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Large mammal diets and paleoecology across the Oldowan–Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses

Kevin T. Uno ^{a, *}, Florent Rivals ^{b, c, d}, Faysal Bibi ^e, Michael Pante ^f, Jackson Njau ^g, Ignacio de la Torre ^h

^a Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA

^b Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain

^c Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

^d Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain

^e Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, 10115 Berlin, Germany

^f Department of Anthropology, Colorado State University, 1787 Campus Delivery, Fort Collins, CO 80523, USA

^g Department of Geological Sciences, Indiana University, 1001 E Tenth Street, Bloomington, IN 47405, USA

^h Institute of Archaeology, University College London, 31–34 Gordon Square, London WC1H 0PY, UK

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ABSTRACT

The well-dated Pleistocene sediments at Olduvai Gorge have yielded a rich record of hominin fossils, stone tools, and vertebrate faunal remains that, taken together, provide insight to hominin behavior and paleoecology. Since 2008, the Olduvai Geochronology and Archaeology Project (OGAP) has undertaken extensive excavations in Bed II that have yielded a large collection of early Pleistocene stone tools and fossils. The strata of Lower, Middle and Upper Bed II at Olduvai Gorge capture the critical transition from Oldowan to Acheulean technology and therefore provide an opportunity to explore the possible role of biotic and abiotic change during the transition. Here, we analyze newly discovered and existing fossil teeth from Bed II sites using stable isotope and tooth wear methods to investigate the diets of large mammals. We reconstruct the dietary ecology of Bed II mammals and evaluate whether vegetation or hydroclimate shifts are associated with the technological change. Combined isotope and tooth wear data suggest most mammals were C₄ grazers or mixed feeders. Carbon isotope data from bulk enamel samples indicate that a large majority of Bed II large mammals analyzed had diets comprising mostly C₄ vegetation (>75% of diet), whereas only a small number of individuals had either mixed C₃–C₄ or mostly C₃ diets (<25% C₄). Mesowear generally indicates an increase of the abrasiveness of the diet between intervals IIA and IIB (~1.66 Ma), probably reflecting increased grazing. Microwear indicates more abrasive diets in interval IIA suggesting stronger seasonal differences at the time of death during this interval. This is also supported by the intratooth isotope profiles from *Equus oldowayensis* molars, which suggest a possible decrease in seasonality across the transition. Neither stable isotope nor tooth wear analyses indicate major vegetation or hydrological change across the Oldowan–Acheulean transition.

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1. Introduction

Olduvai Gorge contains one of the richest early Pleistocene records of stone tools and human-modified bones in eastern Africa,

a record that provides evidence of hominin behavior and their interactions with other mammals on the landscape. Vertebrate fossils in the Gorge were first studied by Hans Reck's team over 100 years ago, then by Mary and Louis Leakey whose artifact and hominin fossil discoveries became world-renowned (Leakey, 1959, 1971; Leakey et al., 1964). The pioneering paleoanthropological work by Mary Leakey and colleagues was placed in a geological framework by Richard Hay (1963, 1976), who defined the stratigraphy of Olduvai Gorge following the original division of Olduvai into Beds I to

* Corresponding author.

E-mail addresses: kevinuno@ldeo.columbia.edu (K.T. Uno), florent.rivals@icrea.cat (F. Rivals), faysal.bibi@mfn-berlin.de (F. Bibi), Michael.Pante@colostate.edu (M. Pante), jknjau@indiana.edu (J. Njau), i.torre@ucl.ac.uk (I. de la Torre).

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IV by Reck (1914, 1951). The Bed II stratigraphic framework established by Hay (1963, 1976) has now been revised by Stanistreet et al. (submitted). Much effort has gone into determining the ages of the fossils and artifacts from Bed I and Bed II sites throughout the Gorge using combined radiometric dating (Curtis and Hay, 1972; Manega, 1993; Deino, 2012) and correlation of volcanic tuffs when direct dating was not possible (McHenry, 2012; McHenry et al., 2016; Habermann et al., 2016a).

One exceptional feature of Olduvai Gorge is that it is one of only a handful of places known to capture the Oldowan–Acheulean transition (Leakey, 1971). Renewed excavations at Bed II sites by the Olduvai Geochronology and Archaeology Project (OGAP), especially at the Henrietta Wilfrida Korongo East East site (HWK EE; Fig. 1), have produced more than 18,000 artifacts and nearly 30,000 fossils (de la Torre et al., submitted) that when combined with other, younger Bed II sites (e.g., EF-HR, MNK, FC East and FC West, HWK E-Tembo and FLK West), shed new light on the Oldowan–Acheulean transition, tool use, and hominin–carnivore interactions from ~1.7 to 1.6 Ma (Pante et al., submitted). Reconstructing the paleoenvironment at Olduvai Gorge is essential to understanding the role of environmental change during this major archaeological transition.

A multitude of approaches to reconstructing paleoenvironments have previously produced a wealth of information on the flora and fauna of Olduvai Gorge, especially for Bed I. These have focused on vertebrate remains (e.g., Gentry and Gentry, 1978; Plummer and Bishop, 1994; Kovarovic et al., 2013; Bibi et al., submitted), plant macro- and micro-fossils (Bonnefille, 1984; Bamford et al., 2006, 2008; Barboni et al., 2010; Albert and Bamford, 2012; Bamford, 2012; Albert et al., 2015a), paleopedology (Ashley et al., 2014), and isotopic studies of soil carbonates and organic matter (Cerling and Hay, 1986; Sikes, 1994; Sikes and Ashley, 2007), mammalian teeth (Van der Merwe, 2013), and plant biomarkers (Magill et al., 2013 a,b, 2016). Three main conclusions arise from these studies: first, the Olduvai region has long been a semi-arid to arid ecosystem

(Bonnefille, 1984). Second, there is an overall shift towards more arid conditions sometime between ~1.9 Ma and the present (Cerling and Hay, 1986; Sikes and Ashley, 2007). Third, within the context of a semi-arid to arid ecosystem, the Olduvai landscape was varied spatially (Barboni et al., 2010; Magill et al., 2016) and temporally (Bamford, 2012; Magill et al., 2013b), with associated temporal changes in fauna as well (Kappelman, 1984).

Fossil teeth of large herbivores can be used to reconstruct past environments based on their morphology, microwear texture, and geochemistry. Both stable isotope and tooth wear methods are commonly used for paleodietary and paleovegetation reconstructions, yet these powerful and well-established methods have not yet been applied to Bed II fossil teeth. The recent excavation of new fossil teeth by the OGAP team, combined with the existing teeth collected by Mary Leakey's team in the early 1970s, present an opportunity to reconstruct the paleoenvironment and mammal diets during the Oldowan–Acheulean transition (see also Rivals et al., 2017). Here, we use stable isotope analysis and tooth wear methods to evaluate diet, vegetation, and hydroclimate, and to provide a robust assessment of the paleoenvironment during the Oldowan–Acheulean transition at Olduvai Gorge.

2. Materials and methods

2.1. Teeth analyzed for stable isotopes, mesowear and microwear

Fossil teeth sampled for stable isotope analysis come from the Leakey and OGAP research collections. Teeth were sampled from the HWK EE, FC East, FC West, MNK, FLK West, HWK E-Tembo, and EF-HR sites (Fig. 1). They represent a wide range of mammals, including Proboscidea (Elephantidae, Deinotheriidae), Perissodactyla (Rhinocerotidae, Equidae), Artiodactyla (Bovidae, Girafidae, Hippopotamidae, Suidae), Carnivora (Hyaenidae), and Primates (Cercopithecidae) (see Table 1).

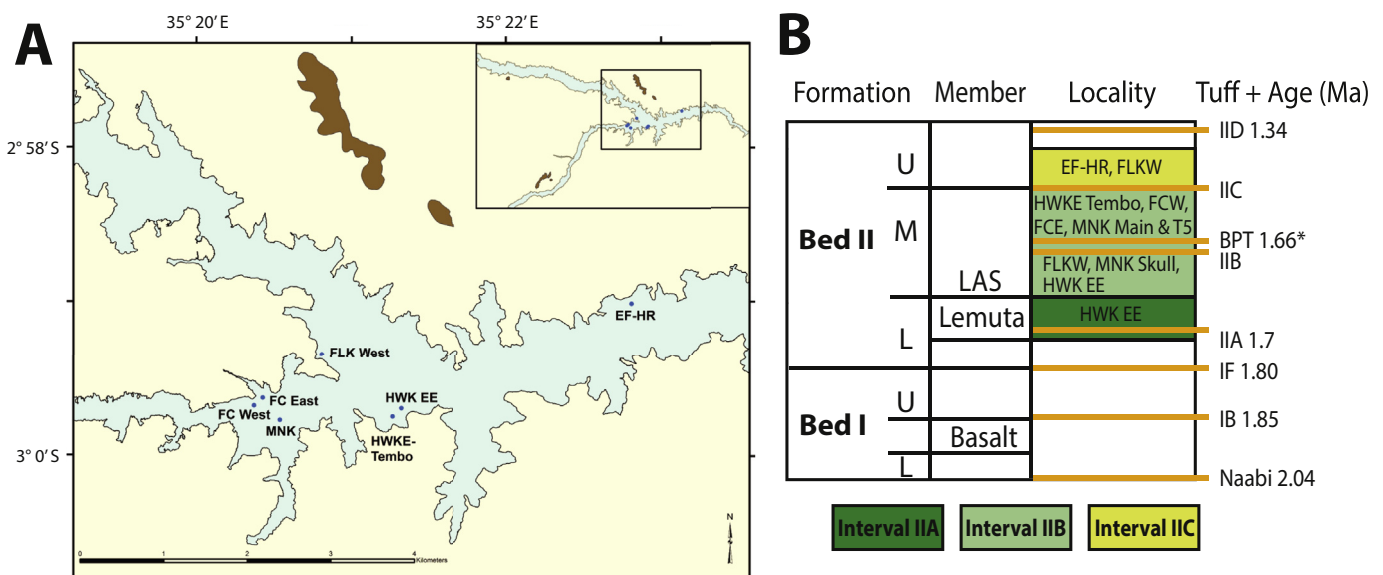


Figure 1. A) Map of Olduvai Gorge with the Bed II sites from which fossil teeth analyzed in this study come from. Interval IIA teeth (~1.7 Ma) are from the HWK EE, FLK West, and MNK Skull sites; Interval IIB (~1.66 Ma) teeth are from the HWK EE, HWK E-Tembo, FC West, FC East, and MNK Main sites; the interval above IIC includes teeth from the FLK West and EF-HR sites. B) A simplified stratigraphic framework based on Hay (1976) and Stanistreet et al. (submitted), following the proposal to use the top of Lemuta to separate Lower Bed II from Middle Bed II (see Stanistreet et al., submitted). Intervals defined in this study are shown in colored boxes. Sampled sites are listed by interval. Tuffs are marked in orange and their ages are from Curtis and Hay (1972), Deino (2012), and Domínguez-Rodrigo et al. (2013). *Approximate age of Bird Print Tuff (BPT) is derived from dating of a tuff denominated FLKWb by Diez-Martin et al. (2015), which Uribealrea et al. (2017) place at ~25 cm below the level of the BPT nearby.

Table 1

Number of teeth analyzed for carbon and oxygen isotope ratios by mammalian family from intervals IIA, IIB, and above IIC.

Family	Interval IIA	Interval IIB	Interval above IIC
Bovidae ^a			
Alcelaphini	17	16	–
Antilopini/Aepycerotini	7	–	1
Bovini	1	–	–
Hippotragini	4	2	–
Reduncini	3	1	–
Tragelaphini	2	4	–
Indet.	2	–	–
Cercopitheciidae	1	3	–
Deinotheriidae	2	–	–
Elephantidae	–	1	–
Equidae	9	11	4
Giraffidae (<i>Giraffa</i>)	1	–	1
Giraffidae (<i>Sivatherium</i>)	2	3	–
Hyaenidae	1	3	–
Hippopotamidae	2	16	–
Rhinocerotidae	5	2	–
Suidae	4	10	–
Total	63	72	6

^a Bovidae are further specified to tribe.

The sampling strategy for stable isotope and tooth wear analyses is designed to include as many taxa from the faunal assemblage as possible and to capture the full dietary diversity. It is also designed to reflect relative faunal abundances observed in the faunal assemblage. For example, abundant taxa such as Alcelaphini and Equidae in Bed II at Olduvai are also the most abundant taxa in the isotope and tooth wear data sets. Where possible, at least five specimens from each clade were analyzed to represent the dietary breadth present. This was not always possible for rarer taxa, such as Deinotheriidae and *Giraffa*. In some cases, analyzed samples for very abundant taxa are underrepresented (e.g., Alcelaphini), and for rare taxa it is possible for them to be under- or over-sampled with respect to their relative abundance in the faunal assemblage.

To evaluate whether the specimens sampled for isotope analysis represent the entire faunal assemblage, we calculate the coefficient of determination between the relative abundance of the number of individual specimens (NISP) from the OGAP fossil tooth database (Bibi et al., submitted) and that of the isotope data set. If the two data sets are similar, then community level interpretations of the isotope data can be applied to the NISP data set.

A second important consideration is fossil provenance. Patterson et al. (2017) demonstrate that Pleistocene paleontological and archaeological sites have different faunal compositions for large mammals in the Turkana Basin. At Olduvai, where the archaeological deposits are thicker and therefore likely more palimpsest in nature, we consider the Bed II fauna as a combination of archaeological and paleontological in provenance.

Most of the teeth (135 of 141) from these sites can be assigned to two stratigraphic intervals that span the Bed II subformations (Lower, Middle, and Upper), as defined by Hay (1976; see also Stanistreet et al., submitted). The ages of the two intervals, denoted here as interval IIA and interval IIB, are based on associated radiometric ages of tephra layers. Sixty-three teeth recovered from HWK EE trenches, HWK E-Tembo, Trench 73 at FLK West, and Trench 36 and the Skull site at MNK are assigned an age of ~1.7 Ma, based on the updated ages of 1.68 and 1.76 Ma of Tuff IIA by Manega (1993) and Curtis and Hay (1972), respectively, that have been recalculated by McHenry (submitted) using an updated potassium-40 decay constant and the same reference standard, the Fish Canyon sanidine. These trenches are all stratigraphically positioned between Tuff IIA and Tuff IIB, and are here included in what we term interval IIA. Seventy-two teeth come from between Tuff IIB

and IIC, and are grouped within what we term interval IIB. Interval IIB teeth are assigned an age of ~1.6 Ma based on their proximity to the Bird Print Tuff (BPT), which lies just above Tuff IIB. The BPT has been stratigraphically placed ~25 cm above Tuff FLKWb (Uribelarrea et al., 2017), with a reported age of 1.664 ± 0.019 Ma (Diez-Martín et al., 2015). Interval IIB includes fossil teeth from all FC East and West trenches, the MNK Main and T5 trenches, and HWK E-Tembo. Six teeth come from above Tuff IIC (IIC interval), which include three from EF-HR and three from FLK Trench 69. Tuff IIC is not dated. Tuff IID is dated around 1.48 Ma (Manega, 1993) or 1.34 Ma in age (Domínguez-Rodrigo et al., 2013).

