Dietary flexibility of *Australopithecus afarensis* in the face of paleoecological change during the middle Pliocene: faunal evidence from Hadar, Ethiopia

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Abstract

One approach to understanding the context of changes in hominin paleodiets is to examine the paleodiets and paleohabitats of contemporaneous mammalian taxa. Recent carbon isotopic studies suggest that the middle Pliocene was marked by a major shift in hominin diets, characterized by a significant increase in C₄ foods in *Australopithecus*-grade species, including *Australopithecus afarensis*. To contextualize previous isotopic studies of *A. afarensis*, we employed stable isotopes to examine paleodiets of the mammalian fauna contemporaneous with *A. afarensis* at Hadar, Ethiopia. We used these data to inform our understanding of paleoenvironmental change through the deposition of the Hadar Formation. While the majority of the taxa in the Hadar fauna were C₄ grazers, most show little change in the intensity of C₄ food consumption over the 0.5 million-year interval sampled. Two taxa (equids and bovins) do show increases in C₄ consumption through the Hadar Formation and into the younger, overlying Busidima Formation. Changes in the distributions of C₄-feeders, C₃-feeders and mixed-C₃/C₄-feeders in the sampled

intervals are consistent with evidence of dietary reconstructions based on ecomorphology, and with habitats reconstructed using community structure analyses. Meanwhile, *A. afarensis* is one of many mammalian taxa whose C_4 consumption does not show directional change over the intervals sampled. In combination with a wide range of carbon and oxygen isotopic composition for *A. afarensis* as compared to the other large mammal taxa, these results suggest that the C_3/C_4 dietary flexibility of *A. afarensis* was relatively unusual among most of its mammalian cohort.

Keywords: stable isotope, environment, ecology, diet, hominin, tooth enamel

Introduction

Recent studies of early hominin tooth enamel have challenged conventional ideas regarding the evolution of hominin diets and feeding behaviors (Cerling et al., 2011; Henry et al., 2012; Lee-Thorp et al., 2012; Cerling et al., 2013; Klein, 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). These analyses have also raised new questions regarding interactions between early hominins and other species and their environments. In particular, they allow researchers to reexamine explanations for the links between dentognathic configurations, food material properties and hominin dietary adaptations. Stable isotopic and other biogeochemical data from fossil tooth enamel provide direct

evidence of the chemistry of the foods consumed by individual hominins and serve as proxies for foraging behavior and habitats.

The carbon isotopic composition of biological apatite in individual teeth reflects the degree to which hominins consumed C₄- or CAM-derived foods, such as tropical grasses, sedges, and succulents commonly found in tropical savannas (Lee-Thorp et al., 1994). The oxygen isotopic composition of tooth enamel provides additional paleodietary and paleophysiological information for individual specimens, while an analysis of taxa with a range of thermophysiological adaptations and behaviors may provide additional paleoclimatic information (Levin et al., 2006). The recent surge of stable isotopic data from hominins also makes it clear that the middle Pliocene marked significant hominin paleodietary change, when hominins first began to exploit substantial C₄/CAM-based foods in more open environments (Lee-Thorp et al., 2012; Cerling et al., 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). The timing of this C₄ dietary expansion, combined with other middle Pliocene discoveries, including possible hominin tool use and manufacture (McPherron et al., 2010; Harmand et al., 2015) and potentially increased diversity of hominin taxonomic diversity (Wood and Boyle, 2016), have heightened interest in the ecological, dietary, and behavioral patterns of hominins in the middle Pliocene (~3.8 – 3.0 Ma).

Abundant fossils from the middle Pliocene Hadar Formation in Ethiopia's lower Awash Valley provide a unique opportunity to address the paleoecological context of hominin evolution during this key time period. The Hadar Formation has produced the majority of the *Australopithecus afarensis* hypodigm (Kimbel and

Delezenne, 2009). Recent stable isotopic analyses of *A. afarensis* dental enamel (Wynn et al., 2013), as well as material from other hominins (Levin et al., 2015), showed that the earliest perceptible transition to significant consumption of C₄/CAM-derived food resources began in the middle Pliocene in *Australopithecus*-grade hominins (Sponheimer et al., 2013; Levin et al., 2015). The analyzed specimens of *A. afarensis* (from ca. 3.45 – 3.0 Ma), distributed throughout well-dated strata of the Hadar Formation, while highly variable, show no evidence of a temporal change in the overall proportion of C₄-derived foods despite faunal and other evidence for paleoenvironmental shifts across this time period (Wynn et al., 2013). Thus, the long-term stability of C₄/CAM food consumption by *A. afarensis* was marked by a high degree of intraspecific variation in the degree to which these foods were used. This variation spans the range between C₃-specialists such as *Giraffa* and C₄-specialists such as Alcelaphini, indicating that *A. afarensis* occupies a position within the isotopic dietary spectrum of the Hadar mammalian community that is distinct from most other taxa (Wynn et al., 2013).

Although additional direct biogeochemical evidence from hominin teeth is needed to understand hominin dietary evolution better, a more complete picture of the ecological context and evolutionary drivers of patterns in early hominin diets can be derived from associated floras and faunas (Bobe et al., 2007; Potts, 2012; Behrensmeyer and Reed, 2013; Sponheimer et al., 2013). While fossil faunas preserved with hominins are often studied using a variety of non-isotopic approaches (Bobe et al., 2007; Reed, 2008; Behrensmeyer and Reed, 2013), one of several productive approaches has been to couple isotopic analysis of hominins with

similar data from associated mammalian faunas (White et al., 2009; Bedaso et al., 2013; Levin et al., 2015). In particular, new approaches using the isotopic composition of micromammals may provide more detailed information on vegetation structure and composition (Leichliter et al., 2016). In this paper, we provide stable isotopic data from the Hadar mammalian fauna to provide a broader and more comprehensive context for the interpretation of the diet and ecology of *A. afarensis*. In particular, we examine whether the lack of change in C₄ food consumption in *A. afarensis* through half a million years of environmental fluctuation is reflected in the broader Hadar mammalian faunal community. Specifically, we compare the isotopic signature of *A. afarensis* to the cohort of large mammalian fauna in general and to those that survived the last known appearance *A. afarensis* and continued into the Busidima Formation. We also use these data in an exploration of new approaches to integrated study of paleoecological and paleoenvironmental change combining stable isotopic information with other data from of mammalian fauna.

