



## Dietary traits of the ungulates from the HWK EE site at Olduvai Gorge (Tanzania): Diachronic changes and seasonality



Florent Rivals <sup>a, b, c, \*</sup>, Kevin T. Uno <sup>d</sup>, Faysal Bibi <sup>e</sup>, Michael C. Pante <sup>f</sup>, Jackson Njau <sup>g</sup>, Ignacio de la Torre <sup>h</sup>

<sup>a</sup> ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

<sup>b</sup> Institut Català de Paleoeologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

<sup>c</sup> Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain

<sup>d</sup> Division of Biology and Paleo Environment, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, 10964, USA

<sup>e</sup> Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, D-10115 Berlin, Germany

<sup>f</sup> Department of Anthropology, Colorado State University, 1787 Campus Delivery, Fort Collins, CO 80523, USA

<sup>g</sup> Department of Geological Sciences, Indiana University, 1001 E Tenth Street, Bloomington, IN 47405, USA

<sup>h</sup> Institute of Archaeology, University College London, 31-34 Gordon Square, WC1H 0PY London, United Kingdom

### ARTICLE INFO

#### Article history:

Received 11 April 2017

Accepted 8 August 2017

Available online 2 September 2017

#### Keywords:

Carbon stable isotopes

Oxygen stable isotopes

Tooth mesowear

Tooth microwear

Oldowan

Bed II Olduvai Gorge

### ABSTRACT

The Oldowan site HWK EE (Olduvai Gorge, Tanzania) has yielded a large fossil and stone tool assemblage at the transition from Lower to Middle Bed II, ~1.7 Ma. Integrated tooth wear and stable isotope analyses were performed on the three most abundant ungulate taxa from HWK EE, namely *Alcelaphini*, cf. *Antidorcas recki* (Antilopini) and *Equus oldowayensis* (Equini), to infer dietary traits in each taxon. Some paleodietary changes were observed for cf. *A. recki* and *E. oldowayensis* based on tooth wear at the transition from the Lemuta to the Lower Augitic Sandstone (LAS) interval within the HWK EE sequence. Stable carbon and oxygen isotope data show no significant changes in bulk diet or hydroclimate between the Lemuta and LAS intervals. The combined tooth wear and stable isotope data suggest similar paleoecological conditions across the two HWK EE intervals, but that differences in vegetation consumed among ungulates may have resulted in changes in dietary niches. Integrating tooth wear and stable isotope analyses permits the characterization of ungulate diets and habitats at HWK EE where C<sub>4</sub> dominated and minor mixed C<sub>3</sub> and C<sub>4</sub> habitats were present. Our results provide a better understanding of the paleoenvironmental conditions of the Lemuta and LAS intervals. The LAS assemblage was mostly accumulated during relatively dry periods at Olduvai Gorge when grasses were not as readily available and grazing animals may have been more nutritionally-stressed than during the formation of the Lemuta assemblage. This helps to contextualize variations in hominin and carnivore feeding behavior observed from the faunal assemblages produced during the two main occupations of the site.

© 2017 Elsevier Ltd. All rights reserved.

## 1. Introduction

Recent excavations at Henrietta Wilfrida Korongo East East (HWK EE) by the Olduvai Geochronology Archaeology Project (OGAP) combined with Mary Leakey's original unpublished collections together yield a remarkable assemblage of stone tools and faunal remains that are critical for understanding hominin habitat and behavior during the late Oldowan to Acheulean technological transition (de la Torre et al., 2018; de la Torre and Mora, 2018; Pante

et al., 2018; Pante and de la Torre, 2018). In that regard, reconstructing the dietary behavior of ungulates at HWK EE provides data on any paleoecological change associated with the technological transition at this site.

The objectives of this paper are 1) to detect dietary shifts between two main stratigraphic intervals preserved at the site, namely the Lemuta Member and the Lower Augitic Sandstone (LAS), and 2) to characterize seasonal patterns in the dietary intake of the most common herbivores in these two stratigraphic intervals. To achieve the first objective, we analyzed paleodiet through tooth mesowear and microwear and stable isotope analysis of tooth enamel of the most abundant taxa at HWK EE:

\* Corresponding author.

E-mail address: [florent.rivals@icrea.cat](mailto:florent.rivals@icrea.cat) (F. Rivals).

Alcelaphini, cf. *Antidorcas recki* and *Equus oldowayensis*. For the second objective, we assessed two aspects of seasonality. First, we examined variability in microwear within a population from a species or tribe to assess whether the fossil assemblage derives from a single event or a seasonal or longer term accumulation. Second, we used intratooth stable isotope analyses to evaluate seasonal changes in diet and hydroclimate.

Although stable isotopes are widely used to study dietary changes in various areas in the Plio-Pleistocene of eastern Africa (e.g., Kingston and Harrison, 2007; Bibi et al., 2013; Cerling et al., 2015), tooth wear studies on ungulate communities are still scarce, whether for microwear or mesowear. Most work to date has focused on specific taxa in southern Africa (Franz-Odenaal et al., 2003; Franz-Odenaal and Solounias, 2004; Kaiser and Franz-Odenaal, 2004; Merceron and Ungar, 2005; Schubert et al., 2006; Ungar et al., 2007; Stynder, 2009, 2011; Boisserie and Merceron, 2011; Peter et al., 2016) or central Africa (Blondel et al., 2010).

The combination of three dietary proxies, namely microwear, mesowear, and stable isotopes, provides data on three different timescales within the lifetime of an animal. Tooth microwear reflects the diet of the last days or week of life (Grine, 1986), mesowear indicates the last weeks or months (Fortelius and Solounias, 2000), and carbon and oxygen isotopes in tooth enamel reflect an animal's diet over the period of tooth formation (Kohn and Cerling, 2002). Development of the permanent dentition in ungulates usually occurs during the first 1–5 years of life (e.g., Brown et al., 1960; Hoppe et al., 2004). Discrepancies resulting from the integration of these three dietary proxies are usually due to changes in diets across the different timescales recorded by each proxy (Ecker et al., 2013; Marín Leyva et al., 2013; Mayte et al., 2016; Sánchez-Hernández et al., 2016). This is the first study to combine tooth wear (both mesowear and microwear) and stable isotope approaches to the archaeological record at Olduvai Gorge.