The material studied for meso- and micro-wear was selected from all the specimens available in the collections from HWK EE, FC East, FC West, and MNK. We analyzed large herbivorous mammals among Proboscidea (Elephantidae, Deinotheriidae), Perissodactyla (Rhinocerotidae, Equidae), and Artiodactyla (Giraffidae, Hippopotamidae, Suidae, Bovidae). For Bovidae, where identification of isolated teeth to species level is difficult, we used tribe level: Alcelaphini, Antilopini, Bovini, Caprini, Hippotragini and Reduncini. For other groups, we used the lowest level of identification possible (genus or species). All taxonomic assignments follow the updated faunal list provided in Bibi et al. (submitted). A total of 298 specimens were molded and screened to assess their suitability for microwear and mesowear analyses. After excluding teeth where both buccal cusps were broken or damaged, 171 specimens were suitable for mesowear analysis. After an examination of the epoxy casts under the stereomicroscope, specimens with taphonomic alterations which damaged the original microwear pattern were discarded, leaving a total of 248 specimens suitable for microwear analysis.

2.2. Sampling and analytical methods

2.2.1. Stable isotopes in teeth Stable carbon and oxygen isotope ratios of tooth enamel are determined by an animal's diet and body water, respectively, and therefore can be used to reconstruct herbivore diets, vegetation, and local hydroclimate (Levin et al., 2006; Kingston and Harrison, 2007; Uno et al., 2011; Van der Merwe, 2013). Tooth enamel carbon isotope ratios of large herbivores reflect the proportion of C₃ to C₄ vegetation in their diet during the time in which the tooth formed (see Supplementary Online Material [SOM] for details). Oxygen isotopes in enamel (or other mammalian bioapatites) are primarily controlled by the isotope ratio of precipitation but also influenced by food water, plant water, evaporative processes in soils, plants, and water sources, and animal physiology (Luz et al., 1984; Kohn et al., 1996; Levin et al., 2006). Stable carbon and oxygen isotope ratios are reported as delta (δ) values relative to the Pee Dee Belemnite (PDB) standard using permil (‰) notation where

$$\delta^{13}\text{C}(\text{or } \delta^{18}\text{O}) = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000 \quad (1)$$

and R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ($^{18}\text{O}/^{16}\text{O}$) ratios in the sample and in the standard, respectively, and the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of PDB are defined as 0‰.

2.2.2. Enamel sampling, pretreatment, and isotope analysis Sampling of fossil teeth for stable isotopes was performed at the Olduvai field station, at University College London, and at Lamont-Doherty Earth Observatory of Columbia University. Fossil teeth were selected from 10 mammalian families, with identification primarily done by Bibi et al. (submitted), but also by F.R. and M.P. in some cases. Prior to drilling, each tooth was inspected, photographed, and a sampling location on the tooth was evaluated.

A detailed description of the sampling methods, enamel pretreatment, and isotope analysis are available in the SOM. Briefly, a cordless rotary drill with a carbide or diamond grit bit was used to clean off the outermost enamel and expose a fresh surface. Approximately 2–5 mg of enamel were removed by drilling. Enamel powder was pretreated with 3% sodium hypochlorite followed by 0.1 M buffered acetic acid. Samples were dried, weighed, then heated in vacuo prior to analysis via dual inlet isotope ratio mass spectrometry.

We calculated the dietary contribution of C_4 vegetation to diet using the C_3 and C_4 endmember enamel $\delta^{13}C$ values of $-11.9 \pm 4\%$ and $+2.8 \pm 2\%$, respectively, where uncertainty is based in observed variability in C_3 and C_4 eastern African plants (e.g., Cerling and Harris, 1999; Cerling et al., 2003a). We applied a two-end member mixing model, where the percent of C_4 vegetation in diet is determined as

$$\%C_4 = (\delta^{13}C_{C_3} - \delta^{13}C_{\text{enamel}}) / (\delta^{13}C_{C_3} - \delta^{13}C_{C_4}) \times 100, \quad (2)$$

where $\delta^{13}C_{\text{enamel}}$ is the measured $\delta^{13}C$ value of the sample and $\delta^{13}C_{C_3}$ and $\delta^{13}C_{C_4}$ are the calculated C_3 and C_4 endmember values for enamel. We propagated the uncertainty in both the dietary endmember values and in the analytical procedure ($\pm 0.1\%$), which resulted in uncertainties of 12–30%. We note that uncertainties in the calculated $\%C_4$ in diet are higher towards the C_4 end of the continuum due to the larger uncertainty of the C_3 endmember value, which is $\pm 4\%$. We define C_3 -dominated diets as those with $\delta^{13}C$ values of $< -8\%$ ($\sim < 25\% C_4$), mixed C_3 – C_4 diets as having values from -8 to -1% (~ 25 – $75\% C_4$), and C_4 -dominated diets as those with $\delta^{13}C$ values of $> -1\%$ ($\sim > 75\% C_4$). We use a three-term ratio to describe the percentage of C_4 -dominated, mixed, and C_3 -dominated diets for a given time period. We adopt a simplified version of that used by Sponheimer et al. (1999) and one that is similar to that of Cerling et al. (2015), who used carbon isotope data to classify Turkana Basin mammals as C_4 grazers:mixed C_3 – C_4 feeders: C_3 -browsers. Ours differs from Cerling et al. (2015) in that we take a more conservative approach and maintain the vegetation type (C_3 versus C_4) rather than infer feeding habit (browsing versus grazing), because tooth wear data suggest that C_3 grasses or C_4 shrubs may have been minor dietary components of the Olduvai Bed II mammals.

We compared tooth enamel carbon and oxygen isotope data from Olduvai Bed II mammals with that of modern mammals from Tanzania ($n = 72$) published by Van der Merwe (2013). We corrected for the difference in the modern $\delta^{13}C_{\text{atm}}$ value (-8%) and the calculated early Pleistocene values for Bed II (-6.7% , see SOM for details) by adding 1.3‰ to all modern $\delta^{13}C_{\text{enamel}}$ values. To compare the modern $\delta^{18}O$ values to Bed II values, we re-calculated the modern values, originally calculated using the calcite-based acid fractionation factor, using a tooth enamel specific, temperature dependent acid fractionation factor from Passey et al. (2007: their Eq. (3)). This is necessary so that the $\delta^{18}O$ values from both data sets can be directly compared. To do this, we converted the modern $\delta^{18}O$ values from mineral back to CO_2 gas $\delta^{18}O$ values using the temperature dependent calcium carbonate acid fractionation factor of Swart et al. (1991). We then applied the tooth enamel acid fractionation factor from Passey et al. (2007). The difference between the originally published and recalculated $\delta^{18}O$ values for the modern enamel samples is $\sim -0.1\%$.

We apply the Mann–Whitney U-test (also called the Wilcoxon test) to compare carbon and oxygen isotope distributions between time intervals (IIA, IIB, and modern) because there is no reason to assume the data are normally distributed.

Finally, because of their semiaquatic lifestyle, Hippopotamidae are overrepresented in the fluvial and lacustrine sediments

compared to terrestrial mammals of similar size (see Weston and Boisserie, 2010 and references therein). To address the overrepresentation of 16 *Hippopotamus gorgops* in interval IIB, where they comprise 24% of all samples, our statistical analyses used only three values from the population, the minimum, median, and maximum values as a conservative approach to representing interval IIB Hippopotamidae.

2.3. Intratooth stable isotope profiles and inverse modeling

Intratooth stable isotope profiles of ungulate tooth enamel provide a time series of the diet and body water over the period in which the tooth enamel formed (Fricke and O’Neil, 1996; Sharp et al., 1998). In extant equids, premolars and molars form over 1.5–2.8 years, inclusive of crown extension and enamel maturation (Hoppe et al., 2004). The time represented in intratooth isotope profiles can therefore be used to evaluate seasonal variability in environmental precipitation, vegetation, and diet (Sharp et al., 1998; Nelson, 2005; Metcalfe et al., 2011). Amelogenesis, or the process of enamel formation, is a two stage process that starts with a secretory stage, where the enamel matrix is deposited, followed by a protracted maturation stage, where density of the original matrix increases significantly (Suga, 1979). As a result, the isotope ratio of a given volume of enamel represents a time integrated signal of the initial period of matrix deposition plus the maturation period. Tooth enamel maturation and isotope sampling methods blur and attenuate the original isotope input signal (Passey and Cerling, 2002; Zazzo et al., 2005). Here we applied the inverse method developed by Passey et al. (2005) to estimate the original input signal for $\delta^{13}C$ (diet) and $\delta^{18}O$ (body water) that more closely reflects the actual diet and body water composition of the equid during the time during in which the tooth formed. A detailed description of the modeling method is given in the SOM.

2.4. Tooth wear methods

2.4.1. Mesowear analysis Mesowear analysis is a method of analyzing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices which is related to the amounts of attritive and abrasive dental wear (Fortelius and Solounias, 2000). Mesowear is analyzed macroscopically from the buccal side of upper molars, preferably the paracone of the M2. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices, are omitted from mesowear analysis (Rivals et al., 2007). Mesowear was applied to Rhinocerotidae, Equidae, Giraffidae and Bovidae because of their suitable tooth morphology when using the Fortelius and Solounias (2000) method. In this study, the standardized method introduced by Mihlbachler et al. (2011) was employed. The method is based on seven cusp categories, ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or MWS (Mihlbachler et al., 2011). For a more detailed description of the method see Rivals et al. (2017).

2.4.2. Microwear analysis Tooth microwear patterns were examined following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). After cleaning, the occlusal surface of each specimen was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. Casts were observed under incident light with a stereomicroscope Zeiss Stemi 2000C at 35 \times magnification. Microwear scars were quantified in a square area of 0.16 mm². We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) which basically

distinguishes pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and are classified as small pits, large pits, or puncture pits. Scratches are elongated microfeatures that have straight and parallel sides. Scratches are divided into fine, coarse and hypercoarse scratches. The presence of some other features, cross scratches (scratches with a different orientation than most scratches) and gouges (large features which have ragged, irregular edges and are much larger and deeper than large pits), is recorded qualitatively. In addition, scratch textures were assessed using the scratch width score (SWS). For a more detailed description of the method see Rivals et al. (2017).

In artiodactyls and perissodactyls, scratches and pits were counted in two areas on the paracone of the upper molars and the protoconid of the lower molars. In proboscideans, the area was selected on a loph in the center of the worn part of the occlusal surface. The results were compared with a database comprising extant ungulate taxa (Solounias and Semperebon, 2002; Rivals et al., 2010). In primates, microwear was counted on the mesio-buccal cusp of upper molars or on the mesio-lingual cusp of lower molars. The results are compared to the database of extant primates from Godfrey et al. (2004).

3. Results

3.1. Stable isotopes

3.1.1. Comparison of NISP and isotope data sets The relative abundances for all tooth specimens from the OGAP and Leakey Bed II fossil assemblage and for the isotope data are given in SOM Table S2. There is close agreement between the relative abundances between the two data sets, with significant coefficients of determination for interval IIA and IIB samples ($R^2 = 0.84$ and 0.81 , respectively; SOM Fig. S1). In most cases, the difference in relative abundance between the NISP and isotope data sets is less than 5%. For more abundant taxa such as Alcelaphini, Equidae, and Hippopotamidae, the difference reaches up to 20% (SOM Table S2). The isotope data set represents the overall fossil assemblage in Bed II and suggests that interpretations of the isotope samples at the community level broadly apply to the fossil community.

3.1.2. Bulk samples Tooth enamel $\delta^{13}\text{C}$ values ($n = 141$) from Bed II at Olduvai span a range of nearly 17‰, from -12.8 to $+4.1$ ‰, with a median value of $+0.7$ ‰. There is a range of 9.4‰ in oxygen isotope values from -4.3 to $+5.1$ ‰, with a median value of -0.1 ‰. All carbon and oxygen isotope values are presented in SOM Table S3, which also includes taxonomic data from Bibi et al. (submitted) and site information. More than 95% of the samples (135 of 141) came from either interval IIA ($n = 63$) or interval IIB ($n = 72$). Six additional samples came from Upper Bed II sites EF-HR and FLK (Fig. 1), positioned above Tuff IIC. However, because of the small sample size we do not discuss samples from interval IIC in detail. Summary statistics from the three Bed II intervals (IIA, IIB, and

IIC) are presented in Table 2 and a cross plot of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for the two main intervals is shown in Figure 2. We also include isotope data from 72 extant large mammals in Tanzania from Van der Merwe (2013), primarily from the Serengeti and Maswa ecosystems that lie to the west of Olduvai Gorge, to compare extant fauna to the main Bed II intervals, IIA and IIB. Histograms of carbon and oxygen isotopes from the modern and Bed II sample populations are shown in Figure 3.

The majority of the mammals from the main Bed II intervals had C_4 -dominated diets. In interval IIA, the distribution of taxa with C_4 -dominated: mixed: C_3 -dominated diets is 71:21:8. In interval IIB the ratio is 83:15:2 ($n = 59$), when corrected for the overrepresentation of Hippopotamidae (see Materials and methods section). The modern community also primarily comprises mammals with C_4 -dominated diets (57:24:19), but about 15–25% less than are present in the Bed II communities, with considerable increases in the percentages of mammals with mixed and C_3 dominated diets.

Mann–Whitney U-test results indicate no significant differences between carbon isotope distributions from the three intervals (Table 3). Median $\delta^{13}\text{C}$ values are nearly identical between intervals IIA, IIB, and the modern distribution. There are, however, significant differences ($p < 0.05$) in the oxygen isotope distributions between fossils and modern distributions (Table 3). The median $\delta^{18}\text{O}$ values in interval IIA and interval IIB are identical ($+0.2$ ‰) when corrected for the overrepresentation of IIB Hippopotamidae. Despite their identical median values, interval IIA has a higher maximum $\delta^{18}\text{O}$ value ($+5.1$ vs. $+3.7$ ‰), which may be indicative of more evaporated water and, likely, more arid conditions during interval IIA times. The modern median $\delta^{18}\text{O}$ value is 1.8‰ more positive than in intervals IIA and IIB.