Background

Geology

The Pliocene Hadar Formation within the Hadar area is composed of nearly 155 m of fluvio-lacustrine sediments. It is divided into four members (Basal [BM], Sidi Hakoma [SH], Denen Dora [DD], and Kada Hadar [KH]) separated by laterally

widespread tephra horizons with radiometric ages. These members are further subdivided by other lithostratigraphic markers, primarily sand bodies, into submembers (*e.g.*, DD-1, -2, -3) that serve as the stratigraphic collecting and analytical units for the fauna (Fig. 1; Campisano and Feibel, 2008). The sediments of the Hadar Formation represent different components of a large-scale fluvio-lacustrine basin that varied significantly in extent during deposition of the sediments. Fluvial and deltaic deposition predominated within the fossiliferous Hadar collecting area. The extensive sand bodies preserved at different stratigraphic levels within the Hadar sequence were deposited by the fluvial system upstream of the stable lacustrine depocenter, located east and northeast of Hadar. At least seven lacustrine transgressive episodes are represented in the Hadar record, occurring in almost all submembers (Figure 1; Campisano and Feibel, 2008). The most significant and persistent lacustrine episodes occur within the Basal Member, mostly exposed at the nearby Dikika site (Wynn et al., 2008), and in the uppermost Sidi Hakoma to lowermost Denen Dora Members (SH-4 to DD-1 submembers).

A regional angular unconformity separates the Hadar Formation from the overlying Busidima Formation (Quade et al., 2008; Wynn et al., 2008). In contrast to the Hadar Formation, the Busidima Formation at Hadar is dominated by cut-and-fill channel conglomerates and silt-dominated paleosols representing a high-energy fluvial system. Laterally discontinuous exposures and a lack of suitable material for dating has complicated the construction of a high-resolution chronostratigraphic framework for much of the Busidima Formation (Campisano, 2012). The Busidima specimens analyzed in this study range in age from ~2.7–0.8 Ma, with the majority

of them likely falling between ~2.4–1.3 Ma (~ BKT-3 to AST-3 levels). Because the age range of fossils analyzed from the Busidima Formation is wide and poorly constrained, and the fauna is not as rich as in the Hadar Formation, these samples were combined into a single stratigraphic bin and used as an “out-group” to the Hadar Formation fauna, which was analyzed at submember resolution.

The majority of the vertebrate fossils from Hadar are associated with fluvial and deltaic sands and silts, particularly channel and overbank deposits. However, the large mammal specimens analyzed in this study are intensively sampled from a subset of the depositional environments represented (SH-1, DD-2, and KH-2 submembers, ~3.40, ~3.23 and ~3.05 respectively), with relatively few specimens from other submembers. The depositional environment of the SH-1 and DD-2 fossiliferous horizons represent distributary channel and overbank deposits across an exposed delta plain, while those of the KH-2 represent channel and overbank deposits of a major meandering fluvial system (Campisano and Feibel, 2008). While the sampling strategy provides reasonably robust data on the large mammal communities for these intervals, the samples analyzed represent only a few windows in time rather than a continuous sequence across the range of depositional environments found in the Hadar Formation. Hence, while these data may be useful in testing for long-term dietary trends, it is not possible to distinguish any cyclical patterns of environmental or ecological change occurring on shorter time scales, such as Milankovitch periodicity.

The Hadar fauna

Ecomorphological characterization of the faunal assemblage, coupled with community structure analysis, has been undertaken for nine Hadar Formation submembers and for the Busidima Formation (Reed, 2008). Of the 64 known large mammal species in the Hadar Formation, 13, including *A. afarensis*, are represented in all of the submembers, while 51 are limited to a subset of the submembers. Of the 36 large-mammal species recovered from Busidima Formation, only 12 are also known in the Hadar Formation. Overall, the mammalian fauna suggests predominance of wooded and wet habitats in the Sidi Hakoma Member, floodplain edaphic grasslands and woodland in the Denen Dora Member, and relatively arid conditions in the Kada Hadar Member (Reed, 2008). The fauna from the Busidima Formation at Hadar suggests wooded grassland with riverine woodland or forest (Reed, 2008). Throughout the Hadar Formation the reconstructed habitats, as represented by the faunas, vary from more closed and mesic to more open and arid. The Busidima Formation habitats at Hadar appear to return to more wooded conditions.

Materials and methods

Enamel was collected from 387 specimens representing a range of taxa and stratigraphic intervals through the Hadar and Busidima Formations (Table 1; full data set provided in Supplementary Online Material [SOM]). The analysis was

limited to taxonomically identifiable isolated and/or fractured teeth. Taxonomic resolution varied by group. For example, most bovids were identified at least to tribe, although in some cases specimens could be identified to genus. In the case of the giraffids, some specimens were identified to genus (*Giraffa*), while others were identified to family (Giraffidae). In cases where nested sets of taxa were sampled, the higher and lower taxa within a nested set were analyzed and interpreted separately due to greater potential dietary variation within the higher taxon.

Enamel was extracted and powdered using a Dremel® Stylus™ rotary drill and diamond-tipped bit. Secondary carbonate was removed using 1.0 M Ca-acetate buffered acetic acid, followed by thorough rinsing and drying in an oven at 60°C. The pretreated enamel powders were analyzed at the Department of Geology Stable Isotope Lab at the University of South Florida. Approximately 2 mg of enamel powder was reacted in 103% phosphoric acid (i.e., superphosphoric acid with excess P₂O₅) at 25°C for 24 hours in He-flushed 4.5 mL borosilicate Labco Exetainer® vials. The carbon and oxygen isotopic compositions of the CO₂ produced from this reaction were analyzed on a Thermo Delta V 3 keV Isotope Ratio Mass Spectrometer (IRMS) coupled to a Thermo Gasbench II device and GCPal autosampler. Standards used for the analysis of tooth enamel carbonate were NBS-18 and an in-house carbonate standard calibrated to the V-PDB scale. Carbon and oxygen isotopic compositions are reported in standard delta (δ) notation:

$$\delta = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right]$$

with delta values reported per mil (i.e., $\times 1000\text{‰}$, Coplen, 2011), where R is the relevant isotopic ratio ($^{13}\text{C}/^{12}\text{C}$, or $^{18}\text{O}/^{16}\text{O}$). The standard used here is the international reference scale V-PDB (Vienna-PeeDee Belemnite). Statistical tests of significance of differences between median values (Kruskal-Wallis, Mann-Whitney U) were calculated using Matlab®. Because many taxa turn over between the Hadar and Busidima Formations, we tested for differences in isotopic compositions in two sets: (1) within the Hadar Formation alone; and (2) by including specimens from the Busidima Formation.