## 2. Material and methods

### 2.1. Material

The HWK EE archaeological site is located in the Junction Area of Olduvai Gorge, stratigraphically positioned in the transitional interval from Lower to Middle Bed II (de la Torre et al., 2018; Stanistreet et al., 2018), and is dated to ~1.7 Ma (McHenry et al., 2016; McHenry and Stanistreet, 2018) (Fig. 1). Teeth analyzed in this paper include specimens from the Leakey assemblage (Pante and de la Torre, 2018) and from the new excavations at the HWK EE site (de la Torre et al., 2018).

Recent fieldwork at HWK EE has distinguished three main stratigraphic intervals, namely (from bottom up) Lemuta, Lower Augitic Sandstone (LAS) and Tuff IIB (see Fig. 1). The Lemuta Member, which contains fluvial and lacustrine sediments, is separated from the upper intervals by a significant disconformity (see details in Stanistreet et al., 2018), after which fluvial deposits dominate the sequence of LAS and the Tuff IIB interval. Site formation processes at HWK EE are complex and most of the archaeological units are interpreted as palimpsests comprising multiple accumulation episodes, including human, carnivore, and abiotic agents (de la Torre et al., 2018).

For the mesowear and microwear analyses, we focused on cf. *A. recki* ( $n = 10$ ), Alcelaphini ( $n = 43$ ) and *E. oldowayensis* ( $n = 13$ ) as they were the taxa present in both the Lemuta and the LAS stratigraphic intervals with significant dental sample sizes suitable for tooth wear analyses (Table 1). Data on other ungulates present at HWK EE, which were also sampled for tooth wear analyses, are discussed by Uno et al. (2018). The diets of Alcelaphini, cf. *A. recki*, and *E. oldowayensis* were examined through tooth mesowear and

microwear analyses. We also sampled fossil teeth from the Lemuta and LAS stratigraphic intervals for stable carbon and oxygen isotope analyses. As with the tooth wear analyses, we focused on the same three abundant taxa (Alcelaphini, cf. *A. recki*, and *E. oldowayensis*), but also included additional stable isotope data from a wide range of mammalian taxa that included additional tribes of Bovidae (Hippotragini, Reduncini, and Tragelaphini), plus Cercopithecidae, Deinotheriidae, Giraffidae, Hippopotamidae, Hyaenidae, Rhinocerotidae, and Suidae. The number of samples analyzed for each taxon in the Lemuta and the LAS intervals are given in Table 2.