The Bed II and modern carbon and oxygen data are shown as box plots for lineages (family, genus or species) for which there are three or more teeth analyzed for at least one interval (Fig. 4). Elephantidae and Deinotheriidae are excluded from the box plots due to their small sample size ($n < 2$) and lack of continuity across intervals. Although not all groups have robust sample numbers (e.g., >5), Hippotragini, Reduncini, Tragelaphini, Equidae, Hippopotamidae, Hyaenidae and *Theropithecus* all show enrichment in ^{13}C between intervals IIA and IIB. There are no consistent $\delta^{18}\text{O}$ changes across the different lineages between intervals.

Finally, we present results of the bulk sampled isotope data by site since the scope of many archaeological studies is focused at that level (SOM Fig. S2). Fossil teeth sampled in this study came primarily from sites HWK EE ($n = 61$; 59 from interval IIA, 2 from interval IIB), FC (East and West; $n = 52$; all from IIB), and MNK ($n = 20$; 3 from IIA, 17 from IIB). FC East and FC West were considered together due to their close proximity and same stratigraphic position. Six teeth from interval IIC came from sites FLK (Trench 69) and EF-HR; data for these sites are not presented here but are listed in SOM Table S3. Carbon and oxygen isotopes from each site are plotted in SOM Figure S2 for HWK EE, MNK, FC East

Table 2
Summary statistics of carbon and oxygen stable isotope data for modern and Bed II taxa.

Interval ^a	n	%C4			$\delta^{13}\text{C}$				$\delta^{18}\text{O}$			
		Median	Max	Min	Median	Max	Min	Range	Median	Max	Min	Range
Modern ^b	72	69	100	0	0.3	4.0	-15.3	19.3	2.0	6.6	-4.2	10.8
Above IIC	6	94	100	15	2.0	3.3	-9.7	13.0	-0.6	2.1	-2.0	4.1
Tuff IIB ^c	59	88	100	23	1.0	4.1	-8.5	12.6	0.2	3.7	-4.3	8.0
Tuff IIA	63	86	100	0	0.7	3.3	-12.9	16.2	0.2	5.1	-3.8	8.9

^a Bed II taxa are divided into the intervals IIA, IIB, and above IIC.

^b Modern enamel $\delta^{13}\text{C}$ values are corrected by $+1.3$ ‰ for recent changes to the $\delta^{13}\text{C}$ value of the atmosphere.

^c Interval IIB does not include all Hippopotamidae as they are overrepresented.

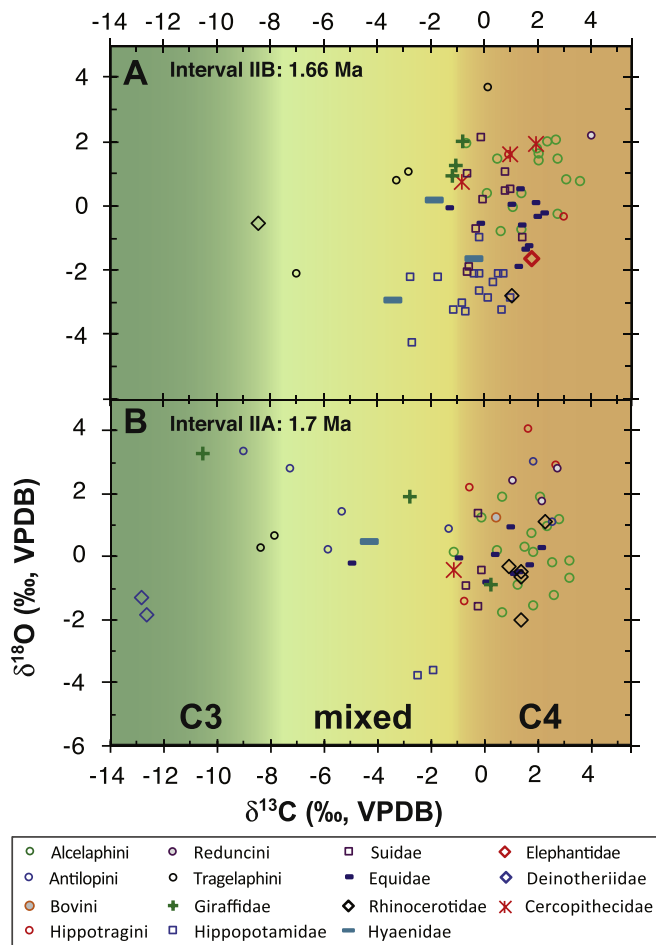


Figure 2. Cross plot of tooth enamel carbon and oxygen isotopes from the two main Bed II intervals, A) Interval IIB (1.66 Ma) and B) Interval IIA (~1.7 Ma). Shaded regions indicate C₃-dominated (green), mixed C₃–C₄ (yellow), and C₄-dominated (orange) diets based on $\delta^{13}\text{C}$ values. Data are plotted at the family level except for Bovidae, which are plotted by tribe. For Giraffidae, the *Giraffa* sp. has a C₃-dominated diet and *Sivatherium* sp. a C₄-dominated diet. VPDB = Vienna Pee Dee Belemnite.

and West, FLK, and EF-HR. All but two HWK EE samples come from interval IIA. At all sites, C₄-dominated diets were prevalent. At HWK EE, the dietary distribution was 71:21:8 (the same as the IIA values). For FC East and FC West, the ratio was 81:17:2 and at MNK it was 90:10:0. Thus, the higher proportion of C₄-dominated diets in FC East/FC West and MNK may suggest greater proportions of C₄ vegetation relative to HWK EE. Nevertheless, median $\delta^{13}\text{C}$ values are nearly identical from the three sites and median $\delta^{18}\text{O}$ values are only slightly (<1‰) more negative at FC East and West and at MNK than at HWK EE (SOM Table S4). Mann–Whitney U-test results show no statistically significant differences ($p > 0.05$) between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ distributions at the three sites (SOM Table S5).

3.1.2.1. Artiodactyls. Bovids are common in the OGAP and Leakey collections (Bibi et al., submitted), and their carbon and oxygen data are presented by tribe in Figure 5. There were shifts towards more positive $\delta^{13}\text{C}$ distributions (median and/or ranges) between intervals IIA and IIB for Tragelaphini, Reduncini, and Hippotragini. Alcelaphin $\delta^{13}\text{C}$ distributions remained unchanged, but their $\delta^{18}\text{O}$ median values increased by ~1‰ between intervals IIA and IIB, a statistically significant change (Mann–Whitney U-test, Table 3). In other bovid tribes, $\delta^{18}\text{O}$ trends between interval IIA to IIB are mixed, probably in part due to small sample sizes. For example,

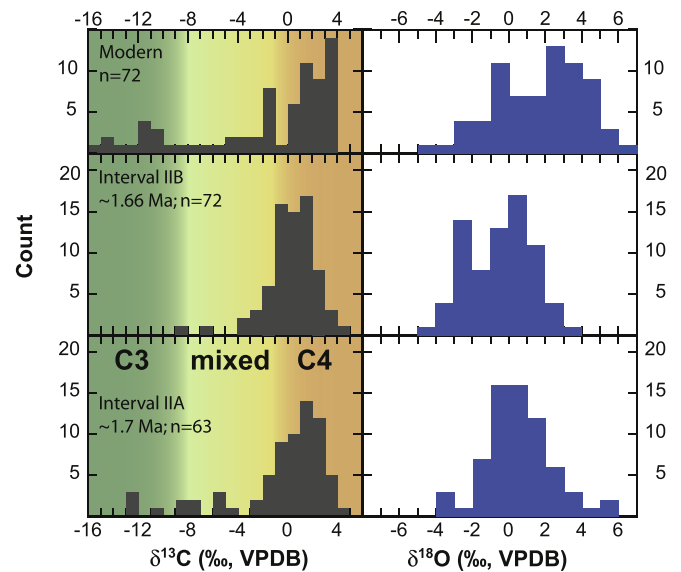


Figure 3. Carbon and oxygen isotope data from the two main Bed II intervals and modern taxa from Tanzania (Van der Merwe, 2013). To compare Bed II and modern samples, we add 1.3‰ to all modern $\delta^{13}\text{C}_{\text{enamel}}$ values (see SOM Table S1). In all three intervals, mammals with C₄-dominated diets are most common with the number of mammals with mixed C₃–C₄ and C₃-dominated diets varying between intervals. Modern $\delta^{18}\text{O}$ values show the broadest range and have a median value that is ~2‰ enriched with respect to Bed II median values (Table 2). Interval IIB includes all Hippopotamidae data ($n = 16$), whereas for statistical analyses only the minimum, maximum and median values are used. VPDB = Vienna Pee Dee Belemnite.

Tragelaphini $\delta^{18}\text{O}$ values increased in range and became more positive in interval IIB, while Hippotragini values became more negative between IIA and IIB (Fig. 5). Among Antilopini, which were sampled from only interval IIA, cf. *Antidorcas recki* had a C₄-dominated diet, whereas the larger form (which might alternately be *Aepyceros*) showed a mixed diet.

Bibi et al. (submitted) divided alcelaphin lower third molars into three taxonomic-size categories: *Megalotragus isaaci* (large size), Alcelaphini spp. indet. (intermediate), and Alcelaphini small spp. (small). Comparisons of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values among these three taxonomic categories show no differences among them (SOM Fig. S3).

Other Bed II artiodactyls had C₄-dominated or mixed diets, with the exception of *Giraffa*, one from HWK EE (interval IIA) and one from EF-HR (interval above IIC). Five *Sivatherium* $\delta^{13}\text{C}$ values, combined from intervals IIA and IIB, indicate C₄-dominated or mixed diets; their $\delta^{18}\text{O}$ values are similar between intervals.

Eighteen *H. gorgops* teeth were sampled, two from interval IIA and 16 from IIB. Interval IIA *H. gorgops* have $\delta^{13}\text{C}$ values of –1.9 and –2.4‰ and $\delta^{18}\text{O}$ values of –3.8 and –3.6‰, the latter of which were the most negative values from all IIA fauna analyzed. In interval IIB, the median $\delta^{13}\text{C}$ value for the 16 *H. gorgops* is –0.1‰ (min: –2.8‰; max: +1.1‰); the median $\delta^{18}\text{O}$ value is –2.6‰ (min: –4.3‰; max: –1.0‰). Hippopotamidae enamel typically yields the most negative $\delta^{18}\text{O}$ values within a given ecosystem (Bocherens et al., 1996; Cerling et al., 2008).

Two suid genera, *Kolpochoerus* and *Metridiochoerus*, had C₄-dominated diets (77–91% C₄), with a median $\delta^{13}\text{C}$ value of –0.1‰ (min: –0.6‰; max: +1.5‰) for Bed II suids. *Kolpochoerus* $\delta^{18}\text{O}$ values are about 1–2‰ more depleted than coeval *Metridiochoerus* values, suggesting different diets, water sources (e.g., due to habitat or dietary preferences), or physiologies.

3.1.2.2. Perissodactyls. Perissodactyls from Bed II comprise relatively rare Rhinocerotidae and abundant Equidae, the latter second

Table 3

Mann–Whitney U-test results comparing carbon and oxygen isotope distributions between the two main intervals (IIA and IIB) and modern Tanzanian taxa from Van der Merwe (2013).

	Intervals IIA and IIB ^a	Interval IIB ^a and modern	Interval IIA and modern
All taxa			
Carbon <i>p</i> -value	0.5557	0.6201	0.9613
Oxygen <i>p</i> -value	0.4607	0.0001^b	0.0015
<i>n</i>	63/59	59/72	63/72
Alcelaphini			
Carbon <i>p</i> -value	0.8451	–	–
Oxygen <i>p</i> -value	0.0445	–	–
<i>n</i>	17/16	–	–
Equidae			
Carbon <i>p</i> -value	0.1754	–	–
Oxygen <i>p</i> -value	0.3312	–	–
<i>n</i>	9/11	–	–

^a Hippopotamidae (*n* = 16) are over represented in the IIB interval so their values were removed and replaced with the maximum, mean, and median values to represent the group.

^b Significant differences in isotope distributions (*p* < 0.05) are in bold.

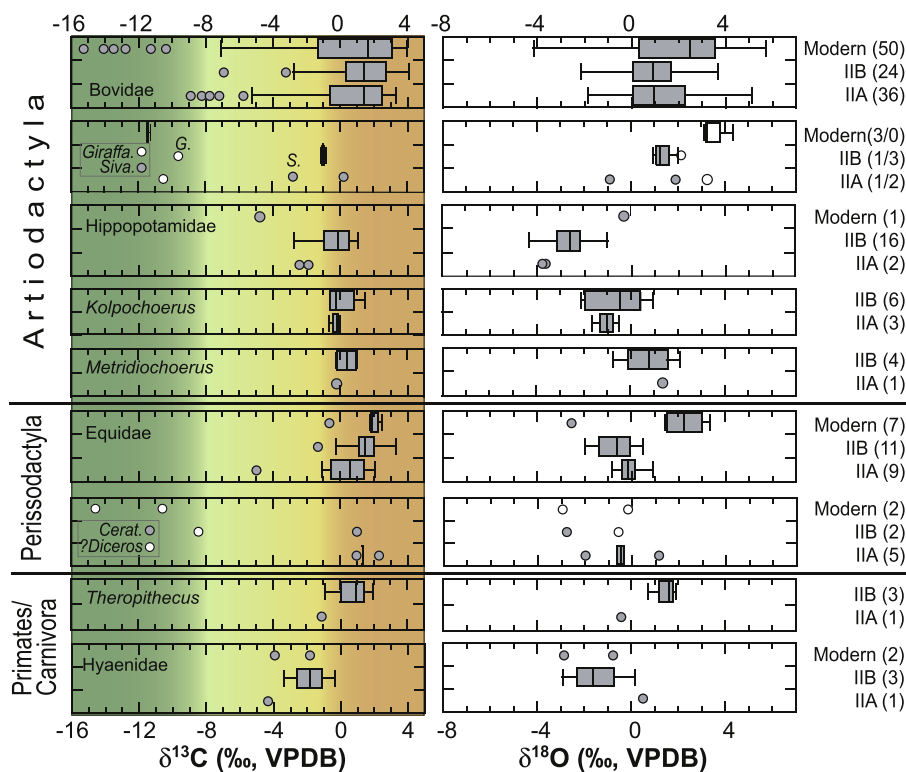


Figure 4. Tooth enamel carbon and oxygen isotope box plots by intervals (IIA, IIB, and modern). The vertical gray line in a box is the median, the box ends are the 1st and 3rd quartiles, and lines (whiskers) define the range of data except for outliers. Taxa are divided at the family level or, where possible, by genera. In the *Giraffa/Sivatherium* panel, *Giraffa* is in white and *Sivatherium* is in gray. In the *Ceratotherium/?Dicerus* panel, *Ceratotherium* is in white and *?Dicerus* is in gray. Abbreviations: *Siva* = *Sivatherium*; *Cerat.* = *Ceratotherium*. VPDB = Vienna Pee Dee Belemnite.

only to Alcelaphini in abundance. In interval IIA, all five rhinocerotid samples – most, if not all, *Ceratotherium* cf. *simum* – indicated C₄-dominated diets (Fig. 4; SOM Table S3). Only two indeterminate specimens were sampled from interval IIB. One of these had a C₄-dominated diet, like the IIA specimens. The other had a C₃-dominated diet suggesting it may well have belonged to the black rhinoceros, *Diceros*, previously recorded from Bed II (Leakey, 1971). The median $\delta^{18}\text{O}$ value of the interval IIA rhino samples is ~1‰ more enriched than those in interval IIB.

