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 Pliocene-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 wooded 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 C3 and C4 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 C3 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 C3/C4 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 18O 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...
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 Laetolil 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.

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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 Laetolil in northern Tanzania represents one of the key paleontological and paleanthropological localities in East Africa. Volcaniclastic sediments exposed in the Laetolil 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).

Palaeoecology 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 Laetolil 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). Laetolil 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 Laetolil to indicate more wooded ecosystems than previously considered. A subsequent assessment supported the notion that, although the composite fauna from Laetolil 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; Kolarovic 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 (Kolarovic et al., 2002) indicate a transition during the later Pliocene at Laetolil to semi-arid scrub or bushland habitats. Stable isotope investigations of paleosol carbonates (Berling, 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 Laetolil 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 (δ13C 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 (δ18O 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. C4 grasses, for example, are considered to be less nutritious than C3 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 Ndoninya 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 Ndoninya Beds? Recent recovery of Paranthropus aethiopicus from the Upper Ndoninya 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 Laetolil succession is exposed over an area of >1600 km², although most of the paleontological collections to date have been recovered from a relatively restricted area (∼100² 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, 1987; Ndessokia, 1990; Manega, 1993). This latter unit is overlain by the Olgoi 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; Tieszen 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...
Table 1
Herbivore carbonate hydroxylapatite δ¹³C and δ¹⁸O of fossil and modern samples collected at the site of Laetoli

<table>
<thead>
<tr>
<th>Sample number</th>
<th>Formation</th>
<th>Taxon</th>
<th>δ¹³C enamel</th>
<th>δ¹⁸O enamel</th>
<th>Element</th>
<th>Locality</th>
<th>Stratigraphic level</th>
</tr>
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<tbody>
<tr>
<td>114</td>
<td>U. Laetoli Beds</td>
<td>Ceratherium praecox</td>
<td>−5.9</td>
<td>−1</td>
<td>Lower cheek tooth</td>
<td>Loc. 9 S</td>
<td>Below tuff 2</td>
</tr>
<tr>
<td>115</td>
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<td>Ceratherium praecox</td>
<td>−11.0</td>
<td>−1.1</td>
<td>Upper molar</td>
<td>Loc. 21</td>
<td>Between tuffs 5 and 8</td>
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<td>Upper molar</td>
<td>Loc. 6</td>
<td>Between tuffs 5 and 6</td>
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<td>Lower molar</td>
<td>Loc. 21</td>
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<td>Loc. 9 S</td>
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<td>4.2</td>
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1.2 Family Giraffidae

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<td>Lower molar</td>
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1.3 Family Gomphotheriidae, Elephantidae, and Deinotheriidae

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### 1.3 Family Gomphotheriidae, Elephantidae, and Deinotheriidae

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### 1.4 Family Suidae

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<th>Stratigraphic level</th>
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### 1.5 Family Equidae

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Table 1 (continued)