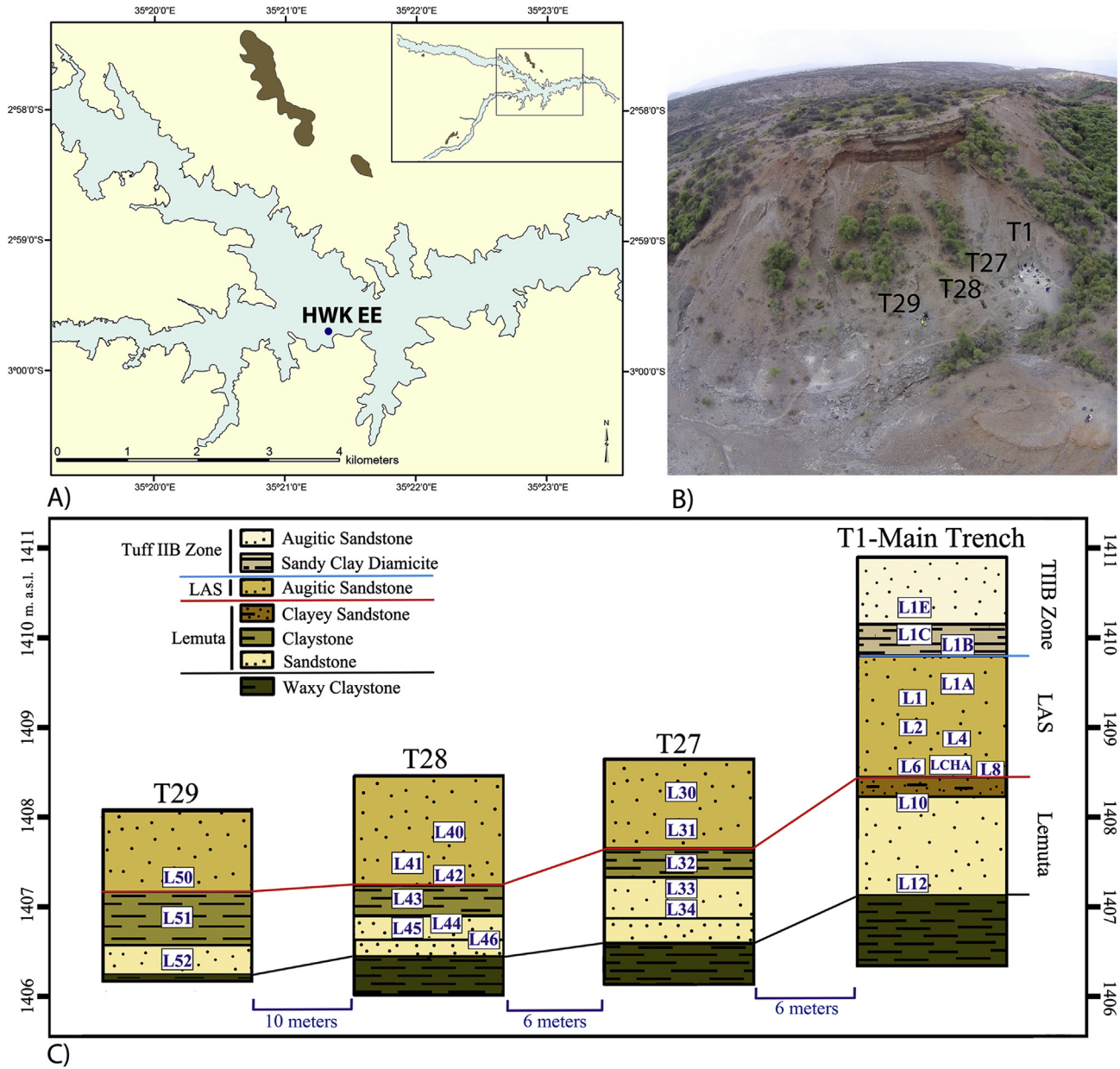
### 2.2. Tooth mesowear analysis

Mesowear analysis, first introduced by Fortelius and Solounias (2000), is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the level of abrasiveness in a species' diet. A diet with low levels of abrasion (high attrition) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices. Mesowear was scored macroscopically from the buccal side of upper molars and lingual side of lower molars, preferably the paracone of upper M2 (Fortelius and Solounias, 2000). Other molars (both upper and lower M1 and M3) were used to increase sample size. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices were omitted from mesowear analysis following Rivals et al. (2007). In this study, the standardized method introduced by Muhlbachler et al. (2011) was employed. The method is based on seven cusp categories (numbered from 0 to 6), 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 dentition corresponds to the 'mesowear score' or MWS (Muhlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher (FR) to reduce inter-observer error, following the recommendations of Loffredo and DeSantis (2014).

### 2.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleaning, molding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). This low-magnification microwear technique has been questioned in relation to repeatability and inter-observer error (Muhlbachler et al., 2012; DeSantis et al., 2013), and indeed such problems may arise when observers are not properly trained in the microwear method or when comparing data that were collected by different researchers. To avoid these issues, in the present study all the data were collected by a single experienced observer (FR).

The occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis, following King et al. (1999). Casts were observed under transmitted light with a Zeiss Stemi 2000C stereomicroscope at 35 $\times$  magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e., elongated scratches and rounded pits) were quantified on the paracone of the upper teeth or the protoconid of



**Figure 1.** A) Location of HWK EE in Olduvai Gorge (map template after [Jorayev et al., 2016](#)). B) Aerial view of HWK EE trenches. C) Correlation of HWK EE trenches, with the three main stratigraphic intervals (Lemuta, Lower Augitic Sandstone (LAS), and Tuff IIB Zone) and position of archaeological units (numbers in white boxes) (simplified from [de la Torre et al., 2018](#), Figure 20).

**Table 1**  
Results from the tooth mesowear and microwear analyses from ungulates sampled from HWK EE.<sup>a</sup>

		Mesowear		Microwear				
		n	MWS	n	NP	NS	SD	CV
<i>cf. Antidorcas recki</i>	LAS	6	1.50	6	16.75	13.25	3.402	0.257
	Lemuta	4	2.75	4	28.75	22.75	3.862	0.170
<i>Alcelaphini</i>	LAS	20	2.80	15	18.07	15.53	2.949	0.190
	Lemuta	23	2.65	19	18.97	18.68	2.750	0.147
<i>Equus oldowayensis</i>	LAS	3	5.00	5	16.40	17.50	2.208	0.126
	Lemuta	4	4.00	8	15.06	17.00	2.478	0.146

<sup>a</sup> MWS = mesowear scores; NP = average number of pits; NS = average number of scratches; SD = standard deviation on NS; CV = coefficient of variation on NS; LAS = Lower Augitic Sandstone.

lower teeth in a square area of 0.16 mm<sup>2</sup> using an ocular reticule. We used the classification of [Solounias and Sempredon \(2002\)](#) and [Sempredon et al. \(2004\)](#) which basically distinguishes pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that are not merely longer than they are wide, but have straight, parallel sides. Using average scratch and pit data, it is possible to discriminate between the dietary categories of leaf browser (i.e., eating woody and non-woody dicotyledonous plants), grazer (i.e., eating grass), and mixed feeders. Finally, following [Rivals et al. \(2015\)](#), two measurements of variability of scratch density, namely the standard deviation (SD) and the coefficient of variation (CV) were used to estimate the duration of the accumulation of the faunal



**Table 2**  
Number of teeth analyzed for carbon and oxygen isotope ratios by mammalian family.<sup>a</sup>

Family	Lemuta	LAS
Bovidae		
<b>Alcelaphini</b>	<b>12</b>	<b>4</b>
<b>Antilopini (cf. <i>A. recki</i>)</b>	<b>3</b>	<b>3</b>
Bovini	–	1
Hippotragini	2	2
Reduncini	2	1
Tragelaphini	1	1
Indet.	1	–
Cercopitheciidae	1	–
Deinotheriidae	–	2
<b>Equidae</b>	<b>5</b>	<b>2</b>
Giraffidae ( <i>Giraffa</i> )	–	1
Giraffidae ( <i>Sivatherium</i> )	1	1
Hyaenidae	–	1
Hippopotamidae	2	–
Rhinocerotidae	3	2
Suidae	1	3
<b>Total</b>	<b>34</b>	<b>25</b>

<sup>a</sup> Bovidae are further specified to tribe, and the three taxa that are the focus of this study are denoted in bold. LAS = Lower Aughtic Sandstone.

assemblages. The integration of these two measurements of variability permitted the classification of each case into one of the following three categories: [A] seasonal or shorter time windows, [B] longer than a season (i.e., two or more contiguous seasons), or [C] separated events that occurred in different non-contiguous seasons.