Equid teeth analyzed for isotopes were mainly of *Equus oldowayensis* (*n* = 18), with a smaller number belonging to *Eurygnathohippus cornelianus* (*n* = 5), and one indeterminate specimen. Equid $\delta^{13}\text{C}$ values indicate C₄-dominated diets for 21 of 24 analyzed

specimens (SOM Table S3 and Fig. 4). $\delta^{13}\text{C}$ values of *E. oldowayensis* and *Eu. cornelianus* largely overlap. *Eurygnathohippus cornelianus* specimens suggest a diet with a higher proportion of C₄ vegetation than *E. oldowayensis*, but sample sizes for the former were very small (SOM Fig. S3C). $\delta^{18}\text{O}$ values show no differences between the two equid species (SOM Fig. S3D).

Overall, equids in interval IIB have more positive median $\delta^{13}\text{C}$ values and smaller interquartile range than in IIA, which suggests decreased dietary breadth during interval IIB times, while $\delta^{18}\text{O}$ values are slightly more negative in IIB (Fig. 4). However, Mann–Whitney U-test results indicate that neither the differences in carbon (*p* = 0.1754) nor oxygen (*p* = 0.3312) are significant (Table 3).

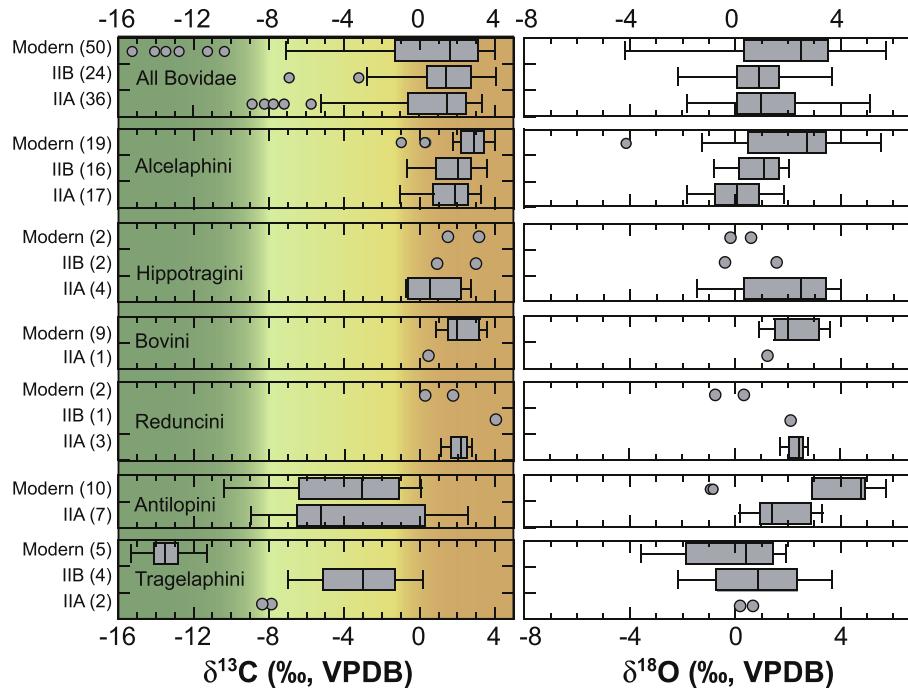


Figure 5. Tooth enamel carbon and oxygen isotope box plots for Bed II and modern Bovidae tribes. All Bovidae data are plotted in the uppermost panel for reference. Sample sizes are given in parentheses. VPDB = Vienna Pee Dee Belemnite.

3.1.2.3. Proboscideans. Proboscidean material is rare from the available data set of Bed II, with only two deinotheres and one elephantid specimen analyzed. The deinotheres from interval IIA yielded the most negative $\delta^{13}\text{C}$ values from Bed II and functionally define a C_3 endmember diet (median = -12.7‰). The $\delta^{18}\text{O}$ values of -1.3 and -1.8‰ are also relatively negative compared to most other values from interval IIA (Fig. 3). With a $\delta^{13}\text{C}$ value of $+1.8\text{‰}$, the single *Elephas recki* specimen from IIB is at the opposite end of the dietary spectrum (93% C_4).

3.1.2.4. Primates. Primates were also rare in Bed II. Four *Theropithecus oswaldi* teeth, one from interval IIA and three from IIB, have a median $\delta^{13}\text{C}$ value of 0.0‰ , indicating C_4 -dominated diets (73–94% C_4). The *T. oswaldi* from interval IIA has more negative $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values than those from interval IIB (Fig. 4).

3.1.2.5. Carnivores. Four hyaenid teeth (*Crocota* sp.) were analyzed from Bed II, one from interval IIA and three from IIB. The IIA specimen has a $\delta^{13}\text{C}$ value of -4.3‰ and the three from interval IIB have values ranging from -3.4 to -0.3‰ (Fig. 4). Carnivore biapatite is depleted $\sim 1.3\text{‰}$ with respect to their diet (Fox-Dobbs et al., 2006), so the *Crocota* prey at Olduvai were herbivores with mixed and C_4 -dominated diets. *Crocota* $\delta^{18}\text{O}$ values ranged from -2.9 to $+0.5\text{‰}$. The Bed II *Crocota* stable isotope values are similar to those of modern hyenas from Tanzania reported by Van der Merwe (2013) and are plotted in Figure 4.

3.1.2.6. Serially sampled equids. The measured and modeled isotope data from the three *E. oldowayensis* intratooth profiles are given in SOM Table S6 and additional model input and output data (E_{meas} , E_{pred} , and ϵ) are provided in SOM Table S7. The intratooth profiles are plotted in Figure 6. The modeled $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the profiles ranged from -2.3 to $+2.1\text{‰}$ and -2.1 to $+1.6\text{‰}$, respectively, which reflect the estimated range of dietary input and body water variability, after being corrected for blurring due to enamel maturation and sampling (SOM Table S6). The tooth from

the Lemuta interval at HWK EE (IIA interval, specimen L10-523) shows greater seasonal variability in both isotope ratios than the other two profiles, L1-48 (MNK Main) and L62-104 (FC West), that came from interval IIB (Fig. 6). For example, the estimated diet of the *E. oldowayensis* from IIA ranged from 66 to 97% C_4 , whereas the diets of the other two ranged from 74 to 87% C_4 (specimen L1-48) and from 91 to 97% C_4 (specimen L62-104). All three profiles indicate mostly C_4 -dominated diets, with indications of seasonally mixed C_3 – C_4 diets in L10-523 and L1-48 (SOM Table S6).

3.2. Tooth wear

All the results from the mesowear and microwear analyses are provided in Table 4 by site for all taxa. Raw data are available in SOM Table S8. Even if all teeth available in the collections had been sampled, the sample size for many taxa would still be very low. The results from taxa with small sample size ($n < 3$) are reported but will not be used in the interpretations (see Discussion).

Small samples excluded, mesowear scores range from $\text{MWS} = 1.8$ in Reduncini to $\text{MWS} = 5.2$ in Equidae (Table 4). This range of values corresponds to those for extant grass-dominated mixed feeders and grazers (Fortelius and Solounias, 2000; Muhlbachler et al., 2011). In comparison to extant reference samples, the microwear patterns observed correspond to the range of extant mixed feeders and grazers (Fig. 8; Table 4). The detailed results are reported for each taxon, comparing the assemblages from intervals IIA and IIB.

3.2.1. Artiodactyls Bovidae are represented by six tribes (Table 4). In general, bovids plot among the extant mixed feeders (Fig. 8A). Sample size is sufficiently large for further analysis for Alcelaphini, Antilopini, and Reduncini.

Alcelaphini provided the largest sample, both at IIA ($n = 45$ for mesowear, $n = 35$ for microwear) and IIB ($n = 38$ for mesowear, $n = 40$ for microwear). The two samples show mesowear scores similar to extant grass-dominated mixed feeders and grazers. The sample from IIB has higher values than in IIA, but the values overlap

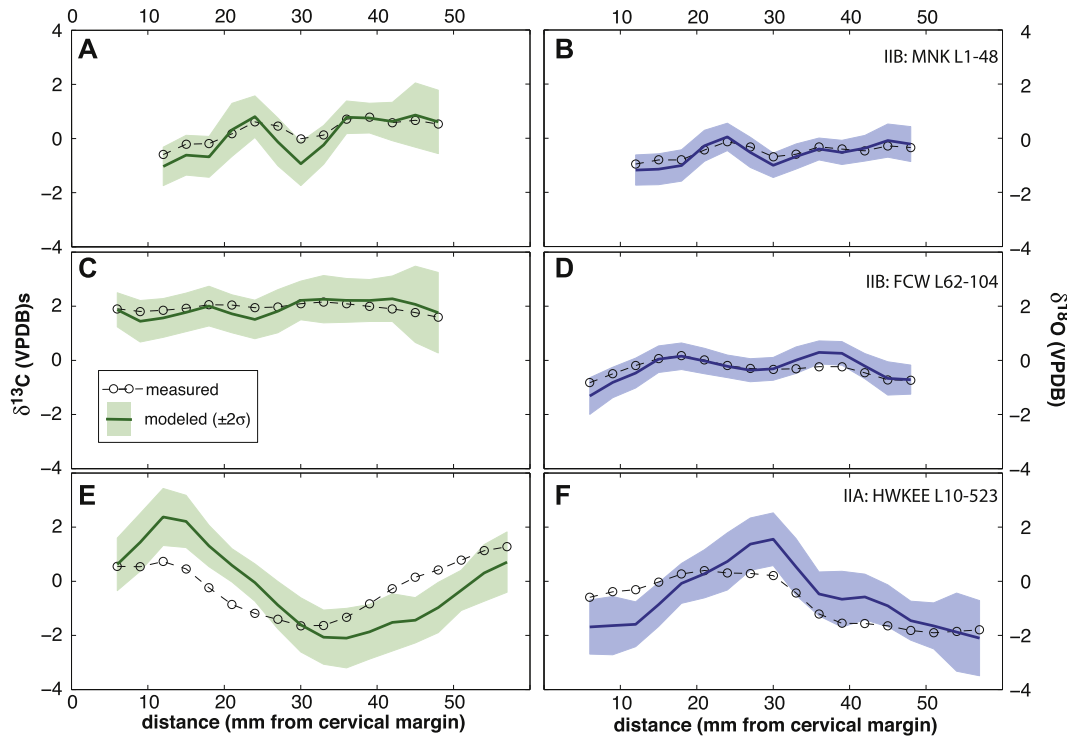


Figure 6. Intratooth *Equus oldowayensis* isotope profiles from interval IIB (MNK Main L1-48 and FC West L62-104; panels A–D) and interval IIA (HWK EE L10-523; panels E and F). Open circles are measured data (smoothed with a 3 pt weighted mean; see text for details), the thick line is the mean of 100 inverse model solutions for the estimated input signal (i.e., diet or body water), and the shaded area is $\pm 2\sigma$ of the solutions. The IIA interval profile exhibits greater variability than the two profiles from the IIB interval. VPDB = Vienna Pee Dee Belemnite.

slightly (Fig. 7). The microwear pattern with intermediate numbers of scratches is characteristic of mixed feeders (Fig. 8A). In terms of numbers of pits and scratches, the microwear pattern is very similar in the two stratigraphic units (Table 4). However, some differences are reported with a higher percentage of large pits and

hypercoarse scratches, as well as wider scratches (higher SWS) in interval IIA.

Hippotragini, even with relatively small sample sizes, show mesowear and microwear values which are very similar to those previously reported for the Alcelaphini (Fig. 7 and Fig. 8A). The two

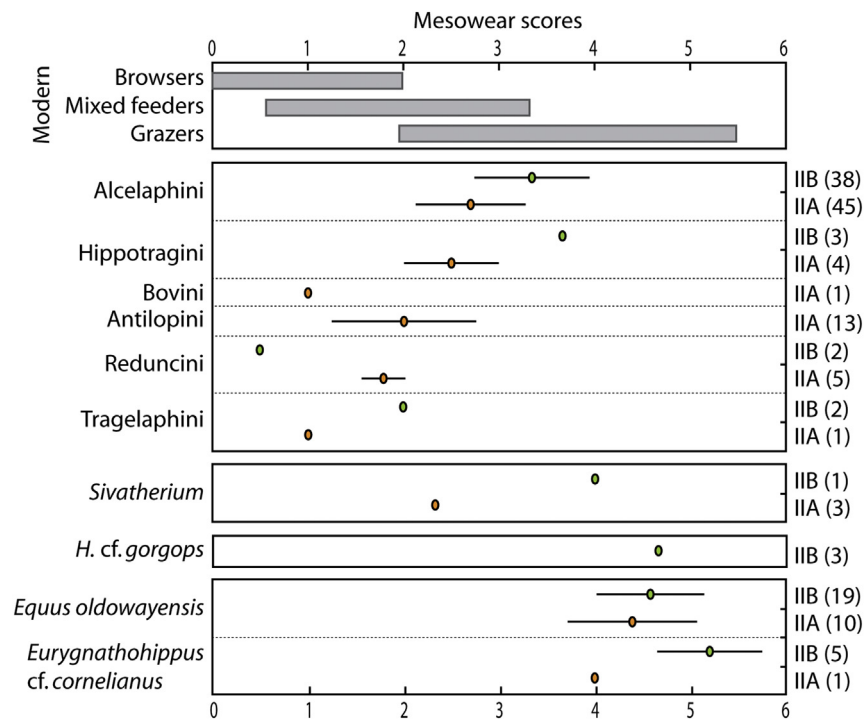


Figure 7. Mesowear scores for the taxa from Bed II intervals IIA and IIB. Sample size is given in parenthesis for each taxon. The data from modern browsers, mixed feeders and grazers are taken from Fortelius and Solounias (2000).