Comparisons of $\delta^{13}\text{C}$ values between modern and fossil tooth enamel are made after a 1.5‰ correction for the effect of fossil fuel-derived carbon in modern tooth enamel (as in Cerling et al., 2003), which is based on data from CO_2 trapped in ice cores (Friedli et al., 1986). Comparisons between $\delta^{13}\text{C}$ values of tooth enamel and diet are made after applying a ^{13}C -enrichment factor ($\epsilon_{\text{A-B}} = R_{\text{A}}/R_{\text{B}} - 1$, with values reported in per mil (‰) notation, i.e., $\times 1000$, where A and B are two species, in this case enamel and bulk diet) of $\epsilon_{\text{enamel-diet}} = 14.1\text{‰}$ (as in Cerling et al., 2003). In order to estimate the $\delta^{18}\text{O}$ value of meteoric water, we apply the method of Bedaso et al. (2013), using the most negative $\delta^{18}\text{O}_{\text{enamel}}$ value of hippopotamids (obligate drinkers), after conversion of $\delta^{18}\text{O}_{\text{enamel}}$ from the V-PDB to the V-SMOW (Vienna-Standard Mean Ocean Water) scale using ($\delta^{18}\text{O}_{\text{SMOW}} = 1.03091 (\delta^{18}\text{O}_{\text{PDB}}) + 30.91$; Coplen, 1988). We then use an ^{18}O -enrichment factor $\epsilon_{\text{enamel-drinking water}}$, assuming body water temperature of 37°C (from Luz and Kolodny, 1985; Bryant et al., 1996), to calculate $\delta^{18}\text{O}_{\text{drinking water}}$ of hippopotamids, which serves as a proxy for $\delta^{18}\text{O}_{\text{meteoric}}$

water, reflecting that of mean annual rainfall. We also apply the aridity index of Levin et al. (2006) to estimate the evaporative water deficit (potential evapotranspiration–mean annual precipitation). The ^{18}O -enrichment, as defined above, between evaporation-sensitive taxa (ES) and evaporation-insensitive taxa (EI), $\epsilon_{\text{ES-EI}}$, provides a proxy of paleo-aridity because water deficit is correlated with $\epsilon_{\text{ES-EI}}$ in modern taxa (Levin et al., 2006). We follow prior work in the selection of a specific regression equation and taxa used to define ES and EI endmembers from the Hadar (Bedaso et al., 2013) and Busidima Formations (Bedaso et al., 2010).

Ecomorphological measurements of fauna from Hadar were compared with those from modern taxa to provide predictions of paleodiet. Measurements and ecomorphological analyses of Bovidae and Giraffidae follow methods in Sponheimer et al. (1999). The width and unworn height of lower third molars from Perissodactyla and Suidae were used to determine hypsodonty indices and compared with those from modern taxa (Janis, 1988). The predicted values for paleodiets for these taxa were then used in correspondence analyses (CA) of submember assemblages to explore habitat clusters at Hadar through time (Reed, 2008). This method of using actual indices and the subsequent predictions in CA allow for community structure analyses, as the habitats of fossil taxa are reflected in community structure as represented by diet and substrate use. We compare these previous results with the new stable isotopic data presented here.

Results and discussion

The 387 samples from the Hadar mammalian assemblage constitute one of the largest stable isotopic data sets from fossil tooth enamel from a Pliocene hominin site. The data represent 27 taxa, mostly from three submembers of the Hadar Formation (Fig. 2), and from the Busidima Formation (Fig. 3) strata exposed at Hadar. The range of $\delta^{13}\text{C}_{\text{enamel}}$ values is useful to validate two primary assumptions in the estimation of the paleoecological and paleoenvironmental parameters of fossil communities. First, the range of $\delta^{13}\text{C}_{\text{enamel}}$ values across the spectrum from C_3 -browsers to C_4 -grazers, combined with taxonomic separation between these categories, indicates the overall lack of diagenetic resetting of carbon isotopic compositions (Lee-Thorp and van der Merwe, 1987). Second, the range of $\delta^{13}\text{C}_{\text{enamel}}$ values confirms the continued presence of both C_3 and C_4 vegetation throughout the period considered.

Carbon isotopic composition and paleodiets

We use the range and median $\delta^{13}\text{C}_{\text{enamel}}$ values for each taxon to differentiate dietary intake into three carbon isotopic categories: C_4 , mixed C_3/C_4 , and C_3 feeders (Table 2; Figure 2; Sponheimer and Lee-Thorp, 2003). C_3 feeders are defined as those which eat 80% or more C_3 vegetation (median $\delta^{13}\text{C}_{\text{enamel}} < -8\text{‰}$), C_4 feeders defined as those which consume 80% or more C_4 vegetation (median $\delta^{13}\text{C}_{\text{enamel}}$

> -1‰), and mixed C₃/C₄ feeders fall between these modes (Sponheimer and Lee-Thorp, 2003).

The distribution of $\delta^{13}\text{C}_{\text{enamel}}$ values from the entire Hadar faunal data set shows a bimodal distribution, with a minor mode at about -10‰ and a major one at 0 – 1‰, representing C₃ and C₄ feeders, respectively (Fig. 2). C₃ taxa are *Deinotherium*, *Giraffa*, *Sivatherium* and *Parapapio* (the latter two have 25th -75th quartile ranges that span into mixed-C₃/C₄-feeders). C₄ taxa are more diverse and exemplified by *Eurygnathohippus* and the bovids alcelaphini, reduncini, and *Aepyceros*, as well as hippopotamids and elephantids (all but the alcelaphines have 25th – 75th quartile ranges that span into mixed-C₃/C₄-feeders). Overall, mixed-C₃/C₄ feeders predominate, with many taxa having a range of 25th – 75th quartiles of $\delta^{13}\text{C}_{\text{enamel}}$ values that span the mixed-C₃/C₄-feeder to C₄ feeder range with median $\delta^{13}\text{C}_{\text{enamel}}$ values within or tending towards the C₄ endmember. C₄-biased mixed feeders (with 25th – 75th quartile ranges of $\delta^{13}\text{C}_{\text{enamel}}$ values that extend into the range of mixed-C₃/C₄-feeders, but with median values within the C₄ range) include *Ugandax* and *Notochoerus*. Similarly, C₃-biased mixed -C₃/C₄-feeders include *Tragelaphus* and *Australopithecus*. Other mixed-C₃/C₄-feeder taxa include an antilopin and those with carnivorous or omnivorous diets of mixed C₃/C₄-derived foods (the hyaena *Crocota*, the primate *Theropithecus*, and the suids *Kolpochoerus* and *Nyanzachoerus*).