#### 2.4. Stable isotope analysis

Stable carbon and oxygen isotope ratios of tooth enamel are determined by an animal's diet and body water, respectively, and can therefore be used to reconstruct herbivore diets, ecosystem vegetation, and local hydroclimate (e.g., 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 C<sub>3</sub> to C<sub>4</sub> vegetation in their diet during the time in which the tooth formed. Oxygen isotopes in enamel 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). The fidelity of stable isotopes in fossil enamel is well established. Enamel was shown to be resistant to isotopic alteration over geologic timescales based on modeling studies (Wang and Cerling, 1994). The C<sub>3</sub> dietary signal from the teeth of known browsers (i.e., *Giraffa* and *Deinotherium*) and a C<sub>4</sub> signal from known grazers (e.g., Equidae) from the same fossil site supports the preservation of the primary diet signal in carbon isotopes (Kingston, 2011). Evidence for the preservation of oxygen isotopes in fossil enamel comes from the consistently low values of hippo enamel relative to other taxa, which is a result of their semi-aquatic lifestyle (Bocherens et al., 1996).

Methods for tooth sampling (serial and bulk), enamel pretreatment, and analysis on an isotope ratio mass spectrometer (IRMS) are provided in the Supplementary Text in Uno et al. (2018). Briefly, 1–5 mg of powdered enamel was pretreated with a weak oxidizer followed by buffered acetic acid, then ~0.5 mg of powder was analyzed on a dual inlet Thermo Delta V+ IRMS via acid hydrolysis on a Kiel IV (70 °C; 10-min reaction time).

Stable carbon and oxygen isotope ratios are reported as delta (δ) values relative to the Pee Dee Belemnite (PDB) standard using permil (‰) notation where

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

and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  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‰.

Today in eastern Africa nearly all woody vegetation uses the C<sub>3</sub> photosynthetic pathway, or Calvin cycle, while nearly all low elevation (<1500 m) grasses, some sedges (e.g., *Cyperus papyrus*), and some shrubs (e.g., some Amaranthaceae) use the C<sub>4</sub> pathway, or Hatch–Slack cycle (Tieszen et al., 1979; Livingstone and Clayton, 1980; Young and Young, 1983; Cerling and Harris, 1999). The carbon isotope ratio of C<sub>3</sub> plants is on average around –28‰ with an observed range of about –36 to –23‰. The wide range in  $\delta^{13}\text{C}$  values in C<sub>3</sub> 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‰). C<sub>4</sub> plants exhibit a narrower range of values, from about –14 to –10‰ in eastern Africa (Cerling et al., 2003a).

We established end-member  $\delta^{13}\text{C}$  values in tooth enamel ( $\delta^{13}\text{C}_{\text{enamel}}$ ) for C<sub>3</sub> and C<sub>4</sub> diets using an estimated atmospheric  $\delta^{13}\text{C}$  value of –6.7‰ and published values for the enrichment in  $^{13}\text{C}$  between diet and tooth enamel (+14.1‰). This is described further in the Supplementary Text in Uno et al. (2018). Using these values, we calculated C<sub>3</sub> and C<sub>4</sub> end member enamel values of  $-11.9 \pm 4\%$  and  $+2.8 \pm 2\%$ , respectively, where uncertainty reflects the range of variability in the  $\delta^{13}\text{C}$  values of C<sub>3</sub> and C<sub>4</sub> vegetation in the region today. These end member values are applied to a mixing model to calculate the percentage of C<sub>4</sub> vegetation in an animal's diet, where

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

and  $\delta^{13}\text{C}_{\text{enamel}}$  is the measured value in tooth enamel, and  $\delta^{13}\text{C}_{C_3}$  and  $\delta^{13}\text{C}_{C_4}$  are the end member values listed above. We propagated the uncertainty in both the dietary end member values ( $\pm 4$  and  $\pm 2\%$ ) and in the analytical procedure ( $\pm 0.1\%$ ), which results in uncertainties of 12–30%. Uncertainties in %C<sub>4</sub> in diet are higher towards the C<sub>4</sub> end of the continuum. We defined C<sub>3</sub>-dominated diets as those with  $\delta^{13}\text{C}$  values of  $\leq -8\%$  (ca. <25% C<sub>4</sub>), mixed C<sub>3</sub>–C<sub>4</sub> diets as having values from –8 to –1‰ (ca. 25–75% C<sub>4</sub>), and C<sub>4</sub>-dominated diets as those with  $\delta^{13}\text{C}$  values of  $\geq -1\%$  (ca. >75% C<sub>4</sub>).

We serially sampled a single *E. oldowayensis* tooth from the Lemuta interval to evaluate seasonality of diet and hydroclimate. Although limited to a single sample, the intratooth isotope profile provides an important snapshot of diet and body water over ~1–3 years of time that the tooth formed (Hoppe et al., 2004). To ameliorate blurring of the isotope signal recorded in the tooth due to enamel maturation and sampling geometry, we apply the inverse model developed by Passey et al. (2005) to reconstruct the primary input signal, although we recognize that the inverse modeling approach of Passey et al. (2005) assumes constant growth of the tooth, which we realize is likely not the case in determinant ungulate molars (Zazzo et al., 2012; Bendrey et al., 2015). A description of the sampling methods are given in the Supplementary Online Material in Uno et al. (2018) and inverse modeling methods are detailed in Passey et al. (2005).

#### 2.5. Statistics

The chi-square test was used to test for differences in the preservation of the microwear patterns between Lemuta and LAS intervals. Analysis of variance (ANOVA) and Tukey's HSD test was used to test for differences in numbers of pits and scratches among

the three taxa from the Lemuta and LAS intervals. The Mann–Whitney U test was employed to compare carbon and oxygen isotope distributions between Lemuta and LAS intervals for all taxa, the three most abundant (Alcelaphini, cf. *A. recki*, and *E. oldowayensis*), and just the Alcelaphini. For all tests, significance level was set to  $p = 0.05$ .