Table 4
Summary of mesowear and microwear data for the fossil assemblages from Olduvai Bed II intervals IIA and IIB.

Stratigraphy	Taxa	Mesowear			Microwear					%LP	%G	SWS	%XS	%PP	%HC	
		n	MWS	SD	n	NP	SD (NP)	NS	SD (NS)							
Interval IIA	Antilopini	13	2.00	1.53	11	22.41	8.43	16.50	5.94	27.27	18.18	1.0	0.00	0.00	0.00	
	Bovini	1	1.00		2	17.75		13.75		0.00	0.00	1.0	0.00	0.00	0.00	
	Caprini				1	9.00		12.50		0.00	0.00	1.0	0.00	0.00	0.00	
	Hippotragini	4	2.50	1.00	3	19.83	7.52	17.67	2.47	33.33	0.00	1.3	0.00	0.00	33.33	
	Reduncini	5	1.80	0.45	3	24.17	6.17	22.17	1.04	66.67	0.00	1.0	0.00	0.00	0.00	
	Tragelaphini	2	1.00		1	33.00		10.50		100.00	0.00	1.0	0.00	0.00	0.00	
	Alcelaphini	45	2.69	1.14	35	17.50	4.82	17.66	3.09	28.57	0.00	1.2	2.86	2.86	34.29	
	<i>Equus oldowayensis</i>	10	4.40	1.35	18	15.92	4.75	15.92	2.32	5.56	5.56	1.2	0.00	0.00	16.67	
	<i>Eurygnathohippus cornelianus</i>	1	4.00		5	13.50	4.95	19.25	1.71	0.00	0.00	1.0	0.00	0.00	0.00	
	<i>Sivatherium maurusium</i>	3	2.33		3	30.00		14.00		33.33	33.33	2.0	33.33	0.00	33.33	
	<i>Hippopotamus gorgops</i>	3			3	10.17		18.83		33.33	33.33	1.0	100.00	0.00	0.00	
	<i>Ceratothorium cf. simum</i>				3	19.67		19.17		0.00	0.00	0.7	33.33	0.00	0.00	
	<i>Kolpochoerus</i> sp.				11	18.00	5.77	20.32	2.75	63.64	18.18	1.0	90.91	18.18	0.00	
	<i>Metridiochoerus</i> sp.				2	10.50		17.25		50.00	50.00	1.0	100.00	50.00	50.00	
	Interval IIB	Bovini	1			1	12.50		16.50		0.00	0.00	1.0	0.00	0.00	0.00
		Hippotragini	3	3.67		2	15.00		16.50		0.00	0.00	1.0	0.00	0.00	0.00
		Reduncini	2	0.50		1	14.50		20.00		0.00	0.00	1.0	0.00	0.00	0.00
Tragelaphini		1	2.00													
Alcelaphini		38	3.34	1.21	40	16.38	6.66	17.59	3.92	20.00	7.50	1.0	0.00	2.50	2.50	
<i>Equus oldowayensis</i>		19	4.58	1.12	32	15.92	4.29	18.17	2.96	40.63	9.38	1.0	6.25	0.00	0.00	
<i>Eurygnathohippus cornelianus</i>		5	5.20	1.10	8	16.81	6.60	20.06	1.97	12.50	0.00	1.4	0.00	0.00	12.50	
<i>Sivatherium maurusium</i>		1	4.00		2	15.25		12.50		0.00	0.00	1.0	0.00	0.00	0.00	
<i>Hippopotamus gorgops</i>		3	4.67		18	10.47	3.58	15.47	2.73	22.22	11.11	1.7	94.44	0.00	5.56	
<i>Kolpochoerus</i> sp.					14	16.18	6.26	17.82	4.77	21.43	21.43	1.1	92.86	0.00	14.29	
<i>Metridiochoerus</i> sp.					5	13.40	2.22	18.30	2.71	0.00	0.00	1.2	100.00	0.00	20.00	
<i>Elephas recki</i>					1	17.00		16.00		0.00	0.00	2.0	0.00	0.00	0.00	
Intervals IIA + IIB		<i>Theropithecus oswaldi</i>	3			3	14.67		26.00		33.33	0.00	1.3	66.67	0.00	0.00

Abbreviations: n = Number of specimens; MWS = Mesowear score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width score; %XS = Percentage of specimens with cross scratches; %HC = Percentage of specimens with hypercoarse scratches; %PP = Percentage of specimens with puncture pits; SD = standard deviation.

samples from intervals IIA and IIB plot among the mixed feeders. Nevertheless, the sample from interval IIA displays a higher percentage of large pits and wider scratches than in interval IIB as well as the presence of hypercoarse scratches.

Antilopini provided data in only interval IIA ($n = 13$). The mesowear score plots among the mixed feeders, at the limit of the values for extant browsers and grazers (Fig. 7). The same result is obtained from microwear (Fig. 8A). The Antilopini show high percentages of large pits (Table 4) like the Alcelaphini and the Hippotragini from interval IIA, but the pits differ from those found in the latter in being associated with gouges, which indicate the presence of large-sized particles of grit on the vegetation consumed.

Reduncini show low mesowear scores corresponding to browsing or browse-dominated mixed feeding (Fig. 7), but high numbers of scratches indicating grazing (Fig. 8A). There is a clear discrepancy between the two proxies, especially for the sample from interval IIA (the sample size from interval IIB is very small).

Bovini and Tragelaphini are represented by only very small samples. Specimens from interval IIA show low mesowear values and low numbers of scratches consistent with browsing (Fig. 7 and Fig. 8A). Specimens from interval IIB were studied from only a single proxy, i.e., microwear for the Bovini and mesowear for the Tragelaphini. For Bovini, microwear shows intermediate values consistent with mixed feeding (Fig. 8A). For Tragelaphini, the single mesowear value suggests mixed feeding (Fig. 7). However, the low sample size prohibits confident interpretation of the results.

Caprini are represented by only a single specimen of uncertain stratigraphic provenience (surface find). The low number of scratches would suggest a browsing trend, but sample size limits the significance of this interpretation (Fig. 8A).

The giraffid *Sivatherium maurusium* shows intermediate mesowear and microwear values. The mesowear values show a tendency

toward grazing (MWS > 2), while the microwear pattern, with a low number of scratches (NS < 17), suggests more browsing at the time of death (Fig. 8B). As previously reported for most of the bovids, the samples from interval IIA show higher percentages of large pits, gouges, hypercoarse scratches, but also cross scratches, than in interval IIB (Table 4). Consequently, due to the presence of hypercoarse scratches, the SWSs are generally also high in interval IIA. These higher scores, i.e., wider scratches in interval IIA, would suggest the presence of high quantities of grit ingested together with the vegetation.

For *H. gorgops*, tooth mesowear indicates grazing (in interval IIB), while microwear suggests mixed feeding (in both intervals IIA and IIB). The microwear pattern is also characterized by a high frequency of cross-scratches in intervals IIA and IIB, and the presence of coarse and hypercoarse scratches (high SWS) in interval IIB (Table 4).

The suids *Kolpochoerus* sp. and *Metridiochoerus* sp. were analyzed only through microwear. The four samples plot in the grazing confidence ellipse or among the grass-dominated mixed feeders (Fig. 8B). All samples have high percentages of cross scratches (from 90 to 100%) and many samples display large pits, gouges, puncture pits and hypercoarse scratches. The combination of all these features would suggest these species consumed leaves, grasses, wood bark, and importantly, might have relied on a rooting diet (Medin et al., 2015).

3.2.2. Perissodactyls The equids *E. oldowayensis* and *Eu. cornelianus* have high mesowear values (MWS = 4 to 5.2) which correspond to extant grazers (Fig. 7). Mesowear values for the two species in interval IIB are higher than those in interval IIA, suggesting more abrasive diets in the samples from interval IIB. Regarding microwear, *E. oldowayensis* shows fewer scratches than *Eu. cornelianus*, indicating that *Eu. cornelianus* was more of a grazer than *E. oldowayensis* (Fig. 8B). In each assemblage,

E. oldowayensis also has more large pits and gouges than *Eu. cornelianus*. It is also significant that the samples from interval IIB show a higher number of scratches than those from interval IIA, indicating more abrasion in interval IIB, which is consistent with the previously reported mesowear results.

For *C. cf. simum*, the sample from interval IIA ($n = 3$) displays a high number of scratches with values tending towards the extant grazers (Fig. 8B). The absence of large pits and gouges and the presence of mostly fine scratches (low SWS value) also confirm grass-dominated diets (Table 4).

3.2.3. Proboscideans *Elephas recki* is represented by a single specimen showing a microwear pattern with an intermediate number of scratches, plotting in between extant browsers and grazers (Table 4 and Fig. 8B).

3.2.4. Primates Primates are represented by three specimens attributed to *T. oswaldi*. In comparison to extant primates with known diets (Godfrey et al., 2004), the specimens from intervals IIA and IIB plot among the species which feed on grass such as *Theropithecus gelada*, *Hapalemur griseus* and *Hapalemur simus* (Fig. 9).

3.2.5. Tooth wear summary Mesowear scores are generally higher in the samples from interval IIB compared with those from interval

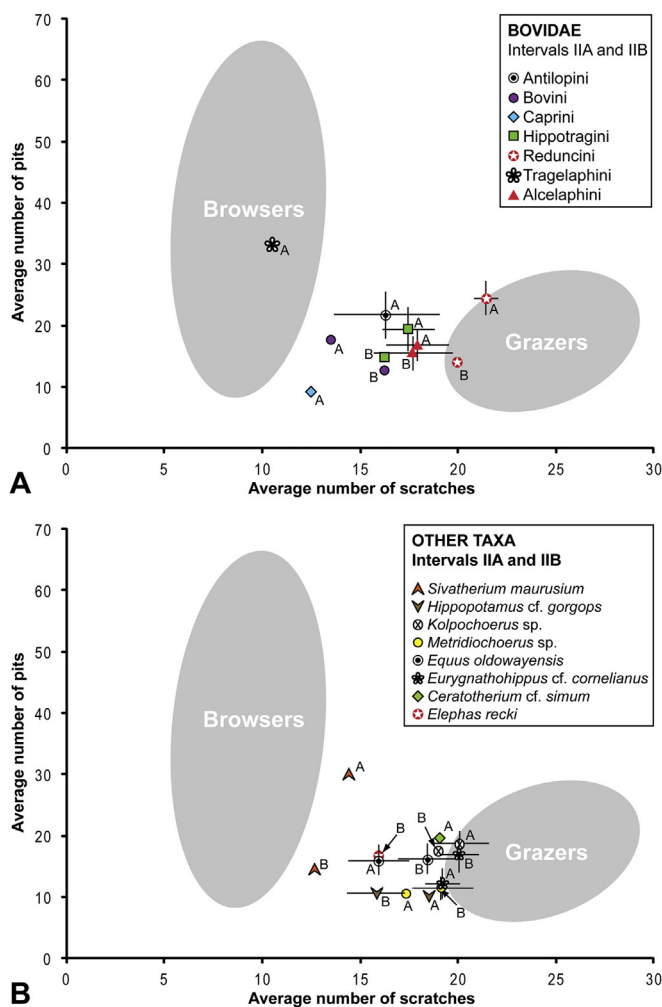


Figure 8. Bivariate plot of the average numbers of pits and scratches for the Bovidae (A) and the other taxa (B). Bars correspond to standard deviations for the fossil samples. Gray areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the modern leaf browsers and grazers based on Solounias and Sempregon (2002) and Rivals et al. (2010).

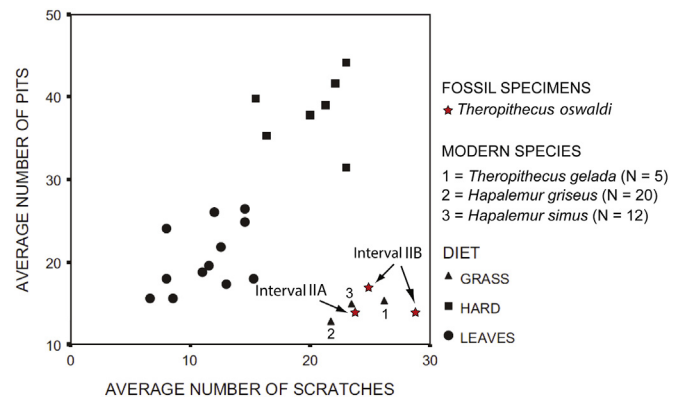


Figure 9. Bivariate plot of the average numbers of pits and scratches for primates (modified from Godfrey et al., 2004) with the three *Theropithecus oswaldi* specimens from Olduvai Bed II intervals IIA and IIB plotted as red stars. *Theropithecus oswaldi* plots among extant primates feeding on grass.

IIA, with the exception of the small sample of Reduncini (Fig. 7). This would indicate a more abrasive diet for the populations of herbivores from interval IIB.

In terms of tooth microwear, the samples from interval IIA and IIB have the same ranges of scratches, but the samples from interval IIA tend to have higher numbers of pits than those from interval IIB. The samples from interval IIA usually have more large pits and gouges, and wider scratches (higher SWS and presence of hyper-coarse scratches) than those from interval IIB (Table 4). All these features would suggest the ingestion of exogenous particles (dust, grit) related to drier conditions in interval IIA.

4. Discussion

4.1. Dietary reconstructions

We find no major shifts in overall dietary ecology across the Oldowan–Acheulean transition, although there are changes at the tribe or family level. The stable isotope data suggest a decrease in the number of mammals with mixed and C_3 -dominated diets in interval IIB. However, limited sample size for the isotope data set and hominin preference for mammals with C_4 -dominated diets (e.g., Alcelaphini) may bias the record against browsers (Patterson et al., 2017). Mesowear scores generally increase between intervals IIA and IIB, suggesting an increase in grazing. Microwear data indicate more abrasive diets in interval IIA based on the higher occurrence of scratches. The combination of tooth wear and stable isotope analyses provides two independent methods for reconstructing mammalian diets. A combined approach has the potential to yield more refined paleodietary and paleovegetation reconstructions.