Oxygen isotopic composition and paleoaridity

The wide range of $\delta^{18}\text{O}_{\text{enamel}}$ values (-11.6‰ to +7.8‰) may represent a large degree of variation between taxa having water-dependent and water-independent physiologies, although temporal variation in mean annual $\delta^{18}\text{O}$ values of drinking water may also contribute to this range. We first examine the stability of $\delta^{18}\text{O}$ values of drinking water through the Hadar Formation using the $\delta^{18}\text{O}_{\text{enamel}}$ values of hippopotamids, which are aquatic and can be assumed to have negligible ^{18}O -enrichment (i.e., are extremely water-dependent). All of the hippopotamids sampled in this study come from the Hadar Formation (median $\delta^{18}\text{O}_{\text{enamel}}$ = -7.5‰, n = 10), with no apparent difference in the median values from the earlier Sidi Hakoma Member (-7.0‰, n = 6) to the later Denen Dora/Kada Hadar Members (-7.5‰, n = 4, p = 0.81). For the entire Hadar Formation sample, the estimated mean $\delta^{18}\text{O}$ value of drinking water is -3.1‰ (on the SMOW scale), which may be used as an approximation of the $\delta^{18}\text{O}$ value of meteoric water. This estimate for the Hadar fauna is close to the value calculated by Bedaso et al. (2013) using hippopotamid $\delta^{18}\text{O}_{\text{enamel}}$ values from the Basal and Sidi Hakoma Members of the Hadar Formation at Dikika (-4.0‰ on the SMOW scale). Previous work suggests that mean $\delta^{18}\text{O}$ of meteoric water increased by about 2‰ between the Hadar and Busidima Formations, based on $\delta^{18}\text{O}$ values of paleosol carbonate and similar estimates from water-dependent hippopotamids (Aronson and Hailemichael, 2010; Bedaso et al., 2010, 2013; Wynn and Bedaso, 2010). We did not sample hippos from the Busidima Formation, so we cannot address any change across this boundary. However, the

lack of a temporal trend in hippopotamid $\delta^{18}\text{O}_{\text{enamel}}$ values within the Hadar Formation supports the notion that the temporal variation of meteoric water $\delta^{18}\text{O}$ values over the Hadar period represented was likely very small ($\sim 2\text{‰}$) compared to the overall variation within the large mammal fauna (almost 20‰). As such, this range can largely be attributed to physiological variation and behavioral differences between $\delta^{18}\text{O}$ values of water sources such as springs, rivers, ponds and lakes.

The $\delta^{18}\text{O}_{\text{enamel}}$ values from the entire Hadar faunal data set (Fig. 4) show a bimodal distribution, with a major mode at about -5‰ and a minor one at 0‰ . Using these values, the median $\delta^{18}\text{O}_{\text{enamel}}$ values for each taxon can be used to differentiate endmember physiological habits and used to classify taxa as water-dependent ($\delta^{18}\text{O}_{\text{enamel}} < -5\text{‰}$) or water-independent taxa ($\delta^{18}\text{O}_{\text{enamel}} > 0\text{‰}$). The endmembers of these two adaptations are represented by hippopotamids, which show the lowest median $\delta^{18}\text{O}_{\text{enamel}}$ values (water-dependent or evaporation-insensitive of Levin et al., 2006), and giraffids, especially *Sivatherium*, which show consistently high $\delta^{18}\text{O}_{\text{enamel}}$ values (water-independent or evaporation-sensitive of Levin et al., 2006). Other water-dependent taxa include *Australopithecus* and *Kobus*, while water-independent taxa include *Aepyceros* and antilopins. Although the two modes of $\delta^{18}\text{O}_{\text{enamel}}$ values do suggest that these physiological differences are real, it is also notable that a number of taxa show a similar bimodal distribution of $\delta^{18}\text{O}_{\text{enamel}}$ values, both in the Hadar data set and that from Dikika (Bedaso et al., 2013), even within relatively narrow stratigraphic bins (member or submember level). This may indicate that confounding factors contribute to differences in $\delta^{18}\text{O}_{\text{enamel}}$ values beyond physiological water dependence. This additional variation

may be explained by factors such as temporal variation in $\delta^{18}\text{O}$ values of rainfall, local variation in groundwater versus surface water sources, or different surface waters with varying degrees of evaporative fractionation, as might be expected for rivers versus highly evaporated lakes or ponds. Given the variable depositional environments represented by the Hadar Formation, one would expect significant differences in both the spatial and temporal distribution of the isotopic composition of water sources.

After establishing that physiological differences are largely responsible for variation in $\delta^{18}\text{O}_{\text{enamel}}$ values, we use the entire sample of evaporation-sensitive (ES) and evaporation-insensitive (EI) taxa from the Hadar Formation to calculate the ^{18}O -enrichment between ES and EI taxa is $\varepsilon_{\text{ES-EI}} = 3.6\text{‰}$, resulting in an estimated water deficit of 1344 mm (Fig. 4). This value is within the error of the estimate previously calculated from the Sidi Hakoma Member nearby at Dikika (1217 mm, Bedaso et al., 2013); both are roughly similar to the modern water deficit near Lake Magadi and Amboseli National Park, Kenya (Levin et al., 2006). The estimated water deficit for the sample of taxa from the Busidima Formation at Hadar is 1294 mm ($\varepsilon_{\text{ES-EI}} = 3.2\text{‰}$; Fig. 5). Because these values are well within the errors of the proxy, we cannot interpret such small differences (on the order of 100 mm/yr) as significant until we better understand some of the potential non-physiological factors that lead to variation of $\delta^{18}\text{O}_{\text{enamel}}$ within a given taxon.

Paleodietary and paleoenvironmental change

One of the primary objectives of this study was to use stable isotopic data as a source of taxon-specific paleodietary information to test for paleoecological and paleoenvironmental change through the course of deposition of the Hadar and Busidima Formations. It is well known that the carbon-isotopic composition of fossil faunas provides direct evidence of the presence or absence of various C₃- and C₄-vegetation communities (e.g., Cerling et al., 1997). Relatively few studies have approached faunal carbon isotopic data with an explicit focus to develop methods for reconstructing paleoenvironments (Sponheimer and Lee-Thorp, 2003, 2009; Kingston and Harrison, 2007; Bedaso et al., 2010, 2013; Cerling et al., 2015; Leichliter et al., 2016). Here, we explore these and new approaches to begin to capitalize on the paleodietary information in the stable isotopic composition of fossil tooth enamel.