### 3. Results and preliminary discussion

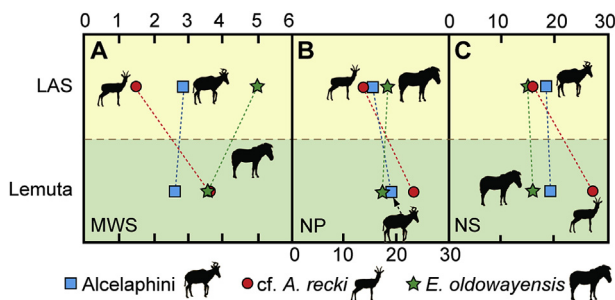
#### 3.1. Tooth wear

Tooth mesowear and microwear data are summarized in Table 1, and given in full in Supplementary Online Material (SOM) Table S1.

**3.1.1. Preservation of tooth microwear** The preservation of microwear on the enamel surface of ungulate teeth from HWK EE was very good. As reported from the taphonomic analysis (de la Torre et al., 2018; Pante et al., 2018), bone preservation was also generally very good and the majority of bones in both intervals do not exceed Behrensmeyer's (1978) weathering stage 1, suggesting rapid burial. Preservation of microwear patterns was slightly higher in the LAS assemblage (80% of the 55 teeth sampled) than in the Lemuta (72% of the 54 teeth sampled), but a chi-square test ( $p = 0.34$ ,  $X^2 = 0.91$ , d.f. = 1) showed these differences to be insignificant.

**3.1.2. Diachronic changes from Lemuta to LAS stratigraphic intervals** Mesowear scores (MWS), which register the dietary signal on a timescale of several weeks to months (Fortelius and Solounias, 2000), showed a smaller range of values in Lemuta (from MWS = 2.65 for Alcelaphini to MWS = 4 for *E. oldowayensis*) and a much broader range of values in LAS (from MWS = 1.5 for cf. *A. recki* to MWS = 5 for *E. oldowayensis*) (Fig. 2A). Moreover, in the Lemuta the values for *E. oldowayensis* and cf. *A. recki* overlap, suggesting diets with similar abrasive properties for the two taxa. Among the three taxa considered in this study, the temporal trends in the two intervals were different. Mesowear scores show opposite changes for the equid *E. oldowayensis* and cf. *A. recki* (Fig. 2A). *Equus oldowayensis* displayed a grass-dominated mixed feeding dietary signal in the Lemuta and a grazing signal in the LAS stratigraphic interval. Mesowear values indicate increased abrasion towards the LAS interval. The mesowear scores of cf. *A. recki* were similar to those of extant mixed feeders, but microwear values shift from grazing in the Lemuta to browsing in the LAS. Finally, the Alcelaphini plot among mixed feeders and show a stable mesowear signal throughout the two stratigraphic intervals (Fig. 2A).

Regarding tooth microwear, the actual numbers of microwear features, numbers of scratches (NS) and numbers of pits (NP), do not show significant variation between the two stratigraphic intervals,



**Figure 2.** Changes in dietary traits in equids and bovids between the Lemuta and Lower Augitic Sandstone (LAS) intervals indicated by (A) tooth mesowear scores (MWS) and the microwear variables: (B) number of scratches (NS) and (C) number of pits (NP).

except for cf. *A. recki* (Fig. 2B–C). cf. *Antidorcas recki* shows a significant decrease in both the numbers of scratches and of pits from Lemuta to LAS (Table 3), corresponding to a decrease in the proportion of grass in the diet, as previously reported for the mesowear data. The differences reported for *E. oldowayensis* and the Alcelaphini between the two stratigraphic intervals were not significant (Table 3).

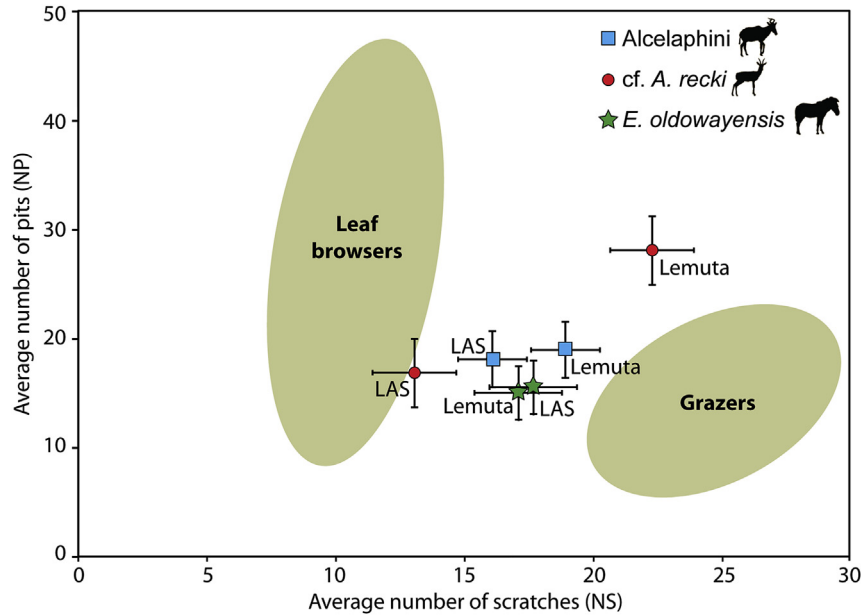
The bivariate plot of average pits and scratches values show the intermediate position of the Alcelaphini and *E. oldowayensis* between the extant leaf browser and grazer ecospace (Fig. 3). There are no significant differences within these taxa when comparing Lemuta and LAS specimens (Table 3). In contrast, cf. *A. recki* shows significant differences in both the numbers of pits and of scratches between the Lemuta and LAS intervals (Fig. 3 and Table 3). cf. *Antidorcas recki* from the LAS plots close to the leaf browser ecospace, while those from the Lemuta have a larger number of scratches. Moreover on Figure 3, Lemuta cf. *A. recki* plots above the extant grazers due to a larger number of pits. In general, tooth microwear results for all taxa in the Lemuta suggest mixed feeding and grazing, while for LAS they suggest mixed feeding and browsing.