Dietary interpretations based on tooth wear and isotope data are summarized in Table 5. Throughout the ensuing discussion of dietary reconstructions based on tooth wear and stable isotopes, it is important to keep in mind that each method records diet over different periods of an animal's life. Microwear analysis represents diet over the previous days or weeks before death; mesowear over months to years; and stable carbon isotopes record diet during tooth formation, which ranges from ~1 to 2 years in ungulates and up to a decade or more in proboscideans (Hoppe et al., 2004; Uno et al., 2013). Discrepancy in reconstructed diet can occur due to long-term (e.g., ontogenetic) or short-term (i.e., seasonal) differences in diet. Dietary discrepancies are expected to be more frequently observed among mixed feeders or dietary generalists than in dedicated grazers or browsers.

Table 5
Summary of dietary interpretations based on tooth wear and stable carbon isotope data.

Taxon	Interval IIA			Interval IIB		
	Isotopes ^a	Mesowear ^b	Microwear ^b	Isotopes	Mesowear	Microwear
Bovidae						
Alcelaphini	C ₄	MF-G, G	MF-G	C ₄	MF-G, G	MF-G
Antilopini/Aepycerotini	C ₃ , MF-C ₃ , C ₄	MF	MF	–	–	–
Bovini	(C ₄)	(B)	(B)	–	–	(MF)
Hippotragini	C ₄	MF-G	(MF-G)	(C ₄)	(MF-G)	(MF-G)
Reduncini	(C ₄)	MF-B	(G)	(C ₄)	(MF-B)	(G)
Tragelaphini	(MF-C ₃)	(B)	(B)	MF-C ₃ to C ₄	(MF)	–
<i>Theropithecus oswaldi</i>	(MF-C ₄)	–	(G)	(C ₄)	–	(G)
Deinotheriidae	(C ₃)	–	–	–	–	–
<i>Elephas recki</i>	–	–	–	(C ₄)	–	(MF)
<i>Equus oldowayensis</i>	MF-C ₃ to C ₄	G	MF	MF-C ₄ , C ₄	G	MF-G
<i>Eurygnathohippus cornelianus</i>	(C ₄)	(G)	G	(C ₄)	G	G
<i>Giraffa</i> spp.	(C ₃)	–	–	–	–	–
<i>Sivatherium maurisium</i>	(MF-C ₄)	(MF-G)	(MF-B)	(MF-C ₄ , C ₄)	(MF-G)	(MF-B)
<i>Crocota</i> sp.	(MF-C ₄ based)	–	–	MF-C ₄ , C ₄ based	–	–
<i>Hippopotamus gorgops</i>	(MF-C ₄)	–	(MF)	MF-C ₄ , C ₄	(G)	MF
<i>Ceratotherium cf. simum</i>	C ₄	–	(G)	(C ₄)	–	–
? <i>Diceros</i>	–	–	–	(C ₃)	–	–
<i>Kolpochoerus</i> sp.	(C ₄)	–	G	C ₄	–	MF-G
<i>Metridiochoerus</i> sp.	(C ₄)	–	(MF)	C ₄	–	MF-G, G

^a C₃ = C₃-dominated diet (<25% C₄), MF-C₃ = C₃ mixed feeder (25–50% C₄), MF-C₄ = C₄ mixed feeder (51–75% C₄), and C₄ = C₄-dominated diet (>75% C₄). Parentheses around diet class indicate $n < 3$.

^b B = browser, MF-B = browse-dominated mixed feeder, MF = mixed feeder, MF-G = grass-dominated mixed feeder, and G = grazer. Parentheses around diet class indicate $n < 3$.

Tooth enamel carbon isotope values indicating C₄-dominated diets in eastern Africa are taken to signify grazing taxa, whereas values indicative of C₃-dominated diets are taken to represent browsing taxa. This assumption is probably valid for taxa younger than ~10 Ma, when carbon isotopes of plant wax biomarkers first show evidence of C₄ vegetation in eastern Africa (Uno et al., 2016). It is further supported by the earliest record of C₄-dominated diets in eastern African from equids at 9.9 Ma, and being widespread among Artiodactyla, Perissodactyla, and Proboscidea by ~7 Ma (Uno et al., 2011). There is evidence for the presence of C₃ grasses in the Pliocene of Laetoli (Rossouw and Scott, 2011), but it is unlikely that C₃ grasslands were ever widespread in eastern Africa during this timeframe, as this would require longstanding C₄-feeders like equids to have grazed selectively based on photosynthetic pathway (or some associated characteristics). It is possible that C₄-dominated diets might have included some proportion of C₄ shrubs (e.g., Amaranthaceae), a question that can be further addressed through a combined tooth wear and isotope approach.

In Olduvai Bed II, the combined tooth wear and stable isotope data indicate C₄ grass-dominated diets for most taxa (Figs. 2–5), with tooth wear data also suggesting that C₃ grasses or C₄ shrubs may have been minor dietary components. The tooth wear data indicate that taxa from interval IIA were grass-dominated mixed feeders and grazers while those from IIB were mostly grazers (Table 5). Taxa from interval IIB tend to show a stronger grazing signal in comparison to their IIA counterparts (Fig. 8), suggesting more abrasive vegetation during interval IIB. This could suggest an increase in the availability of grass or more open habitats in the IIB interval. The carbon isotope data similarly indicate a greater representation of C₃-dominated and mixed diets in interval IIA than in IIB (Fig. 2 and Fig. 3). The percentages of mammals with C₄-dominated, mixed, and C₃-dominated diets for all Bed II fauna are 77:18:5. Between intervals, the dietary distribution shifts from 71:21:8 (IIA) to 82:17:1 (IIB). However, given the low sample number of mixed feeders and browsers and the fact that the fossil teeth analyzed represent a subset of a larger palimpsest collection of paleontological and archaeological material which have their own taphonomic and accumulation biases, we view these

distributions as broadly representative of the diets of the large mammal community at Olduvai. A more detailed look at the combined tooth wear and isotope data among different taxonomic groups further illustrates the utility of combining the two methods (Table 5).

4.1.1. Artiodactyls Tooth wear of Alcelaphini indicate grazing and grass-dominated mixed feeding (Fig. 8A). This differs slightly from the carbon isotope data, which indicate C₄-dominated diets (Fig. 3 and Fig. 5). The grass-dominated mixed feeding signal in Alcelaphini comes from a low number of scratches (<20) in the microwear data (Table 4) that places these samples outside the 95% confidence ellipse for grazers. Their mesowear scores fall within the modern range of grazers and the upper half of the mixed feeding range (Fig. 7). Grazing on soft, mesic C₄ grasses could lead to the combination of relatively high occlusal relief and strong C₄ isotope signal, as has been observed in extant Reduncini. Hippotragini data are similar, with carbon isotopes indicating C₄-dominated diets (75–100% C₄), mesowear scores in the lower range of extant grazers (but based on a small sample size), and microwear data outside the 95% confidence ellipse for grazers. The low frequency of scratches in both Alcelaphini and Hippotragini could also possibly be a result of browsing on C₄ shrubs, which would reconcile the microwear and carbon isotope data. Bonnefille (1984) identified pollen from a C₄ shrub from the family Amaranthaceae, *Aerva javanica* (listed as *Aerva persia* in that publication) in a single sample in Lower Bed II at locality VEK. This does not constitute evidence for widespread C₄ shrubs, but it does at least document their presence during Bed II times.

Both tooth wear and the isotope data for the antilopin cf. *A. recki* point to predominantly mixed feeding (Table 5). The other bovid tribes have sample sizes that are too small ($n < 4$) to apply these methods, so interpretations have lower confidence. Tooth wear on Tragelaphini indicate browsing, whereas isotope data ($n = 6$) suggest a wide dietary breadth ranging from C₃- to C₄-dominated diets.

Reduncini are deemed C₄ grazers based on the agreement between carbon isotopes and microwear, but have somewhat low mesowear scores (mean of 0.5–1.80 in IIA and IIB, respectively, with $n = 5$ and 2, respectively). Extant reduncins are grazers (Cerling

et al., 2003b), but the mesowear characteristics of *Redunca redunca* and *Kobus ellipsiprymnus* show high relief and rounded cusps, two features associated with browsing or mixed feeding (Fortelius and Solounias, 2000). Their preference for soft (C_4) grasses often found in wetlands is our preferred explanation for the discrepancy between the isotope and mesowear signature. Two Bovini, one from each interval, are classified as mixed feeders based on their microwear and a single mesowear value, whereas the isotope value from a single sample in IIA yields a C_4 -dominated diet (84% C_4).

Carbon isotope data from a small number of cf. *Sivatherium* or *S. maurusium* ($n = 5$) place their diets on the boundary of C_4 -dominated and mixed diets, which is supported by the mean mesowear scores based on a small sample size ($n = 1$ and 3 in IIA and IIB, respectively) that suggest mixed to grazing diets in both intervals (Fig. 7). However, the microwear data indicate browse-dominated mixed diets. A seasonal dietary shift from grazing to browsing could be invoked to reconcile the isotope and microwear data.

Sixteen of 18 Hippopotamidae analyzed for isotopes come from interval IIB, and their diets range from mixed to C_4 -dominated. Interval IIA hippos have C_4 grass-dominated mixed diets based on isotope and microwear data. In interval IIB, carbon isotope values from MNK are more positive than those from FC East and West (SOM Fig. S2), possibly illustrating habitat variability over very short distances (Fig. 1), but collectively indicating mixed and C_4 -dominated diets. Mesowear scores in interval IIB should be taken with caution because sample size is small, but they indicate a grazing diet. Microwear data indicate a grass-dominated mixed diet in IIA and mixed diets in IIB (Table 5).

The two suid genera from Bed II, *Metridiochoerus* and *Kolpochoerus*, had C_4 -dominated diets that cannot be differentiated by isotopes (Fig. 5). From our limited sample size, there does not appear to be any difference in $\delta^{13}C$ values between the two *Kolpochoerus* lineages present at Olduvai. Three *Kolpochoerus limnetes/paiceae* from FC East and FC West have nearly identical $\delta^{13}C$ values, suggesting a narrow dietary niche. *Kolpochoerus phillipi/majus* from HWK EE and FC West all have similar $\delta^{13}C$ values with slightly more variability than in *K. limnetes/paiceae* (SOM Table S3). Microwear data support the dietary differences posited by Souron et al. (2015): a higher number of scratches in *K. limnetes/paiceae* suggests a diet focused on grasses whereas a lower number and greater range of scratches in *K. majus* indicates a more varied diet. We do not have enough data to evaluate dietary differences among species of *Metridiochoerus*.

While carbon isotopes indicate little niche partitioning between *Metridiochoerus* and *Kolpochoerus* species, oxygen isotopes and microwear data provide a different view. *Kolpochoerus*, which is the more abundant of the two suid genera (Bibi et al., submitted), has more negative $\delta^{18}O$ values and a higher percentages of pits than *Metridiochoerus*. More negative $\delta^{18}O$ values likely indicate a greater water dependence for *Kolpochoerus*, but could also be the result of differences in diet, physiology, or feeding behavior. While the specific cause is not certain, this pattern is also present in Turkana Basin suids (Harris and Cerling, 2002). There is little to no temporal change in suid diets between intervals IIA and IIB and relative abundances of the two genera are relatively stable between intervals: *Kolpochoerus* makes up 86% of the suid dental remains in IIA and 79% in IIB, whereas around this same period in the Turkana Basin in the KBS member of the Koobi Fora Formation, the relative abundance of the two suid genera is reversed: *Metridiochoerus* makes up ~65%, *Kolpochoerus* ca. 34%, and *Notochoerus* ~1% (Patterson et al., 2017).

4.1.2. Perissodactyls Olduvai Equidae were primarily C_4 grazers based on large sample sizes of tooth wear and carbon isotope results (Table 4 and Table 5 and SOM Table S3). Mean Equidae

mesowear scores range between 4.0 and 5.2, values associated with extant grazers (Fig. 7 and Table 4). Microwear results suggest grass-dominated mixed feeding to grazing (Fig. 8B). Carbon isotopes from bulk and serial sampling indicate primarily C_4 -dominated diets with seasonal mixed diets (Fig. 3, Fig. 4 and Fig. 6). The minor amounts of C_3 vegetation in their diets may have included some C_3 grasses, although the microwear data suggest minor browsing (Fig. 8B). Modern equids (zebra) from Tanzania have similar $\delta^{13}C$ values to those from Bed II, whereas modern $\delta^{18}O$ values are about 3‰ more positive than Bed II values (Fig. 4).

Tooth wear and isotope data suggest possible niche-partitioning between the two equid species in Bed II, but sample size is limited. The most abundant large mammal species in Bed II, *E. oldowayensis*, had a mixed to C_4 -dominated diet that likely included occasional browse, whereas the smaller *Eu. cornelianus* had a diet comprising C_4 grasses almost entirely (SOM Fig. S3C). This is also supported by a higher average mesowear score and a higher number of scratches in the latter. *Equus oldowayensis* also shows a higher range of variation in the number of scratches, suggesting it had a more variable diet (Table 4).

Bed II rhinocerotids had similar diets to extant white and black rhinos. All sampled specimens have a narrow range of carbon values indicative of C_4 -dominated diets (e.g., *Ceratotherium*) except for a single specimen from IIB with a C_3 -dominated diet (e.g., *Diceros*). Microwear data from three teeth in IIA are in agreement with the isotope data (Table 5).

4.1.3. Proboscideans Isotope data from a single *Elephas* molar suggest a C_4 -dominated diet similar to that of *Elephas* of similar age (1.9–1.55 Ma) from the Turkana Basin (Cerling et al., 2015). Microwear data on this specimen, however, indicate a mixed diet (Table 5). Specimens of *Elephas* are rare in the Bed II collection (Leakey, 1971; Bibi et al., submitted). This is intriguing for several reasons. First, C_4 vegetation and open habitats preferred by *Elephas* were abundant. Second, although Middle Bed II exhibits a top-heavy faunal structure (Bibi et al., submitted) relative to the modern Serengeti fauna, it seems mega- herbivores (>1000 kg) like *Elephas* were much rarer than the macro- herbivores (100–1000 kg), most of which were grazing Bovidae or Equidae. This could be the result of the larger bones of mega- herbivores being differentially preserved in the Olduvai fossil assemblages due to their lower potential for burial and fossilization (Behrensmeyer and Boaz, 1980). However, it must also be considered that the assemblages analyzed here were likely accumulated, at least in part, by hominins. HWK EE and MNK T5 show evidence of hominins butchering proboscideans, but few skeletal parts of these animals are represented at the sites, suggesting some of the fossils that are present in the collections were selectively transported by hominins from an off-site location where the initial butchery took place (see Pante et al., submitted). The carcasses of macro- herbivores are more evenly represented and were likely acquired by hominins more often than those of mega- herbivores based on their relative dominance in the collections.