Figure 6 depicts temporal changes in $\delta^{13}\text{C}_{\text{enamel}}$ values of taxa that are well represented in at least three of the intensively sampled units of the Hadar Formation (SH-1, DD-2, KH-2) and the Busidima Formation. The only significant within-taxon differences in $\delta^{13}\text{C}_{\text{enamel}}$ values between submembers of the Hadar Formation are within the genera *Eurygnathohippus* (Kruskal-Wallis, $p = 0.022$) and *Ugandax* ($p = 0.012$), both of which indicate increased C₄ grazing through time. When the Busidima Formation is included in the analysis, there is a significant change within Bovini (genera *Syncerus*, *Pelorovis* and *Ugandax*, $p = 0.026$), Equidae ($p = 0.004$), and *Kolpochoerus* ($p = 0.022$), implying an additional shift toward

increased C₄ dietary intake across the >750 thousand year temporal gap represented by the unconformity. Within the Bovini, the $\delta^{13}\text{C}_{\text{enamel}}$ values of *Ugandax* shift from values indicating mixed feeding in the SH-1 submember to values indicating grazing in the KH-2 submember. In the Busidima Formation, the bovins *Syncerus* and *Pelorovis* have $\delta^{13}\text{C}_{\text{enamel}}$ values indicating pure grazing diets. Likewise, the equid *Eurygnathohippus* from the Hadar Formation has $\delta^{13}\text{C}_{\text{enamel}}$ values that shift from grazing and mixed-feeding in SH-1 submember to pure C₄-grazing in the DD-2 and KH-2 submembers. In the Busidima Formation, $\delta^{13}\text{C}_{\text{enamel}}$ values indicate pure grazing for *Equus*. Within *Kolpochoerus*, $\delta^{13}\text{C}_{\text{enamel}}$ values shift from mixed feeding in the SH-1 and DD-2 submembers to purely grazing in the KH-2 submember and Busidima Formation.

Figure 7 depicts temporal changes in $\delta^{18}\text{O}_{\text{enamel}}$ values of taxa represented through at least three of the four stratigraphic units that were intensively sampled. Three taxa show significant differences in $\delta^{18}\text{O}_{\text{enamel}}$ values between submembers of the Hadar Formation (*Ugandax*, Kruskal-Wallis, $p=0.040$, *Tragelaphus*, $p=0.048$, and *Aepyceros*, $p=0.014$). All have lower $\delta^{18}\text{O}_{\text{enamel}}$ values in the DD-2 submember compared to the SH-1 and KH-2 submembers. The lower $\delta^{18}\text{O}_{\text{enamel}}$ values for these bovids in the DD-2 submember may reflect lower $\delta^{18}\text{O}_{\text{meteoric water}}$ values during this interval (~3.22 Ma), or alternatively, that they fed on abundant mesic grasses in which evaporative ¹⁸O-enrichment of leaf water may be less significant than it is in dry grasses (Flanagan and Ehleringer, 1991), such as in seasonally-flooded grasslands or at the forest fringe. The latter interpretation implies abundant mesic grassland habitats and is supported by the relatively high abundance of *Kobus*

fossils in the DD-2 submember (Reed, 2008). When the Busidima Formation is included in comparisons of the stratigraphic bins of $\delta^{18}\text{O}_{\text{enamel}}$ values, however, the differences among taxa discussed above are not significant. Meanwhile, the equids show significant differences in $\delta^{18}\text{O}_{\text{enamel}}$ values, with a trend from more ^{18}O -depleted values of *Eurygnathohippus* in the Hadar Formation to more ^{18}O -enriched values of *Equus* in the Busidima Formation (Kruksal-Wallis $p = 0.024$). Given the water dependency of equids (Levin et al., 2006), this change across the Hadar-Busidima Formation boundary likely reflects a change in the average $\delta^{18}\text{O}$ value of rainfall across this transition (Aronson and Hailemichael, 2010; Bedaso et al., 2010, 2013; Wynn and Bedaso, 2010).

It is remarkable that the majority of the taxa analyzed show no significant change in $\delta^{13}\text{C}_{\text{enamel}}$ or $\delta^{18}\text{O}_{\text{enamel}}$ values through the Hadar Formation (Figs. 6 and 7), suggesting relative stability of the isotopic dietary niches of these taxa. This fact, combined with the presence of significant quantities of both C_3 and C_4 endmember vegetation, validates assumptions underpinning paleoenvironmental analysis based on changes in taxonomic distributions of the fauna over time. That such indicator taxa as *Aepyceros*, *Tragelaphus*, *Notochoerus*, *Theropithecus*, Elephantids, Giraffidae and Deinotheridae show no significant change in their relative taxonomic contribution through the sampled interval suggests that the abundance of these taxa may provide a robust method of analyzing paleoenvironmental changes over this period.

With such large data sets as those described here, one approach to reconstructing paleoenvironments is to compare the overall distribution of

$\delta^{13}\text{C}_{\text{enamel}}$ values between defined stratigraphic intervals while controlling for abundance. Figure 8 (A – E) shows a model of variation in the distributions of $\delta^{13}\text{C}_{\text{enamel}}$ values of large-mammalian faunas, and comparisons of the model (Fig. 8F) to measured distributions from the four intensively sampled units of the Hadar and Busidima Formations. The model uses a cross-plot of the 80th versus 20th percentile values of the total distribution of $\delta^{13}\text{C}_{\text{enamel}}$ values (Fig. 8E) to distinguish the relative contributions from three carbon isotopic dietary categories: C_4 -feeders, C_3 -feeders, and mixed- C_3/C_4 -feeders. We use the 80th versus 20th percentile values as they mimic the >80% C_3 and <20% C_3 values that define our C_3 and C_4 feeders and which reliably capture what are commonly called “grazers” and “browsers” (see data in Sponheimer and Lee-Thorp, 2003). Thus, if the 80th percentile value for a site is -5‰ (above our C_3 feeder threshold of -8‰) it is obvious that there are few C_3 -feeders or browsers in the dataset. Using other percentiles is certainly possible, but they would not map as well onto the convenient and broadly used browser, grazer, and mixed-feeder categories.