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<td></td>
</tr>
<tr>
<td>14</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-4.0</td>
<td>0.6</td>
<td>Upper M2</td>
<td>Loc. 13</td>
<td>Between tuffs 6 and 8</td>
</tr>
<tr>
<td>20</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-8.0</td>
<td>-0.1</td>
<td>Upper M2</td>
<td>Loc. 10 E</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>34</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
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<td>0.3</td>
<td>Upper M2</td>
<td>Loc. 10 E</td>
<td>Between tuffs 6 and 7</td>
</tr>
<tr>
<td>40</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
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<td>2.5</td>
<td>Lower molar</td>
<td>Loc. 10 W</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>47</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-6.4</td>
<td>-1.3</td>
<td>Upper M3</td>
<td>Loc. 10</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>120</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-4.6</td>
<td>-2.0</td>
<td>Upper molar</td>
<td>Loc. 2</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>121</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-9.8</td>
<td>-0.2</td>
<td>Lower M3</td>
<td>Loc. 2</td>
<td>Between tuffs 5 and 7</td>
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<tr>
<td>122</td>
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<td>Lower M2</td>
<td>Loc. 8</td>
<td>Between tuffs 5 and 6</td>
</tr>
<tr>
<td>123</td>
<td>U. Laetolil Beds</td>
<td>Gazella janenschii</td>
<td>-1.9</td>
<td>4.5</td>
<td>Upper molar</td>
<td>Loc. 15</td>
<td>Between tuffs 6 and 8</td>
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<tr>
<td>76</td>
<td>U. Ndolanya Beds</td>
<td>Gazella janenschii</td>
<td>-7.8</td>
<td>-2.0</td>
<td>Upper M2</td>
<td>Loc. 18</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-8.6</td>
<td>-2.0</td>
<td>Upper molar</td>
<td>Loc. 1</td>
<td>Between tuffs 6 and 8</td>
</tr>
<tr>
<td>19</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-8.0</td>
<td>-0.9</td>
<td>Upper M1</td>
<td>Loc. 10 E</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>33</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
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<td>-0.8</td>
<td>Lower M3</td>
<td>Loc. 10 E</td>
<td>Between tuffs 6 and 7</td>
</tr>
<tr>
<td>40</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-2.2</td>
<td>-0.4</td>
<td>Lower M2</td>
<td>Loc. 10 W</td>
<td>Below tuff 3</td>
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<tr>
<td>42</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-2.6</td>
<td>0.3</td>
<td>Upper M1</td>
<td>Loc. 10W</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>43</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-0.4</td>
<td>-1.6</td>
<td>Lower M2</td>
<td>Loc. 10W</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>46</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-1.1</td>
<td>-0.2</td>
<td>Upper M1</td>
<td>Loc. 10</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>9</td>
<td>U. Ndolanya Beds</td>
<td>Parmularius pandatus</td>
<td>-0.0</td>
<td>3.1</td>
<td>Lower M3</td>
<td>Loc. 2</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>31</td>
<td>U. Laetolil Beds</td>
<td>Aleclaphini sp.</td>
<td>-0.1</td>
<td>1.5</td>
<td>Upper molar</td>
<td>Loc. 10E</td>
<td>Between tuffs 6 and 7</td>
</tr>
<tr>
<td>74</td>
<td>U. Ndolanya Beds</td>
<td>Aleclaphini, medium sp.</td>
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<td>-0.4</td>
<td>Lower M3</td>
<td>Loc. 18</td>
<td></td>
</tr>
<tr>
<td>73</td>
<td>U. Ndolanya Beds</td>
<td>Aleclaphini, large sp.</td>
<td>0.6</td>
<td>1.0</td>
<td>Lower M2</td>
<td>Loc. 18</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-9.1</td>
<td>1.7</td>
<td>Upper molar</td>
<td>Loc. 1</td>
<td>Between tuffs 6 and 8</td>
</tr>
<tr>
<td>21</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-5.0</td>
<td>0.7</td>
<td>Lower molar</td>