4.1.4. Primates This is the first study to our knowledge to combine microwear and stable isotope data from *T. oswaldi*, and the first isotope and tooth wear data reported from Olduvai for this species. Carbon isotope data indicate a diet of 81% C_4 vegetation, equivalent to the diet of *Paranthropus boisei* from Bed I (Van der Merwe et al., 2008). The microwear data fall within the range of the extant *T. gelada*, which has a grass- dominated diet (Fig. 9). Thus, there is strong concision from the isotope and tooth wear approaches that support C_4 grazing by *T. oswaldi* (Table 5).

The median $\delta^{13}C$ value of *T. oswaldi* from Olduvai is 1.0‰ more positive than that from coeval *T. oswaldi* (median = -1.0‰; $n = 24$)

reported from the Turkana Basin from 1.95 to 1.5 by Cerling et al. (2013). The median $\delta^{18}\text{O}$ values of *T. oswaldi* from the two regions are indistinguishable: Bed II is +1.2‰ and Turkana is +1.1‰.

4.2. Paleoenvironmental reconstruction

4.2.1. Vegetation We infer a preponderance of C_4 grass on the landscape during the accumulation of Bed II sediments based on dietary reconstructions from isotope ($n = 141$), mesowear ($n = 171$), and microwear ($n = 248$) analyses of fossil teeth. The data show no evidence for significant vegetation change across the Oldowan–Acheulean transition. This view of abundant C_4 grass on the landscape is consistent with carbon isotope based vegetation reconstructions from Lower Bed II and Lemuta soil carbonates (Cerling and Hay, 1986; Sikes, 1994). We converted these published soil carbonate $\delta^{13}\text{C}$ values to fraction woody cover (f_{wc}), a more tangible representation of vegetation, following the equation developed by Cerling et al. (2011), where values >0.4 represent bushland or shrubland vegetation classifications, values from 0.4 to 0.1 represent wooded grasslands, and values <0.1 represent grasslands. The f_{wc} values from Lower Bed II and the Lemuta Beds range from 0.42 to 0.03 with a median value of 0.22. The majority of the soil carbonate data fall within the wooded grassland vegetation classification, and there is no evidence for forested or closed canopy conditions ($f_{\text{wc}} > 0.8$), which might otherwise have been present along water courses and the shore of paleo Lake Olduvai. A relatively open wooded grassland, perhaps with minor pockets of denser woody cover, fits well with the overall proportion of grazing mammals recovered from Bed II deposits (Bibi et al. submitted) and from our tooth wear and isotope data.

Carbon isotopes from n -alkanes (plant waxes) were used to reconstruct vegetation from slightly older (1.9–1.8 Ma) Bed I sediments (Magill et al., 2013a). Plant wax data show precessionally driven vegetation changes that range from forest to grassland over the ~100 ka interval. The Bed I plant wax record suggests there were periods with more woody C_3 vegetation (high f_{wc}) on the landscape, especially during Middle Bed I to lowermost Upper Bed I times, around 1.85 to 1.83 Ma, where n -alkanes values are 3–4‰ more negative than other “wet” cycles in the plant wax records. Faunal records show a temporary shift towards more humid or wooded conditions during Middle Bed I times based on an increase in Reduncini and Tragelaphini, taxa associated with humid and wooded environments, respectively (Kappelman, 1984, figure 4 in Bibi et al., 2017). Both lines of evidence point to greater water availability and woody vegetation in Middle Bed I compared to Bed II. Bed II faunal distributions (Bibi et al., submitted; Prassack et al., submitted), dietary reconstructions presented here and in Rivals et al. (2017), and previously published soil carbonate data do not support the presence of widespread, dense woody cover at any period studied in Bed II.

Paleovegetation in Upper Bed I and Bed II has also been reconstructed from plant remains. Aside from an early study using pollen (Bonnefille, 1984), most work has focused on the use of phytoliths (e.g., Albert et al., 2009, 2015a; Barboni et al., 2010) and plant macrofossils (Bamford et al., 2006, 2008; Bamford, 2012; Habermann et al., 2016b). There is good agreement between the vegetation reconstructions derived from phytoliths and the tooth wear and enamel isotope data presented from intervals IIA and IIB.

New phytolith assemblages from HWK EE trenches include abundant short rondels produced by Poaceae (grasses) in nearly all samples. In some samples, elongate and spheroid morphotypes belonging to the Arecaceae (palms) dominate (de la Torre et al., submitted). Assemblages from Lower Bed II, including the Lemuta

member, also include grass and palm morphotypes, with the latter being more abundant in the Lemuta sandstone. Some Lemuta samples also yielded short saddle forms ascribed to the C_4 Chloridoideae subfamily of grasses, as well as bulliform and trichome morphotypes associated with grasses (de la Torre et al., submitted). The abundance of palm, wood or bark phytoliths in the HWK EE phytolith data might seem at odds with the low abundance of browsers as identified in the faunal and dental analyses. However, there is evidence that Serengeti palms (e.g., *Hyphaene* and *Phoenix*) produce high numbers of phytoliths that may be more robust and have greater preservation potential over other forms, and that wood and bark phytoliths are overrepresented in modern soils (Bamford et al., 2006; Albert et al., 2006, 2015b). This may explain the discrepancy.

4.2.2. Hydroclimate Hydroclimate change across the Oldowan–Acheulean transition can be assessed through bulk and intratooth $\delta^{18}\text{O}$ isotope values (Fig. 3 and Fig. 6). Our oxygen isotope data from bulk sampling of tooth enamel show no evidence of significant hydroclimate change between intervals IIA and IIB (Table 3). Intratooth profiles from *E. oldowayensis* molars for both carbon and oxygen isotopes, however, show greater variation in interval IIA than in IIB (Fig. 6), suggesting reduced seasonality of vegetation and rainfall in interval IIB. Intratooth isotope profiles from *E. oldowayensis* molars are limited in number, so the interpretation of seasonality we draw is preliminary.

With respect to secular trends across the Oldowan–Acheulean transition, previously published $\delta^{18}\text{O}$ data from pedogenic carbonates similarly show no major changes in $\delta^{18}\text{O}$ values, although there is an overall trend towards more positive $\delta^{18}\text{O}$ values, presumably indicative of increasing aridity, from Bed I through the Masek and Ndutu Formations (Cerling and Hay, 1986; Sikes, 1994).

5. Conclusions

Stable isotope and tooth wear analyses of Bed II fauna reveal most large herbivores had C_4 -dominated diets, and microwear analyses indicate these mostly comprised grasses. Carbon isotope and tooth wear data show that the two most abundant taxa from Lower and Middle Bed II, Alcelaphini and Equidae, as well as Hippotragini, Bovini, Reduncini, *S. maurusium* *H. gorgops*, *Kolpochocerus* spp., *Metridiochoerus* spp., *C. cf. simum*, *E. recki*, and *T. oswaldi*, were C_4 grazers or mixed grazers. The antilopin cf. *A. recki* and Tragelaphini were the only true mixed feeders. A few taxa (*Giraffa*, *?Dicerops*, *Deinotherium*) had C_3 -dominated diets. Carbon isotope values in hyaenid teeth indicate they fed primarily on grazers and mixed feeders. The evidence suggests that abundant C_4 grasses supported a large and taxonomically diverse assemblage of grazers and mixed feeders. C_3 vegetation, while less significant on the landscape, was a minor dietary resource for many large mammals, and the primary resource for at least three large (>1000 kg) browsing species.

There is no evidence for major vegetation or hydroclimate change across the Oldowan–Acheulean transition at Olduvai based on tooth wear or stable isotope data. Local climatic and vegetation change does not seem to have played a significant role in the advent of Acheulean technology at Olduvai. A limited sample of equid intratooth profiles does, however, suggest decreased seasonality in vegetation and precipitation between intervals IIA and IIB, and future work should explore this further, as well as expand isotopic records from Bed I and lowermost Bed II to evaluate possible ecosystem change prior to the Oldowan–Acheulean transition.

This study demonstrates that a combined approach of stable isotope and tooth wear analyses can yield more detailed and robust dietary reconstructions than a single method alone and can help

resolve inconsistencies in dietary reconstructions that may be related to temporal scale (e.g., annual, seasonal, daily) and not detectable by the application of a single method alone.

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Supplementary Online Material

Supplementary online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2018.01.002>.

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Supplementary Text for Uno et al., Large mammal diets and paleoecology across the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses

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Tooth enamel stable isotopes and vegetation

Today in eastern Africa nearly all woody vegetation uses the C₃ photosynthetic pathway, or Calvin cycle, and nearly all low elevation (<1500 m) grasses, some sedges (e.g., *Cyperus papyrus*), and select shrubs (e.g., Amaranthaceae) use the C₄ pathway, or Hatch-Slack cycle (Cerling and Harris, 1999; Jones and Milburn, 1978; Livingstone and Clayton, 1980; Sage et al., 2007; Tieszen et al., 1979; Young and Young, 1983). The carbon isotope ratio of C₃ plants is on average around −28 ‰ with an observed range of about −36 to −23 ‰. The wide range in δ¹³C values in C₃ plants is controlled by environmental conditions: more negative values are found in closed canopy forests whereas xeric conditions—common in lowland eastern Africa—lead to more positive values (e.g., −26 to −23 ‰). C₄ plants exhibit a narrower range of values, from about −14 to −10 ‰ in eastern Africa (Cerling et al., 2003).

To establish the end-member δ¹³C values in tooth enamel (δ¹³C_{enamel}) for C₃ and C₄ diets, the atmospheric δ¹³C value (δ¹³C_{atm}) and the enrichment in ¹³C between diet and tooth enamel must be determined. We use the mean value of −6.7 ‰ for the δ¹³C_{atm} based on the high resolution planktonic foraminifera record from 1.8 to 1.6 Ma from Tipple et al. (2010). We chose the 1.8 to 1.6 Ma interval because it best matches the age range for Olduvai Bed II ages.

We use the δ¹³C_{atm} value of −6.7 ‰ along with biosynthetic fractionation factors for C₃ and C₄ plants to calculate the δ¹³C values for C₃ and C₄ plants from 1.8 to 1.6 Ma (**Table S1**). Next, we apply the enrichment factor (ε*_{enamel-diet}) of 14.1 ± 0.5 ‰ as determined by Cerling and Harris (1999) for large ungulates to calculate δ¹³C_{enamel} endmember values of −11.9 ‰ and + 2.8 ‰ for pure C₃ and C₄ diets, respectively (**Table S1**). The 14.1 ‰ enrichment factor probably doesn't apply to all large ungulates. It likely best describes the enrichment in foregut fermenting bovids. Large mammals with other digestive physiologies that do not match the foregut fermenters in terms of methane production, such as equids, rhinos, proboscideans, suids, and hippos likely have slightly lower ε*_{enamel-diet} values (Passey et al., 2005a). Note that the application of the enrichment factor, ε_{enamel-diet}*, is from rearrangement of the following equation,

$$\varepsilon^* = \alpha^* - 1 \quad (1)$$

from Craig (1954), where alpha (α^*) is the apparent fractionation factor between diet and enamel, defined as

$$\alpha^* = (1000 + \delta^{13}\text{C}_{\text{enamel}}) / (1000 + \delta^{13}\text{C}_{\text{diet}}) \quad (2)$$

We include these equations here as a review of the mathematically correct way to calculate endmember $\delta^{13}\text{C}_{\text{enamel}}$ values from $\delta^{13}\text{C}_{\text{diet}}$ values, rather than simply adding $\epsilon^*_{\text{enamel-diet}}$ (14.1 ‰) to the $\delta^{13}\text{C}_{\text{diet}}$ values to determine endmember $\delta^{13}\text{C}_{\text{enamel}}$ values.

Sampling and Methods

Enamel sampling, pretreatment and isotopic analysis

The protocol for bulk sampling involved drilling along broken enamel surfaces whenever possible, or in some cases a lateral tooth surface, using a Dremel handheld drill with carbide (Brasseler) or diamond grit impregnated (Lasco) bits at low speed (~1000 RPM). No occlusal surfaces were drilled so as to preserve these surfaces for morphological or microwear studies. The sample surface was prepared by abrading the enamel surface with the drill bit. On lateral surfaces, this removed surface adherents and the outermost enamel (*ca.* 100 μm). If present, cementum was drilled away to expose enamel. After visual inspection of the prepared surface with a hand lens, a narrow groove about 1mm deep and 1 to 2 mm wide was drilled parallel to the growth axis of the tooth. Sample groove lengths varied based on tooth geometry (enamel thickness and crown length), but ideally were 10 to 15 mm long to average out potential seasonal variability in diet and water. Sample masses ranged from about 3 to 15 mg.

Three equid molars were serially sampled along the growth axis of the tooth to generate intratooth isotope profiles. Cementum was cleared away using the Dremel to expose a window of the fossil enamel. The exposed area was ~5mm wide and ran the length of the tooth crown (50 to 60 mm). Samples were drilled every 3 mm along the growth axis of the tooth, with sample grooves oriented normal to the growth axis. Sample grooves were ≤ 1 mm deep, ~1 mm wide, and 3 to 6 mm long. Sample masses were about 3-5 mg. Enamel powders from bulk and intratooth profile samples were pretreated at LDEO prior to stable isotope analysis with a weak oxidizer followed by buffered acid. Samples were treated with 3% NaOCl (bleach) for 30 minutes in 1.7 ml centrifuge tubes that were stirred every 10 minutes on a vortex mixer. After the reaction period, samples were centrifuged and the supernatant was removed. Each sample was then rinsed three times with distilled water. The rinse procedure involved adding de-ionized (DI) water, stirring on the vortex mixer, then centrifuging the sample and removing the supernatant. Next, samples were treated with 0.1 M Na-acetate buffered acetic acid for 30 minutes, as above. Following three distilled water rinses, they were loosely covered and dried overnight in a fume hood.