**3.1.3. Variability in dietary signal and seasonality established from tooth wear** The analysis of variability in the microwear signal through the coefficient of variation (CV) and the standard deviation (SD) on the numbers of scratches was used here to characterize seasonality in the accumulation of the ungulate assemblages in Lemuta and LAS stratigraphic intervals (Table 1 and Fig. 4). The combination of these two measurements of variation (CV and SD) has been reported to discriminate seasonal events based on the duration of the accumulation (Rivals et al., 2015). Unfortunately, the Alcelaphini data were not conclusive, neither for the LAS nor for the Lemuta, because the two samples fall on the boundary between zones [A] and [B] (Fig. 4), i.e., in the area where the probability is too high to provide a significant differentiation between the two assemblages ( $p > 0.05$ ). It was not possible to conclude whether the accumulation of the Alcelaphini remains

**Table 3**  
ANOVA and Tukey's HSD test results.<sup>a</sup>

Number of scratches (NS)						
ANOVA results						
Source	df	SS	MS	F-ratio	p	
Model	5	305.54	611.08	6.946	0.0398	
Residual	57	501.45	87.97			
Pair-wise comparisons – q values (Tukey's method); p < 0.05						
	An LAS	An Lem	Al LAS	Al Lem	Eq LAS	Eq Lem
An LAS	–					
An Lemuta	<b>8.868</b>	–				
Al LAS	2.131	<b>6.736</b>	–			
Al Lemuta	<b>4.985</b>	3.882	2.854	–		
Eq LAS	3.100	<b>5.767</b>	0.969	1.885	–	
Eq Lemuta	3.241	<b>5.627</b>	1.110	1.744	0.141	–
Number of pits (NP)						
ANOVA results						
Source	df	SS	MS	F-ratio	p	
Model	5	551.09	110.22	3.756	0.0052	
Residual	57	1672.46	293.41			
Pair-wise comparisons – q values (Tukey's method); p < 0.05						
	An LAS	An Lem	Al LAS	Al Lem	Eq LAS	Eq Lem
An LAS	–					
An Lemuta	<b>6.133</b>	–				
Al LAS	0.673	<b>5.460</b>	–			
Al Lemuta	0.697	<b>5.436</b>	0.024	–		
Eq LAS	0.602	<b>6.736</b>	1.275	1.299	–	
Eq Lemuta	0.412	<b>6.545</b>	1.085	1.109	0.191	–

<sup>a</sup> df = degrees of freedom; SS = sum of squares; MS = mean square; An = cf. *Antidorcas recki*; Al = Alcelaphini; Eq = *Equus oldowayensis*. LAS = Lower Augitic Sandstone. Significant pair-wise comparisons are in bold.



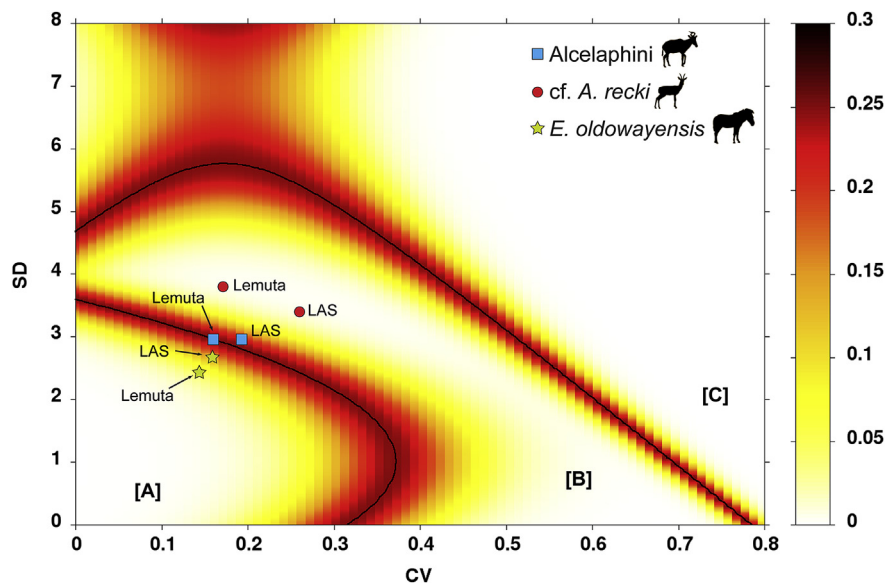
**Figure 3.** Bivariate plot of the average numbers of pits and scratches on the fossil ungulate teeth from HWK EE. Error bars correspond to the standard error of the mean ( $\pm$ S.E.M.) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ( $p = 0.95$ ) on the centroid for the extant leaf browsers and grazers from Solounias and Semprebon (2002).

preserved a seasonal signal or not. The samples of *cf. A. recki* from the LAS and the Lemuta plot in area [B] of the graph (Fig. 4). This area corresponds to long-term accumulation i.e., one or more events spanning more than a single season. The samples of *E. oldowayensis* from the Lemuta plot in area [A], corresponding to seasonal accumulation events, while the sample from the LAS falls on the boundary between zones (Fig. 4). For the LAS assemblage, it was not possible to conclude if the accumulation of *E. oldowayensis* spanned several seasons or occurred every time at the same season. For the Lemuta, the assemblage definitely corresponds to population(s) that died during short events (a single season or less) but occurred every time during

the same season. *Equus oldowayensis* and *cf. A. recki* plot in two different areas of the graph, independently of the stratigraphic context. Consequently, there was no specific pattern related to each stratigraphic interval. In these two intervals, the equids suggested an accumulation during a shorter time frame than *cf. A. recki*, probably related to differences in seasonal availability of the two species in the surroundings of the site.