<td>Loc. 10E</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>35</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-4.0</td>
<td>2.3</td>
<td>Upper molar</td>
<td>Loc. 10 E</td>
<td>Between tuffs 6 and 7</td>
</tr>
<tr>
<td>36</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-7.5</td>
<td>2.8</td>
<td>Upper M1</td>
<td>Loc. 10 E</td>
<td>Between tuffs 6 and 7</td>
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<tr>
<td>45</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-2.3</td>
<td>2.7</td>
<td>Upper M3</td>
<td>Loc. 10 W</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>141</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-4.9</td>
<td>1.3</td>
<td>Upper molar</td>
<td>Loc. 21</td>
<td>Between tuffs 5 and 8</td>
</tr>
<tr>
<td>142</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
<td>-7.7</td>
<td>1.5</td>
<td>Upper molar</td>
<td>Loc. 21</td>
<td>Between tuffs 5 and 8</td>
</tr>
<tr>
<td>143</td>
<td>U. Laetolil Beds</td>
<td>Hippotragini sp.</td>
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<td>1.9</td>
<td>Upper molar</td>
<td>Loc. 8</td>
<td>Between tuffs 5 and 8</td>
</tr>
<tr>
<td>38</td>
<td>U. Laetolil Beds</td>
<td>Madoqua avifluminis</td>
<td>-6.4</td>
<td>-2.7</td>
<td>Upper molar</td>
<td>Loc. 10</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>41</td>
<td>U. Laetolil Beds</td>
<td>Madoqua avifluminis</td>
<td>-10.6</td>
<td>1.6</td>
<td>Upper M3</td>
<td>Loc. 10 W</td>
<td>Between tuffs 5 and 8</td>
</tr>
<tr>
<td>48</td>
<td>U. Laetolil Beds</td>
<td>Madoqua avifluminis</td>
<td>-7.3</td>
<td>-1.8</td>
<td>Lower molar</td>
<td>Loc. 10 E</td>
<td>Between tuffs 5 and 7</td>
</tr>
<tr>
<td>32</td>
<td>U. Laetolil Beds</td>
<td>Trogelaphus sp.</td>
<td>-8.1</td>
<td>-2.5</td>
<td>Upper M2</td>
<td>Loc. 10 E</td>
<td>Between tuffs 6 and 7</td>
</tr>
<tr>
<td>37</td>
<td>U. Laetolil Beds</td>
<td>Trogelaphus sp.</td>
<td>-7.9</td>
<td>-2.1</td>
<td>Upper M3</td>
<td>Loc. 10</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>44</td>
<td>U. Laetolil Beds</td>
<td>Trogelaphus sp.</td>
<td>-8.2</td>
<td>2.9</td>
<td>Upper M1</td>
<td>Loc. 10 W</td>
<td>Below tuff 3</td>
</tr>
<tr>
<td>177</td>
<td>U. Laetolil Beds</td>
<td>Trogelaphus sp.</td>
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<td>-2.2</td>
<td>Upper molar</td>
<td>Loc. 21</td>
<td>Between tuffs 5 and 8</td>
</tr>
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<td>Md64</td>
<td>Modern</td>
<td>Madoqua kirkii</td>
<td>-11.1</td>
<td>-2.2</td>
<td>Lower M3</td>
<td>Laetoli Area</td>
<td></td>
</tr>
</tbody>
</table>
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 deinotherene enamel yielded distinct browsing isotopic signatures while the equids and aelaphines 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 (δ13C) 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; Tieszen 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, 12C and 13C. 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 C3 photosynthetic pathway is characteristic of most trees and shrubs, as well as high altitude grasses that prefer wet, cool growing seasons. The tissues of C3 plants have δ13C 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 C3 plants reflects genetic and environmental factors, such as water stress, nutrient availability, light intensity, CO2 partial pressure, and temperature (Farquhar et al., 1982; Tieszen, 1991; Heaton, 1999). Overall, there tends to be an increase in the amount of 13C in C3 plants from wet to mesic and xeric habitats and the δ13C value of C3 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 CO2 is restricted and light conditions are low, δ13C values can be very negative (<30‰)(Medina and Minchin, 1980; Sterberg et al., 1989; van der Merwe and Medina, 1989). As altitude increases, leaf carbon isotope discrimination (∆) decreases, resulting in more positive δ13C values for C3 plants at higher elevations (Tieszen et al., 1979b; Korner et al., 1991; Sparks and Ehleringer, 1997).