Approximately 300 to 600 μg of powdered enamel sample were weighed out into a silver capsules, along with NBS-19 standard (20-50 μg). Samples and standards were roasted in vacuo for 2 hours at 60° C to remove adsorbed water, then transferred to round bottom,

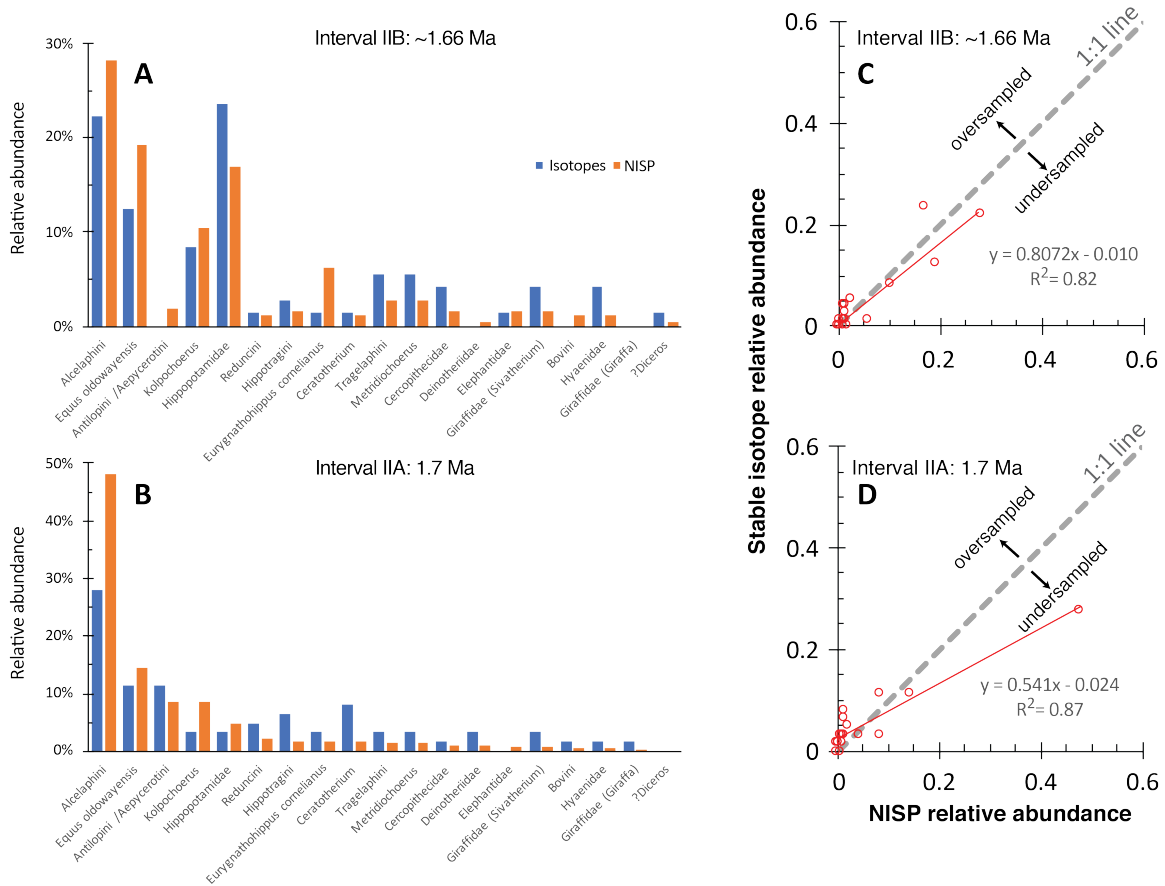
glass reaction vials. A strand of silver wool was added to each vial to oxidize any SO₂ produced in the reaction. Sample vials were loaded immediately into a (Thermo) Kiel IV device or transferred into an oven held at 60° C until analyzed.

Fossil enamel samples were reacted with phosphoric acid at 70° C for 10 minutes in vacuo on a Kiel IV device. Exsolved gases were cryogenically transferred to a microvolume held at -170° C, and then transferred to second microvolume with the first held at -70 °C to remove water. The purified sample CO₂ was inlet into a dual-inlet Delta V Plus isotope ratio mass spectrometer. Carbon and oxygen isotope ratios were corrected using international and internal standards. The standard deviation of NBS-19 throughout sample runs was ~0.05 ‰ for δ¹³C and <0.10 ‰ for δ¹⁸O. Oxygen isotope values were converted from CO₂ (gas) to fossil enamel (mineral) values using a fractionation factor of 1.00799, which was calculated using the temperature dependent equation for fossil enamel (Eq. 4) in Passey et al. (2007).

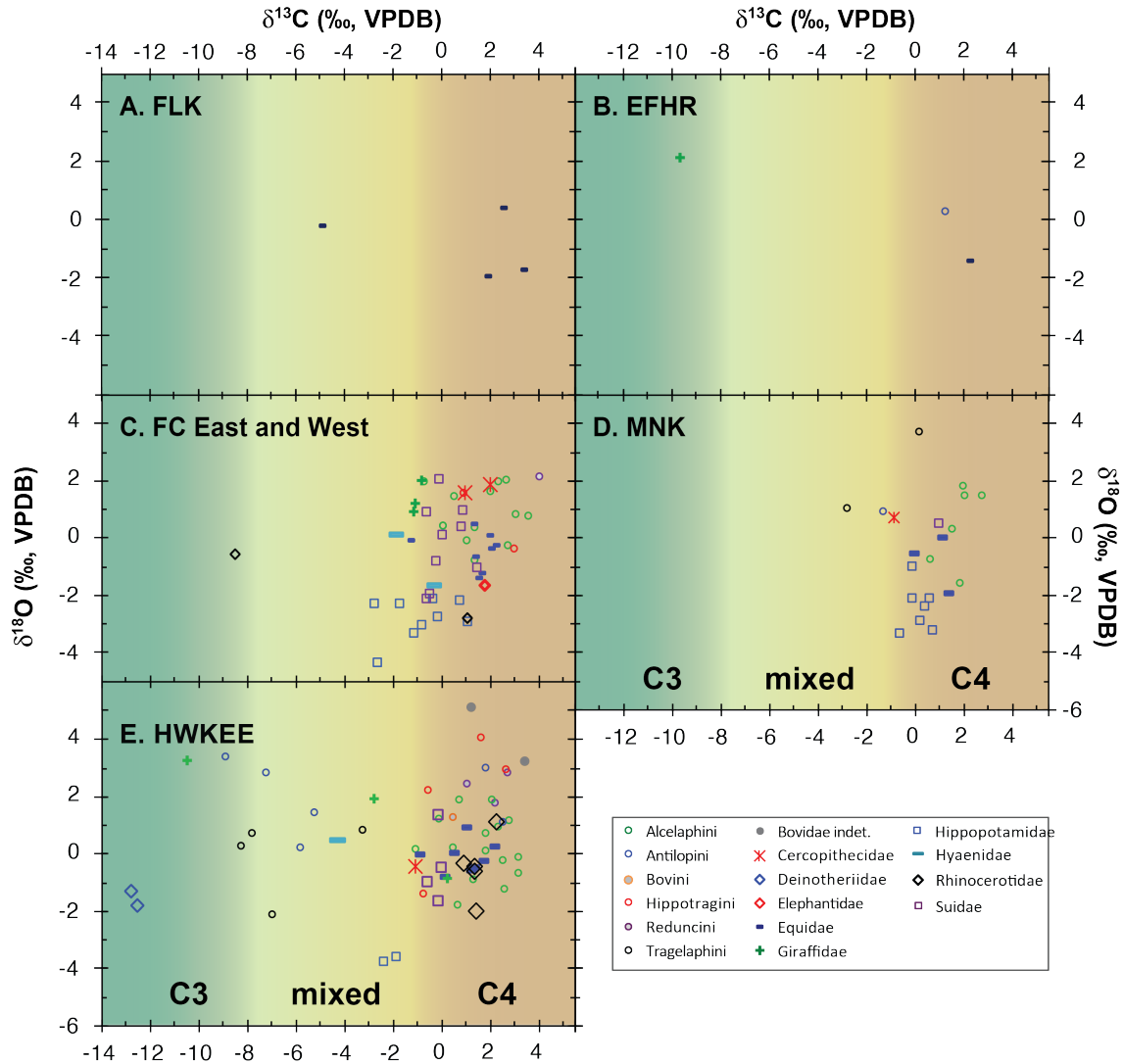
Intratooth stable isotope profiles and inverse modeling procedure

The inverse model requires input parameters related to tooth formation, isotope sampling geometry, and isotope analysis. Input parameters relevant to tooth enamel formation, or amelogenesis, include initial enamel density (f_i), enamel appositional length (l_a) and maturation length (l_m) (Passey and Cerling, 2002). We use parameters measured on *Equus ferus przewalskii* by (Blumenthal et al., 2014) as estimates for *Equus oldowayensis* molars used here, where $f_i = 22\%$, $l_a = 6$ mm, $l_m = 28$ mm. Sample input variables include distance between samples (3 ± 0.5 mm) and depth (0.7 mm \pm 0.2 mm). The final input variables are the measured carbon and oxygen isotope data and their associated uncertainties, which were smoothed with a 3-point weighted mean (0.25:0.5:0.25). A measured error term, E_{meas} , is computed from measurement uncertainties in isotope values and sample measurements. This term ultimately governs model sensitivity it is used to determine an appropriate damping factor (ϵ^2). The model requires selection of a damping factor that minimizes the difference between E_{meas} and the prediction error (E_{pred}). A detailed description of additional model parameters and the regularization method is given in Passey et al. (2005b). Model code was downloaded and adapted from Passey et al. (2005). The inverse model assumes constant growth rate. However, it is widely accepted that ungulate cheek teeth have non-linear growth rates, particularly towards the end of crown extension (Bendrey et al., 2015; Zazzo et al., 2012).

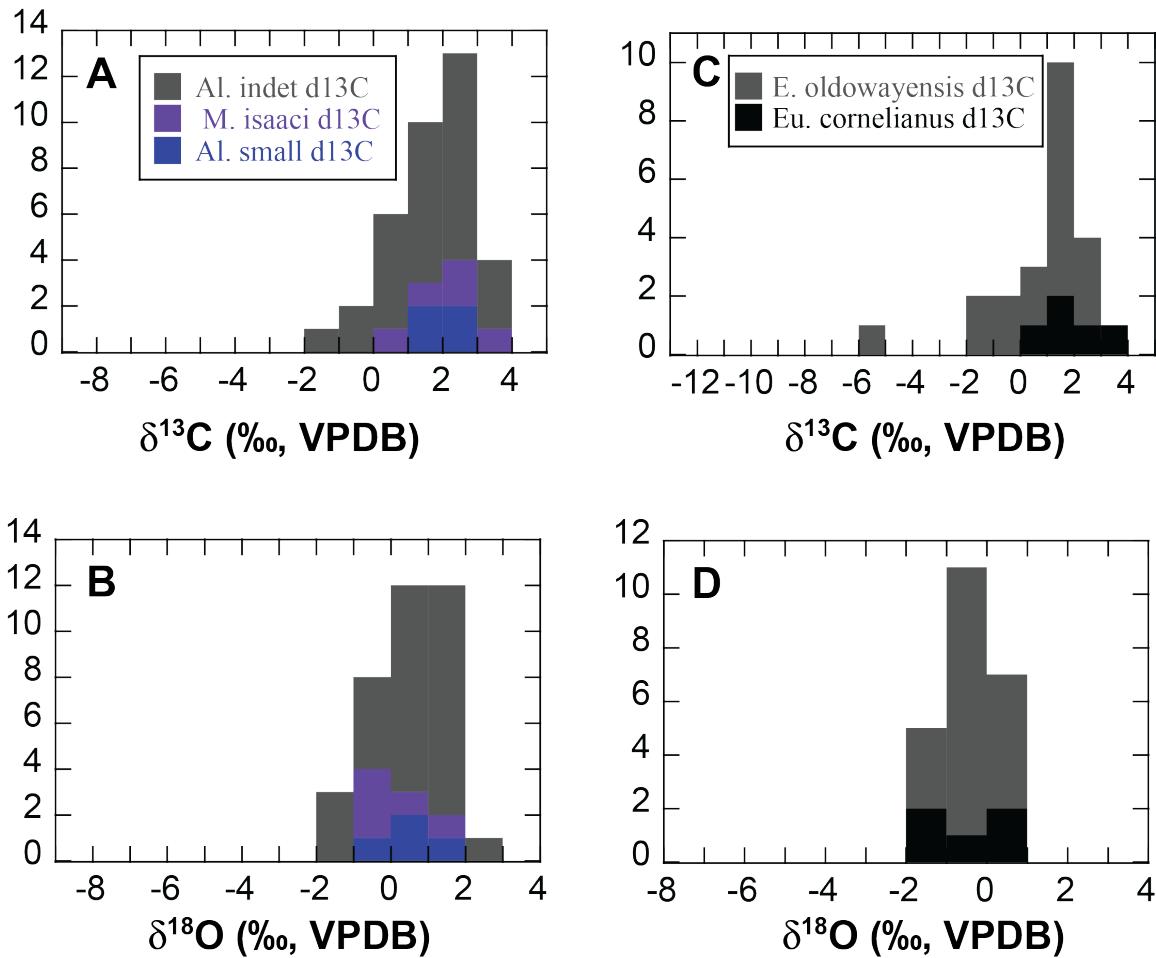
Supplementary Figures



SOM Figure S1. Bar graphs (A, B) and cross plots (C, D) of relative taxonomic abundances of isotope vs. NISP data sets for interval IIA and IIB.



SOM Figure S2. Cross plots of tooth enamel carbon and oxygen isotopes from all sites investigated in this study: A) FLK West, B) EF- HR, C) FC East and West, D) MNK, and E) HWK EE. Shaded regions indicate C₃-dominated (green), mixed C₃-C₄ (yellow), and C₄-dominated (orange) diets based on $\delta^{13}\text{C}$ values. Data are plotted at the family level except for bovinds, which are plotted by tribe.



SOM Figure S3. Histograms of A) $\delta^{13}\text{C}$ and B) $\delta^{18}\text{O}$ for three forms of Alcelaphini (*Megalotragus issaci*, Alcelaphini small sp., and Alcelaphini sp. indet.) from Bed II. Neither isotope shows niche partitioning among the Alcelaphini. Panels C) and D) show $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for the two Equidae species in Bed II, *Equus oldowayensis* and *Eurygnathohippus cornelianus*. The latter tend to have more positive $\delta^{13}\text{C}$ values that indicate a greater proportion of C_4 vegetation in their diet although sample size is small ($n=5$). There is no difference in $\delta^{18}\text{O}$ values.

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