In this 80th – 20th percentile space, model curves in Figure 8E show the trends for purely bimodal distributions (C_4 -feeder and C_3 -feeder endmembers) with distributions also characterized by additional mixed- C_3/C_4 -feeders between the two modes. Example normalized distributions of $\delta^{13}\text{C}$ values are also depicted with specific ratios of C_4 , C_3 and mixed- C_3/C_4 -feeders (Fig. 8A – D). In applying this model to fossil distributions, we must first draw attention to the implicit biases introduced by taphonomic processes, fossil collection strategies, or isotopic sampling strategies (Sponheimer and Lee-Thorp, 2003, 2009). Taphonomic biases may affect the

distributions of individuals or groups that are preserved in the fossil record compared to the living fauna. Collection biases, where specimens are collected versus left behind in the field, and decisions about what specimens are sampled for isotopic analysis, may further affect the distributions of isotopic datasets. However, despite these potential biases, which are common to all fossil faunal analyses (Bobe et al., 2007), we can use this approach to compare similarly collected data and examine relative changes in the distributions of carbon isotopic values to explore whether the results are consistent with expectations based on ecomorphological analyses (Table 2). The critical assumptions are that the collection and sampling biases affected the distributions in similar ways, and the sample size is sufficient to separate trends from noise. Hence, interpretation of the results will be more robust when analysis is carried out on relatively large, comprehensively sampled faunal collections.

Applying this approach to the Hadar isotope data set suggests that the four fossiliferous units sampled are characterized by mixed-C₃/C₄-feeders between the C₃- and C₄-endmembers. The KH-2 submember shows more abundant C₃-feeder $\delta^{13}\text{C}$ values than the SH-1, DD-2 and Busidima Formation, all of which show more abundant C₄-feeder $\delta^{13}\text{C}$ values. That the DD-2 submember shows the highest abundance of C₄-feeder $\delta^{13}\text{C}$ values supports paleoenvironmental inferences of widespread edaphic grasslands based on the abundance of reduncins in this submember (Table 7 in Reed, 2008). This peak of abundance of C₄-feeders in the DD-2 submember at Hadar contrasts with the contemporaneous part of the record from the Pliocene – Pleistocene Shungura Formation, in which C₄-feeders become

increasingly abundant between 3 and 2 Ma and reduncines transition from mixed- C_3/C_4 -feeders to C_4 -feeders after 2.32 Ma (Negash et al., 2015). While the abundance of C_4 -feeders in submember DD-2 is important for the regional record of *A. afarensis* at Hadar, the contrast between the Hadar and Omo-Turkana sedimentary basins underscores the need to understand how regional conditions were influenced by extra-climatic factors, such as tectonic reconfiguration of paleolandscapes. The dominance of C_3 -feeders in KH-2 may reflect the prevalence of shrubland habitats, as was reconstructed by community structure analysis (Reed, 2008). Shrublands have higher percentages of C_3 -feeders as well as mixed- C_3/C_4 -feeders that prefer C_3 -browse because there are usually few ephemeral C_4 grasses (White, 1983). The distribution of $\delta^{13}C_{\text{enamel}}$ values from the KH-2 submember is most similar to that of modern fauna from semi-desert woodlands of Samburu National Park, Kenya (Figure 8F; Cerling et al., 2015). In such shrublands, grasses are mostly seasonal so there is often a predominance of C_3 -browsers. Although this may have been the case at the KH-2 level where the large-bodied C_3 -browsing deinotheres were abundant, this taxon may be oversampled, thus C_3 -browsing taxa may be overestimated in this submember.

Dietary niche of Australopithecus at Hadar

Three key features distinguish the isotopic dietary niche of *A. afarensis* among its cohort of large mammalian fauna at Hadar: (1) a wide dietary range of both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, (2) a range of values that does not significantly overlap those of any other taxa analyzed (Figure 9A) and (3) a range that spans the primary and secondary modes of $\delta^{13}\text{C}$ values for the Hadar large-mammal fauna. The range of both $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values for *A. afarensis* is greater than the range for any other taxon sampled from Hadar (Figure 2). However, the range of $\delta^{13}\text{C}_{\text{enamel}}$ values for *A. afarensis* (-13.0 to -3.0‰) indicates lower consumption of C_4/CAM foods than the majority of the Hadar large mammal fauna, which is dominated in both total abundance and taxonomic diversity by C_4 -feeders (the primary mode is between -1 and 0‰). Although this broad range of $\delta^{13}\text{C}_{\text{enamel}}$ values for *A. afarensis* encompasses the secondary mode for C_3 -feeders (between -11 and -10‰; Figure 2), it does not overlap the primary mode for C_4 -feeders (between -1 and 0‰). As with the wide range of $\delta^{13}\text{C}_{\text{enamel}}$ values, the range of $\delta^{18}\text{O}_{\text{enamel}}$ values for *A. afarensis* (-9.5 to + 5.7‰) is greater than the range for any other sampled Hadar taxon, with a median (-5.7‰) that is well within the range of values typical of obligate drinkers. These data suggest that, although *A. afarensis* had the greatest dietary flexibility in terms of C_3/C_4 food consumption, on the whole its carbon isotopic niche minimally overlapped that of the majority of the Hadar large mammal taxa (e.g., all equids, elephantids, hippopotamids, bovins, reduncins, alcelaphins, aepycerotins, and the suids *Notochoerus* and *Metridiochoerus*).

While its carbon isotopic niche distinguishes *A. afarensis* from its cohort, the combined carbon and oxygen isotopic data more precisely delineate its niche within the large mammalian fauna (Fig. 9A; the closest taxon to *A. afarensis*, in terms of carbon and oxygen isotope space, is the suid *Nyanzachoerus*). Figure 9B shows that despite the change in median values of several taxa through the Hadar Formation, the unique *A. afarensis* dietary niche persists through these changes. Thus, while both the abundance, and in some cases the diets, of many large mammal taxa appear to have responded to paleoenvironmental changes between more and less open conditions 3.4 to 3 Ma, *A. afarensis* endures through these ecological changes with a highly varied intake of C₄ foods. It may be the eurytopic nature of *A. afarensis*, as suggested by Reed (2008), that allowed this species to have persisted through this paleoenvironmental change at Hadar without significant changes in the morphology of the Hadar populations of the species. However, it should be remembered that, within each of the sampled submembers, *A. afarensis* individuals could have focused on different plant foods either during different seasons or different years considering the span of time in each submember. Such variations in diet may be further examined through microanalytical techniques now amenable to analysis of tooth enamel (Passey and Cerling, 2006; Sponheimer et al., 2006; Blumenthal et al., 2014).