C4 physiology is linked almost exclusively to monocotyledons, especially grasses and sedges growing in hot, arid habitats. A mean δ13C value of −13.1‰ ± 1.2‰ has been calculated for C4 plants with a range of about −14 to −11‰ (O’Leary, 1988; Heaton, 1999; Cerling et al., 2003a). There are several C4 subtypes distinguished on the basis of biochemical pathways and anatomy that contribute to the variability. Three sub-pathways are dominant in East African grasses — arid adapted C4 species that utilize the NAD-me and PEP-ck subpathways (Hattersley, 1992; Chapman, 1996) with an average δ13C 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 δ13C 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 C4 and C3 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 CO2 by the CAM (Crassulacean acid metabolism) pathway, C3–C4 intermediates, and C4 dicots potentially complicate this dichotomy, but it is unlikely that these plants comprised a significant component of the equatorial African biomass during the Pleocene.

3.3. Oxygen

The oxygen isotopic composition (δ18O) 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). \(\delta^{18}O\) 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. 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 Buri Member, Koobi Fora Fm.; tb = Tulag Bur Member, Koobi Fora Fm.; l = Lokochot Member, Koobi Fora Fm.; ky = Kaiyumung Member, Nachukui Fm.] Chad [KB = Kossum Bougoudi unit; KL = Kollé unit; KT = Koro Toro unit] Tugen Hills [CH = Chemeron Fm.; LU = Luekino Fm.; MP = Mpesia Fm.; NGG = Ngeringowera Beds, Ngorora Fm.] Gona [GWM-3/5 = Gona Western Margin block 3 and 5 sites] Abu Dhabi [BA = Bayunah Fm.] Storkfornet and Swartvans [mb1–6 = members 1–6]. References: Proboscidea [1] (Cerling et al., 1999, 5) (Bocherens et al., 1996), 5 (Zazzo et al., 2000), 5 (Semaw et al., 2005, 5) (Schoninger et al., 2003)] Rhinocerotidae [1] (Cerling et al., 1999), 5 (Bocherens et al., 1996), 5 (Cerling et al., 2002), 5 (Zazzo et al., 2000, 5) (Kingston, 1992, 5) Suidae [1] (Harris and Cerling, 2002, 5) (Bocherens et al., 1996, 5) (Plummer et al., 1999, 5) (Zazzo et al., 2000, 5) (Lee-Thorp, 1989, 5) Giraffidae [1] (Cerling and Harris, 1999, 5) (Lee-Thorp, 1989, 5) (Semaw et al., 2005, 5) (Zazzo et al., 2000) Equidae [1] (Cerling et al., 2003a, 5) (Cerling et al., 2003b, 5) (Bocherens et al., 1996, 5) (Sponheimer and Lee-Thorp, 1999b, c, d) (Lee-Thorp, 1989, 5) (Lee-Thorp et al., 1994) (Ericson et al., 1981, 5) (Zazzo et al., 2000, 5) (Semaw et al., 2005, 5) (Kingston, 1992, 5) (Sponheimer and Lee-Thorp, 1999b) Bovidae [1] (Cerling et al., 2003c, 5) (Lee-Thorp et al., 2000, 5) (van der Merwe et al., 2003, 5) (Sponheimer et al., 1999, 5) (Zazzo et al., 2000, 5) (Semaw et al., 2005, 5) (Cerling et al., 2003b, 5) (Lee-Thorp, 1989, 5) (Lee-Thorp et al., 1994, 5) (van der Merwe and Thackeray, 1997, 5) (Plummer et al., 1999, 5) (Lee-Thorp and van der Merwe, 1993, 5) (Sponheimer et al., 2003, 5).

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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 CH₃COOH 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 (H₃PO₄) at 90 °C in sealed borosilicate reaction 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 CO₂ and silver were heated to 50 °C to remove impurities, such as SO₂ or H₂S, that could contribute interfering masses. Mass spectrometry was performed at Yale Stable Isotope Laboratory using a MAT-Finnegan 251 mass spectrometer interfaced with a tubercracker and

at the University of Florida, Department of Geoscience Stable Isotope Lab using a VG Prism 602 also interfaced with a tubercracker. Once it was established that SO$_2$ or H$_2$S 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:

\[
\delta^{13}C = \frac{(18)O}{(16)O} = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \\
R = \frac{^{13}C}{^{12}C} \text{ or } \frac{^{18}O}{^{16}O}
\]

Carbon and oxygen values are reported relative to PDB (Pee Dee Belemnite). Precision was ±0.09‰ for $\delta^{13}C$ ratios and ±0.17‰ for $\delta^{18}O$ 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 pCO$_2$ and $^{13}$C values. These variables are not necessarily constant across habitats,
Dietary classification with δ¹³C ranges based on mixing model

