intra-specific variability in both carbon and oxygen isotopes of the herbivore enamel relative to modern African herbivores, suggest generalized foraging ecology with no close modern analog. Evaluated in the context of equivalent data from other fossil localities, Laetoli dietary signatures reveal complex and variable foraging patterns in African herbivore lineages, reflecting dynamic intrinsic biotic and external climatic and tectonic forces on African ecosystems. The limited representation of obligate grazers and the high diversity of mixed feeders and browsers in the assemblage indicates a heterogeneous woodland ecosystem and does not support earlier interpretations of a landscape dominated by grassland-savanna. This reconstruction situates the Laetoli hominins in a 'patchy mosaic ecology' similar to paleoecological reconstructions of other Pliocene hominin sites in East Africa. As a consequence, the preferred ecological range for early hominins becomes more narrowly constrained to woodland or woodland-forest mosaics. This has important implications for developing adaptive explanations for evolutionary innovations such as bipedalism, tool use and manufacture, encephalization, and dietary shifts, all of which have been linked to selective pressures encountered by early hominins foraging in grassland-savannas. However, identifying and characterizing the specific ecological niche of hominins within these heterogeneous ecosystems, ultimately critical for reconstructing adaptive landscapes, remains a considerable challenge.

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