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Table 1: Summary of samples collected for tooth enamel isotopic composition from the Hadar and Busidima Formations

Taxon	Stratigraphic unit						Total, <i>n</i>
	Hadar Fm, total <i>n</i>	SH-1 submember, Hadar Formation	DD-2 submember, Hadar Formation	KH-2 submember, Hadar Formation	Other, Hadar Formation	Busidima Formation, <i>n</i>	
<i>Aepyceros</i>	30	10	9	11	0		30
Alcelaphini	11		10	1	0		11
Antilopini	5			5	5	5	10
<i>Australopithecus</i>	20			8	12		20
Bovini	12	5	6	1	4	4	16
<i>Crocota</i>	2				2		2
<i>Deinotherium</i>	13			6	8	1	14
Elephantidae	26	7	6	13	10	10	36
Equidae	41	8	21	12	5	5	46
<i>Giraffa</i>	15	1	6	6	5	3	18
Giraffidae, other	1		1		1	1	2
Hippopotamidae	10				10		10
<i>Kolpochoerus</i>	29	9	5	14	4	3	32
<i>Metridiochoerus</i>					5	5	5
<i>Notochoerus</i>	39	5	21	13	0		39
<i>Nyanzachoerus</i>	6	6			0		6
<i>Parapapio</i>	8	1		5	2		8
Reduncini	25		23		3	1	26
<i>Sivatherium</i>	5	1		4	1	1	6
<i>Theropithecus</i>	26	13	9	2	11	9	35
<i>Tragelaphus</i>	10		3	7	5	5	15
total	334	66	120	108	93	53	387

Table 2. Multi-method dietary reconstructions of the Hadar mammalian

fauna^a

Taxon	Diet based on: Living relatives, (Taxonomic uniformitarianism)	Diet based on: Ecomorphology	Diet based on: Carbon isotopes	Composite interpretation
<u>Hadar Formation</u>				
Artiodactyla				
<i>Giraffa</i>	B	B	C ₃	C ₃ -B
<i>Sivatherium</i>	B - G	B	C ₃ -(C ₃ /C ₄ -M)	C ₃ -B-C ₃ /C ₄ -M
Hippopotamidae	M		(C ₃ /C ₄ -M)-C ₄	C ₃ /C ₄ -M
<u>Bovidae</u>				
<i>Tragelaphus</i>	B	B, M (2 taxa)	(C ₃)-C ₃ /C ₄ -M	C ₃ -B-C ₃ /C ₄ -M
Alcelaphini	G	M, G (2 taxa)	C ₄	C ₄ -G
<i>Aepyceros</i>	G-M	M	(C ₃ /C ₄ -M)-C ₄	C ₃ /C ₄ -M-C ₄ -G
Reduncini	G	FG	(C ₃ /C ₄ -M)-C ₄	C ₄ -FG
<i>Ugandax</i>	G	FG	C ₃ /C ₄ -M-(C ₄)	C ₃ /C ₄ -M-C ₄ -FG
Antilopini	B		C ₃ /C ₄ -M	C ₃ /C ₄ -M
Perissodactyla				
<i>Eurygnathohippus</i>	G	G	(C ₃ /C ₄ -M)-C ₄	C ₄ -G
Proboscidea				
Elephantidae	(M)-B		(C ₃ /C ₄ -M)-C ₄	C ₄ -G

<i>Deinotherium</i>	B		C ₃	C ₃ -B
Suidae				
<i>Nyanzachoerus</i>	OM	M	C ₃ /C ₄ -M	C ₃ /C ₄ -M
<i>Notochoerus</i>	OM	G	C ₃ /C ₄ -M-(C ₄)	C ₄ -G-C ₃ /C ₄ -M
<i>Kolpochoerus</i>	OM	M	C ₃ /C ₄ -M	C ₃ /C ₄ -M
Primates				
<i>Theropithecus</i>	G-OM		C ₃ /C ₄ -M	C ₃ /C ₄ -OM
<i>Parapapio</i>	OM		C ₃ -(C ₃ /C ₄ -M)	C ₃ -OM
<i>Australopithecus</i>	OM		(C ₃)-C ₃ /C ₄ -M	C ₃ /C ₄ -OM
Carnivora				
<i>Crocota</i>	OM		C ₃ /C ₄ -M	C ₃ /C ₄ -OM
<u>Busidima Formation, where different from Hadar Formation</u>				
Artiodactyla				
<u>Bovidae</u>				
<i>Syncerus</i>	G	FG	(C ₃ /C ₄ -M)-C ₄	C ₃ /C ₄ -M-C ₄ -FG
<i>Pelorovis</i>	M		(C ₃ /C ₄ -M)-C ₄	-C ₃ /C ₄ -M-C ₄ -G
<i>Gazella</i>	M	M	C ₃ -(C ₃ /C ₄ -M)	C ₃ /C ₄ -M
<i>Kobus</i>	G	FG	C ₃ /C ₄ -M	C ₃ /C ₄ -M-C ₄ -FG
<i>Antidorcas</i>	M		C ₃ /C ₄ -M	C ₃ /C ₄ -M
Perissodactyla				
<i>Equus</i>	G	G	C ₄	C ₄ -G
Suidae				

<i>Metridiochoerus</i>	G-OM	G	(C ₃ /C ₄ -M)-C ₄	C ₃ /C ₄ -M-C ₄ -G
<i>Kolpochoerus</i>	OM	M	(C ₃ /C ₄ -M)-C ₄	C ₃ /C ₄ -M
Primates				
<i>Theropithecus</i>	G-OM		C ₃ /C ₄ -M-(C ₄)	C ₃ /C ₄ -OM

^aG= grazer, FG= fresh grass grazer (a category used for grazing in wetlands and edaphic grasses), M = mixed-feeder, B = browser, OM = omnivore (i.e., taxa that are considered to have a significant non-folivorous component to their diet such as frugivory or carnivory). Classification into C₃-, C₄- and C₃/C₄-mixed feeders using carbon isotopic composition is based on the median $\delta^{13}\text{C}$ value for the taxon, with classifications in parentheses when there is overlap of 25th – 75th percentile with adjacent category. Taxonomic uniformitarianism suggests that closely related, extant taxa have the same or very similar diets and provide a diet based on phylogenetic relatedness; ecomorphology suggests what a taxon was capable of eating through the measurement of dietary traits in modern taxa compared with fossil taxa, and the stable values are concrete evidence of the photosynthetic pathway of plants that animals actually ate while the teeth were forming. The ecomorphological assignments in this table are based on measurements of modern comparative samples and the Hadar fauna (Reed, 2008); when the ecomorphology column is blank, there were not enough craniodental remains to ecomorphologically reconstruct diet in the extinct taxa. The stable values refine dietary reconstructions of C₃/C₄-mixed feeders, and the ecomorphological analyses identify differences in grazing and fresh grass grazing, which have similar stable carbon isotopic values.

Figure captions

Figure 1. Composite stratigraphic section of the Hadar and Busidima Formations at Hadar (c = clay, z = silt, s = sand, g = gravel, v = volcanic, b = biogenic). Dated marker beds are labeled; pm indicates level of dated paleomagnetic transitions.