<table>
<thead>
<tr>
<th>Dietary classification</th>
<th>General foraging strategyᵃ</th>
<th>Approximate modern δ¹³C range</th>
<th>+1.5‰ adjusted pre-industrial fossil δ¹³C rangeᵇ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obligate grazer</td>
<td>Almost exclusively monocots (&gt;95%)</td>
<td>&gt;0.5‰</td>
<td>&gt;2‰</td>
</tr>
<tr>
<td>Variable grazer</td>
<td>Predominance of monocots (75–95%) but with seasonal, geographic, or ecological variability in C₃ dicot consumption</td>
<td>0.5 to −2.5‰</td>
<td>2 to −1‰</td>
</tr>
<tr>
<td>Browser–grazer</td>
<td>Mixed diets characterized by intermediate proportions of dicots and monocots</td>
<td>−2.5 to −9.5‰</td>
<td>−1 to −8‰</td>
</tr>
<tr>
<td>Variable browser</td>
<td>Predominance of dicots (75–95%) with seasonal, geographic or ecological variability in C₄ monocot consumption</td>
<td>−9.5 to −12.3‰</td>
<td>−8 to −10.8‰</td>
</tr>
<tr>
<td>Obligate browser</td>
<td>Almost exclusively dicots (&gt;95% C₃ dicots)</td>
<td>&lt;−12.3‰</td>
<td>&lt;−10.8‰</td>
</tr>
</tbody>
</table>

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 C₃/C₄ 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 δ¹³C_{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 C₃ and C₄ endmembers of −25.6±2.0‰ and −13.1±1.2‰ respectively (incorporating +1.5‰ correction for post-industrial ¹³C depletion), a mixing model for C₃–C₄ 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 δ¹³C relative to pre-industrial value (Marino and McElroy, 1991).

In general, δ¹³C_{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 C₃/C₄ 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 successions (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 successions (Fig. 4). The general range of inter- and intra-specific δ¹⁸O_{enamel} variability in the Laetoli assemblage is consistent with that documented in other African fossil assemblages as well as modern herbivores 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 δ¹⁸O depletion in the fossil material relative to potential descendant 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 ¹⁸O compared to modern equatorial assemblages, possibly indicating more humid conditions at Laetoli during deposition of the sequence. Simple comparisons of δ¹⁸O_{enamel} values between geographically and temporally distinct assemblages, however, are complicated by the great diversity in behaviors and local conditions controlling δ¹⁸O (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.

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$_{\text{enamel}}$ 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 Africa. 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$_{\text{enamel}}$ 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).](image-url)
South Africa or Tighenif in Algeria (Bocherens et al., 1996), were excluded, as the paleohabitats at the time appear to be \( \text{C}_3 \) dominated with limited evidence of \( \text{C}_4 \) 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 \( \delta^{13}\text{C}_{\text{enamel}} \). 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 lohps of the upper molars, a progressive elongation of the cranum, 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 δ13C enamel values consistent with a variable to obligate C4 grazing diet averaging about 0.0% and *Diceros bicornis* with a C3 browsing diet with a mean of about −10.5% (Fig. 5a). Cerling and Harris (1999) suggest that more positive δ13C enamel values (ca. −10 to −7‰) of *D. bicornis* from arid habitats, such as Amboseli (Bocherens et al., 1996), Koobi Fora, or Ngurema in Kenya may indicate C4 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 δ13C 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 C3 dietary preference, even though contemporaneous equids exhibit a significant C4 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 C4 grazing, but several million years later (~4–3.5 Ma) (Zazzo et al., 2000). Isotopic signatures of *Ceratotherium* from the Laetoli 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 Laetoli Beds indicates an almost exclusive C4 diet, while several samples, some potentially contemporaneous, reflect a diet consisting of essentially pure C3 browse. The distribution of δ13C for *Ceratotherium* from the Upper Laetoli 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 Laetoli Beds are statistically more 13C 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 δ13C values suggest that *Ceratotherium* was more of an opportunist– 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 Laetoli 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 Laetoli Beds specimens are statistically more depleted in 18O (Mann–Whitney, p<0.01) than modern *Ceratotherium*, with the median of Laetoli fossil δ18O 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 Laetoli Beds has been attributed to three species (Beden, 1987; Harris, 1987a): *Anancus kenensis* from the Lower Laetoli Beds, and
Deinotherium bozasi and Loxodonta exoptata from the Upper Lactolil Beds. Proboscidians 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 M2 and slightly thinner enamel than that from the Lactolil Beds. The isotopic signatures for these taxa indicate diverse foraging strategies that reflect niche partitioning (Fig. 5b). Deinotherium molar δ13C values are consistent with an exclusive C3 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 C3/C4 to variable C4 grazing dietary strategies for Anancus and Loxodonta at Laetoli with δ13C values ranging from ca. −6‰ to 0‰. There are no apparent trends or statistically significant shifts in proboscidian dietary signals through the sequence (Fig. 3).