### 3.2. Stable isotopes

Tooth enamel analyzed from the Lemuta ( $n = 34$ ) and the LAS ( $n = 24$ ) intervals indicated that the majority of large mammals



**Figure 4.** Bivariate plot of the standard deviation (SD) and coefficient of variation (CV) calculated on the numbers of scratches. Boundary lines between the three regions with the error probability (heat map) and the fossil samples from HWK EE. [A] = Season-long or shorter time windows, [B] Longer than a season, [C] Separated events that occurred in different non-contiguous seasons.

had C<sub>4</sub>-dominated diets, with few exceptions. In Table 4, we provide summary statistics of the carbon and oxygen isotope data from all taxa from both intervals. All isotope data and calculated %C<sub>4</sub> values are given in SOM Table S2. We used the median and the range of values to describe the sample populations because diets are derived from a non-normal (i.e., bimodal) distribution of C<sub>3</sub> and C<sub>4</sub> dietary resources. As such, we used a non-parametric statistical test to assess differences in the distributions between the Lemuta and the LAS intervals. A Mann–Whitney U test suggested no significant differences in δ<sup>13</sup>C (*p* = 0.23) or δ<sup>18</sup>O (*p* = 0.52) values of the two populations between the Lemuta and LAS intervals (Table 5). The δ<sup>13</sup>C and δ<sup>18</sup>O data for all taxa are plotted in Figure 5. Median δ<sup>13</sup>C values from the Lemuta and the LAS intervals were +1.1 and +0.3‰, respectively, corresponding to diets comprising 89% and 83% C<sub>4</sub> (Table 4). The range in δ<sup>13</sup>C values was smaller (−8.9 to +3.3‰) in the LAS than in the Lemuta interval (−12.8 to +2.6‰) due to the presence of several browsers (Deinotheriidae and Giraffidae) in the latter interval. The median δ<sup>18</sup>O values from the Lemuta and LAS members were 0.0 and +0.9‰, respectively. The δ<sup>18</sup>O range of values was larger for the Lemuta samples (−3.8 to +5.1‰) than for those from the LAS (−2.0 to +4.0‰). The larger range in oxygen isotope values in the Lemuta may simply be an artifact of the larger sample size from that interval (34 versus 24).

**3.2.1. Stable isotope results of Alcelaphini, cf. *A. recki*, and *E. oldowayensis*** Summary statistics from the three most abundant Lemuta and LAS taxa, the Alcelaphini, cf. *A. recki*, and *E. oldowayensis*, are given in Table 6. The δ<sup>13</sup>C and δ<sup>18</sup>O data for these three taxa from both stratigraphic intervals are plotted together in Figure 6. The carbon isotope data suggested stable diets between intervals, although sample sizes are small, particularly for *E. oldowayensis* in the LAS (*n* = 2) and cf. *A. recki* (*n* = 3) for both intervals. The median δ<sup>13</sup>C values of Alcelaphini in the Lemuta and LAS intervals were +1.8 and +2.2‰, respectively. This is equivalent to diets of 94% and 96% C<sub>4</sub> vegetation, respectively, with a total range of 74%–100% C<sub>4</sub>. For the mixed feeding cf. *A. recki*, median Lemuta and LAS δ<sup>13</sup>C values were −5.8‰ and −4.3‰, corresponding to diets of 41% and 45% C<sub>4</sub> vegetation. Despite the limited sample size (*n* = 3 from each interval), cf. *A. recki* displayed a wide dietary range, spanning 20% to 99% C<sub>4</sub> across both intervals (Table 6). Equid δ<sup>13</sup>C values indicated C<sub>4</sub>-dominated diets. Median δ<sup>13</sup>C values from the Lemuta and the LAS equids were +1.2‰ and −1.4‰, corresponding to diets of 89% and 71% C<sub>4</sub> vegetation, respectively, with a total range of 74%–99% C<sub>4</sub> (Table 6). A Mann–Whitney U test comparing all 29 samples from these three lineages indicated no significant differences between δ<sup>13</sup>C or δ<sup>18</sup>O values from the Lemuta and LAS intervals (Table 5). A further Mann–Whitney U test comparing just the Lemuta and LAS Alcelaphini values also showed no significant differences in either isotope distribution (Table 5). Antilopini and equid samples were too small to be analyzed statistically.

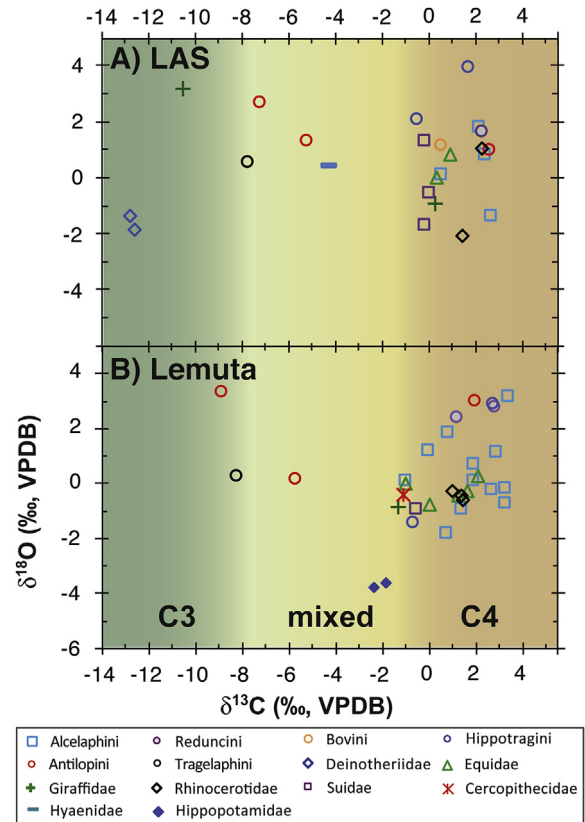
The δ<sup>18</sup>O values from the three most abundant taxa Alcelaphini, cf. *A. recki*, and *E. oldowayensis* exhibit no significant changes throughout the Lemuta and the LAS intervals (Fig. 7). Median δ<sup>18</sup>O