Submembers (analytical units) sampled for this study are in bold and italicized and indicated by the tooth icon, with number of specimens sampled. Submember abbreviations explained in text. . Key to generalized depositional environments: D – deltaic; Fl – fluvial; Fp – floodplain; L – lacustrine; Ns –nearshore (adapted from Campisano and Feibel, 2008).

Figure 2. Box-and-whisker diagram and histogram of the carbon isotopic composition ($\delta^{13}\text{C}$ values, V-PDB scale) of all fauna sampled from the Hadar Formation. In the box and whisker diagram, the central circle shows median value for taxon, the range of the box shows the 25th – 75th percentiles, and the whiskers show the range excluding outliers. Outliers (1.5 x interquartile range) are shown with open circles.

Figure 3 Box-and-whisker diagram and histogram of the carbon isotopic composition ($\delta^{13}\text{C}$ values, V-PDB scale) of all fauna sampled from the Busidima Formation. In the box and whisker diagram, central circle shows median value for taxon, the range of the box shows the 25th – 75th percentiles, and whiskers show the

range excluding outliers. Outliers (1.5 x interquartile range) are shown with open circles.

Figure 4 Box-and-whisker diagram and histogram of the oxygen isotopic composition ($\delta^{18}\text{O}$ values, V-SMOW scale) of all fauna sampled from the Hadar Formation. In the box and whisker diagram, central circle shows median value for taxon, the range of the box shows the 25th – 75th percentiles, and whiskers show the range excluding outliers. Outliers (1.5 x interquartile range) are shown with open circles. *taxa used as evaporation sensitive (ES) in water deficit estimates; **taxa used as evaporation insensitive (EI).

Figure 5. Box-and-whisker diagram and histogram of the oxygen isotopic composition ($\delta^{18}\text{O}$ values, V-SMOW scale) of all fauna sampled from the Busidima Formation. In the box and whisker diagram, central circle shows median value for taxon, the range of the box shows the 25th – 75th percentiles, and whiskers show the range excluding outliers. Outliers (1.5x interquartile range) are shown with open circles. *taxa used as evaporation sensitive (ES) in water deficit estimates; **taxa used as evaporation insensitive (EI).

Figure 6. Temporal variation of carbon isotopic composition ($\delta^{13}\text{C}$ values, V-PDB scale) of fauna represented through submembers of the Hadar Formation (SH-1, DD-2, KH-2) and Busidima Formation. Box-and-whisker diagrams are grouped by taxon. Central circle shows median value for taxon. Range of box shows 25th – 75th

percentile, whiskers show range excluding outliers. Outliers (1.5 x interquartile range) are shown with open circles. *P*-values for Kruskal-Wallis (KW) test are shown for comparisons of all sampling units and within the Hadar Formation only (HF); values in bold with asterisks are significant at the 0.05 level.

Figure 7. Temporal variation of carbon isotopic composition ($\delta^{13}\text{C}$ values, V-PDB scale) of fauna represented through submembers of the Hadar Formation (SH-1, DD-2, KH-2) and Busidima Formation. Box-and-whisker diagrams are grouped by taxon. Central circle shows median value for taxon. Range of box shows 25th – 75th percentile, whiskers show range excluding outliers. Outliers (1.5 x interquartile range) are shown with open circles. *P*-values for Kruskal-Wallis (KW) test are shown for comparisons of all sampling units and within the Hadar Formation only (HF); values in bold with asterisks are significant at the 0.05 level.

Figure 8. Model characterizing the distribution of large mammal faunal carbon isotopic composition using a cross-plot of 80th percentile versus 20th percentile of distributions of $\delta^{13}\text{C}$ values of fossil tooth enamel. **A-E.** Model curves (blue lines in **E** and distributions in **A-D**, *p* = probability in fraction of total) show range of 80th– 20th percentile plots for four endmember distributions ranging from simple bimodal (C_4 -feeders, C_3 -feeders) to bimodal with additional mixed- C_3/C_4 feeders between the two modes. Four example endmember normalized distributions of $\delta^{13}\text{C}$ values are shown: **A.** mixed- C_3/C_4 -feeder dominated (ratio of C_3 -feeders: C_4 -feeders: mixed- C_3/C_4 feeders = 1:1:5); **B.** bimodal, C_4 -feeder dominated (C_3 -feeder: C_4 -feeder = 1:4);

C. bimodal, C₃-feeder dominated (C₃-feeder: C₄-feeder = 4:1); **D.** simple bimodal (C₃-feeder: C₄-feeder = 1). All models are based on $\delta^{13}\text{C}$ values of C₃-feeders with $\delta^{13}\text{C}$ values of $-11.2 \pm 2.3\text{‰}$ (mean $\pm 2\sigma$) from C₃-feeders of $3 \pm 1.1\text{‰}$ (values from Cerling et al., 1999) and mixed-C₃/C₄-feeders of $-4.1 \pm 3.1\text{‰}$. **F.** Cross-plot of 80th percentile versus 20th percentile of distributions from the Hadar and Busidima Formations; open circles show measured data from three sampled submembers (SH-1, DD-2, KH-2) and total samples for Hadar and Busidima Formations (HF and BF, respectively). Data from modern faunas are included for comparison (samples with > 90 specimens from Cerling et al. [2015] and Codron [2006, 2008] with the latter corrected for fractionation using the methods in Sponheimer et al. [2003]).

Abbreviations: KRWL = Kruger National Park woodland, South Africa; SAMB = Samburu National Reserve, Kenya; KRGL = Kruger National Park grassland, South Africa; TSVO = Tsavo National Park, Kenya; LAIK = Laikipia Plateau, Kenya; MARA = Masai Mara, Serengeti Plains, Kenya/Tanzania; ATHI = Athi Plains, Kenya; NBNP = Nairobi National Park, Kenya.

Figure 9. Cross-plot of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for mammalian taxa from the Hadar and Busidima Formations. Central circle shows median value, crosshairs show range of 20th to 80th percentile. **A.** all specimens of each taxa through the entire stratigraphic range sampled. **B.** those taxa whose median $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ values change significantly through the four stratigraphic intervals sampled, overlain on **A.** Arrows show direction of change through intensively sampled intervals (SH-1, DD-2, KH-2,

solid lines = submembers within Hadar Formation dashed lines = Busidima Formation).

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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Bovidae (Bovini, *Tragelaphus*, *Aepyceros*)

Equidae, Giraffidae, Elephantidae

Suidae

Theropithecus

Figure 8

Figure 9

A

B