The low-crowned, thick enameled bunodont teeth of A. kenensis indicate adaptations for crushing and grinding rather than shearing, suggesting a foraging strategy dominated by browsing (Tassy, 1994). The δ13C enamel of a molar fragment of A. kenensis collected from Lower Lactolil Beds is −2.5‰, reflecting a predominantly C4 grass diet. This result lies within the range established for A. kenensis 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 (Longumum Member) (4.5–4.0 Ma) (Cerling et al., 1999, 2003b). These data provide evidence for an almost exclusive grazing strategy for A. kenensis 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 δ13C value of C3 vegetation, suggesting that perhaps earlier forms were variable browsers. This sample, however, derives from prior to the Late Miocene expansion of C4 grasslands when C3 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 proboscidian 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 proboscidian 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 C3 to C4 dominated diets in proboscidians at about 8 Ma. δ13C values indicate that gomphotheriids and elephantids were grazers or mixed feeders more than browsers at least 4 Ma preceding the occurrence of the Laetoli proboscidians. These data do not support the notion that the Laetoli Loxodonta reflect a novel foraging niche.

The range of δ13C values for Laetoli Loxodonta specimens is consistent with material from other fossil localities (Fig. 5b), suggesting similar C4 dominated diets and possibly similar ecosystems. The Laetoli values, especially those of the Upper Laetoli Beds, are in general more 13C-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 elephantids contrast with the δ13C enamel of extant African Loxodonta, which indicate a diet generally dominated by C3 biomass (Cerling et al., 1999). Hypotheses to explain this discrepancy include reduction of C4 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 18O-depleted relative to reported δ18O 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<0.05 for Chad and the Ndolanya Beds *Loxodonta*). These data may also indicate less arid conditions 3.8–3.5 Ma in the Laetolil 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; Kovačovic, 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, Hippostragini, 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 C3/C4 feeding within the tribe (e.g., eland, *Taurotragus oryx* (Lee-Thorp, 1989; Cerling et al., 2003a; Sponheimer et al., 2003). δ13C enamel values of enamel of *Tragelaphus cf. kvaloa* 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 Makaşansgat (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 Laetolil 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, Parenteragorn 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 $^{13}$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 grazer’ 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. cf. 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 alcelaphines) 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 $\delta^{13}C_{\text{enamel}}$ values of modern antelope data from South and East Africa ($n=78$) yields an average dietary signal of $-9.2\%_{\text{oo}}$ ($\pm 1.5\%_{\text{oo}}$) (Sponheimer and Lee-Thorp, 2003) for the tribe. This reflects mixed feeding strategies, but with an emphasis on browsing. Enamel analyses of extant antelopes 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 $\delta^{13}C_{\text{enamel}}$ values corresponding to a diet of essentially pure C$_3$ browse (Cerling et al., 2003c). Antelopes from Laetoli include Gazella janenschii from the Laetolil Beds, and G. janenschii, Antidorcas sp., and Antilopini sp. 1 from the Upper Ndolanya Beds. Gentry (1987) notes that the teeth of G. janenschii are rather generalized and fairly hypsodont and Gentry and Gentry (1978a,b) suggest that G. janenschii is ancestral to G. thomsoni and G. rufifrons. As with the modern gazelles, analyses of G. janenschii from the sequence indicate a variable diet ($-2\%_{\text{oo}}$ to $-10\%_{\text{oo}}$), but with a median of $-7\%_{\text{oo}}$, indicating a foraging strategy focused more on browsing than modern antelopes. Although these represent the only fossil antelopes analyzed from East Africa, isotopic data on fossil antelopes 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 Laetoli 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 thermo-regulatory 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). $\delta^{13}C_{\text{enamel}}$ 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 $-6.5\%_{\text{oo}}$ to $-10.6\%_{\text{oo}}$ with a median over $3\%_{\text{oo}}$ more positive than the modern taxa (using $1.5\%_{\text{oo}}$ correction), suggesting that the extinct forms incorporated 15–20% more grass into their diets.

5.4.7. Summary

Collectively, carbon isotopic analyses of Laetoli bovid diets 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 boids are C$_3$ or C$_4$ specialists that maintain their specialized diets despite forage heterogeneity in home ranges (Sponheimer et al., 2003). The $\delta^{13}C_{\text{enamel}}$ 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 bovid 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 boids, 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 hipparionine 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 Laetolil collections.

In conjunction with a global expansion of C₄ biomass during the late Miocene, equid diets transitioned from C₃ dominated to C₄ 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 C₃ grazing (Fig. 5a). A number of craniodental characters associated with late Miocene equids in Africa (Hipparitherium 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 C₃ grasslands may have been a component of East African ecosystems prior to the Late Miocene isotopic transition. Mixed C₃/C₄ equid diets, allocated to the transition, have been documented at Samburu (Namarungule Fm. ~9 Ma), Abu Dhabi (Bayunnah Fm. ~8–6 Ma), and Lothagam (lowest Lower Nawata ~7.5 Ma). Except at Langebaanweg (South Africa), where C₄ grasses were not established by ~5 Ma (Franz-Obendaal et al., 2002), equid enamel younger than about 7 Ma in tropical and sub-tropical Africa, including all modern samples, have previously yielded δ¹³C enamel values in the range of ~2‰ to 3‰, indicating C₄ dominated to exclusive C₄ 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 C₃ grassland by C₄ grassland 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 C₃ grasslands by C₄ grasslands, more wooded or forested C₃ habitats by C₄ 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 δ¹³C enamel values of ~4‰ for two specimens of Eurygnathohippus from the Upper Laetolil Beds indicate a mixed C₃/C₄ diet at 3.8–3.4 Ma, well after the transitional interval. Laetolil equids were either C₄ grazers supplementing their diet with C₃ browse or C₃ 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 C₄ grasses in East African ecosystems resulted in a dietary switch from C₃ vegetation to a more mixed C₃/C₄ diet as well as the exclusive grazing niche occupied by modern equids, with dietary proportions of dietary C₃ and C₄ 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 C₃ biomass in the diet than equids at other sites or that local C₄ grasses were ¹³C-enriched because they were dominantly classical-NADP subtypes associated with more mesic environments than the arid adapted Nad-me or PEP-ck C₄ grasses (Chapman, 1996). Supporting this later interpretation, δ¹⁸O enamel values for Laetoli Eurygnathohippus are similar to or more negative than those of other fossil localities 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 hypocondonty (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 anti-predator 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 meinertzhageni*) 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 C₄ to mixed C₃/C₄ 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 consistent with the notion that these suids were ecletic feeders, incorporating significant amounts of C₃ biomass into their diet. One specimen, from between Tuffs 7 and 5 in the Upper Laetolil Beds, yielded a δ¹³C enamel signal of −8.2‰, indicative of almost exclusive C₃ 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 C₃ 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 C₃/C₄ 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 δ¹³C 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 C₄ grass. Oxygen isotopic values for *N. euilus* are statistically more ¹⁸O-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 Ndoanyia 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 M3 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 kolpochoeres were exclusive grazers (Harris and Cerling, 2002; Cerling et al., 2005). However, Harris and Cerling (2002) note that the δ18O 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 isotopic to signatures of *K. limnetes* from Olduvai Bed I (Plummer et al., 1999). At Anabo Koma, a ∼1.6 Ma site in Djibouti, the δ13C enamel of a specimen of *K. limnetes* was −6.3‰ suggesting an even greater intake of C3 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 giraffe (*Giraffa stillei* and *G. jumae* respectively) and a sivathere (*Sivatherium cf. maursium*). 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. Sivathere species have been associated with habitats ranging from forest to open woodland (Churcher, 1978; Geraads, 1985). Features of sivathere species, 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 *Samaotherium 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 C3/C4 bimodality, δ13C patterns observed in forests and forest ecotones indicate significant enrichment in 13C in C3 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 13C in closed canopy habitats due primarily to soil-respired 13C-depleted CO2 trapping under forest canopies (i.e., the “canopy effect”) (Medina and Minchin, 1980) and irradiance intensity (Farquhar et al., 1989). The δ18O 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 C₃ 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 δ¹³Cₑnamel variability (Kingston, 2003), exceeding differences between fossil conspecifics and between giraffid species in the Laetoli sequence. Microsampling of a P⁴ and M³ from an individual G. camelopardalis documents almost 2% variation in δ¹³Cₑnamel 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 km² 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 δ¹³Cₑnamel values of −1.6‰ and −2.6‰, indicating a dietary intake of essentially C₄ plants (Kingston, 1999b). Of nine late Miocene herbivore species analyzed from Samos, Greece, Samotherium boissieri displayed the least negative values in δ¹³C (−5.4‰), which was interpreted to indicate that it preferred moisture-stressed C₃ plants, possibly C₃ grasses, or had a C₄ 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 C₄ grazing in early to middle Pliocene. Analyses of S. mauritius enamel from the Upper Laetoli and Upper Ndolanya Beds reveal no evidence of a grazing component in the diet. In fact, the δ¹³Cₑnamel 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 ¹⁸O-enriched oxygen values, with statistically significant more positive δ¹⁸Oₑnamel 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 δ¹⁸Oₑnamel 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 H₂¹⁸O relative to local source water. Differences in δ¹⁸Oₑnamel between the Laetoli giraffid species are not significant. Although both extinct and modern giraffids at Laetoli exhibit the most positive δ¹⁸Oₑnamel 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 ¹⁸O-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 δP,8 rather than adult molars. Analyses of inter-tooth variation in a maxilla of extant G. camelopardalis from Laetoli revealed that earlier formed P⁴ enamel was over 2‰ more positive relative to bulk δ¹⁸Oₑnamel of the M₃ (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 Laetoli beds are statistically ¹⁸O-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 C₃/C₄ feeding and highly variable diets. Although C₄
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 C4 grazing niche. Relatively negative δ13C 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 C3 grass was not available or extremely limited). Other extinct herbivores, such as the suid *Notochoerus eutilus* and the rhinocerotid *Ceratherium*, generally interpreted as grazers, yielded δ13C 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 C3/C4 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 Laetolil 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 C3/C4 diets with δ13C 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 craniomaxillary 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 C4 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; Kovanovic 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 δ13C 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 13C-enriched median carbon isotopic values in the younger Upper Ndolanya Beds, indicating either a greater grazing component, an increase in aridity, shifts in the δ13C of atmospheric CO2, 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

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grazers (the suid *N. euilus*, the rhinocerotid *C. precox*, 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 Laetoli 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 palaeoecological 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 18O-depleted isotopic signatures. While these differences may relate to a number of factors including global or regional shifts in atmospheric 18O, regional variation in the 18O 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 Plioocene 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 C3/C4 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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