**Table 5**

Mann–Whitney U test results comparing carbon and oxygen isotope distributions between Lemuta and LAS intervals for all taxa; Alcelaphini (Al), Antilopini (An), and Equus (Eq); and Alcelaphini.<sup>a</sup>

	All taxa	Al, An, Eq	Al
Carbon <i>p</i> -value	0.2291	0.7992	1
Oxygen <i>p</i> -value	0.5174	0.3171	0.8615
<i>n</i> (Lemuta/LAS)	34/24	20/9	12/4

<sup>a</sup> None of the distributions differs significantly between intervals (*p* < 0.05). LAS = Lower Aughtic Sandstone.



**Figure 5.** Carbon versus oxygen stable isotope ratios for all HWK EE taxa from (A) the Lower Aughtic Sandstone (LAS; *n* = 24) and (B) the Lemuta (*n* = 34) intervals. Most large herbivores from both intervals have C<sub>4</sub>-dominated diets (>75% C<sub>4</sub>), with the exception of some Antilopini (cf. *A. recki*), Deinotheriidae, a *Giraffa stillei*, Hippopotamidae and Tragelaphini. A single Hyaenidae sample from the LAS interval likely had a diet that consisted of mostly grazing herbivores. VPDB = Vienna Pee Dee Belemnite.

values for Lemuta and LAS Alcelaphini were nearly identical, whereas values for cf. *A. recki* decreased by 1.6‰ between the Lemuta and the LAS intervals (Table 6). In contrast, median *E. oldowayensis* δ<sup>18</sup>O values became enriched by 0.8‰.

**3.2.2. *E. oldowayensis* intratooth stable isotope profile** Results from the *E. oldowayensis* intratooth profile, both measured and modeled, are shown in Figure 5 and given in SOM Table S3. The modeled δ<sup>13</sup>C values ranged from −2.3 to +2.1‰, corresponding

**Table 4**

Summary statistics of carbon and oxygen stable isotope data for taxa from the Lemuta and LAS intervals at HWK EE.<sup>a</sup>

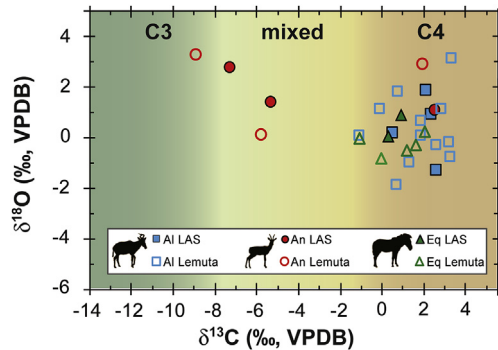
Interval	<i>n</i>	%C <sub>4</sub>			δ <sup>13</sup> C (‰, VPDB)				δ <sup>18</sup> O (‰, VPDB)			
		Median	Min	Max	Median	Max	Min	Range	Median	Max	Min	Range
LAS	24	83	0	99	0.3	2.6	−12.8	15.5	0.9	4.0	−2.0	6.0
Lemuta	34	89	20	100	1.1	3.3	−8.9	12.3	0.0	5.1	−3.8	8.9

<sup>a</sup> LAS = Lower Aughtic Sandstone.



**Table 6**Summary statistics of carbon and oxygen stable isotope data for the three most abundant taxa from the Lemuta and LAS intervals at HWK EE.<sup>a</sup>

Taxon	Interval	n	%C4			$\delta^{13}\text{C}$ (‰, VPDB)				$\delta^{18}\text{O}$ (‰, VPDB)			
			Median	Min	Max	Median	Max	Min	Range	Median	Max	Min	Range
cf. <i>A. recki</i>	LAS	3	45	32	99	-5.3	2.6	-7.2	9.8	1.4	2.8	1.0	1.7
	Lemuta	3	41	20	94	-5.8	1.9	-8.9	10.8	3.0	3.3	0.2	3.1
Alcelaphini	LAS	4	96	85	99	2.2	2.6	0.5	2.1	0.5	1.8	-1.3	3.1
	Lemuta	12	94	74	100	1.8	3.3	-1.1	4.4	0.1	3.1	-1.8	5.0
<i>Equus oldowayensis</i>	LAS	2	—	83	87	—	0.9	0.3	0.6	—	0.9	0.0	0.9
	Lemuta	5	89	74	95	1.2	2.1	-1.1	3.1	-0.3	0.3	-0.8	1.1

<sup>a</sup> Min = minimum; Max = maximum; VPDB = Vienna Bee Dee Belemnite; LAS = Lower Aegitic Sandstone.**Figure 6.** Carbon versus oxygen stable isotope ratios for Alcelaphini (Al), Antilopini (An; cf. *A. recki*), and equids (Eq) from the Lower Aegitic Sandstone (LAS; filled symbols) and Lemuta (open symbols) intervals. The plot illustrates no significant changes occurred between intervals in the  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$  values in the three lineages.

to dietary inputs varying seasonally from  $66 \pm 26\%$  ( $1\sigma$ ) to  $97 \pm 19\%$  C<sub>4</sub> (SOM Table S3). Thus, the modeled data indicated that, seasonally, the equid sampled had a C<sub>4</sub>-dominated to a mixed C<sub>3</sub>–C<sub>4</sub> diet. Seasonal shifts were also evident in body water based on the range of modeled  $\delta^{18}\text{O}$  values ( $-2.1$  to  $+1.6\%$ ).

#### 4. Discussion

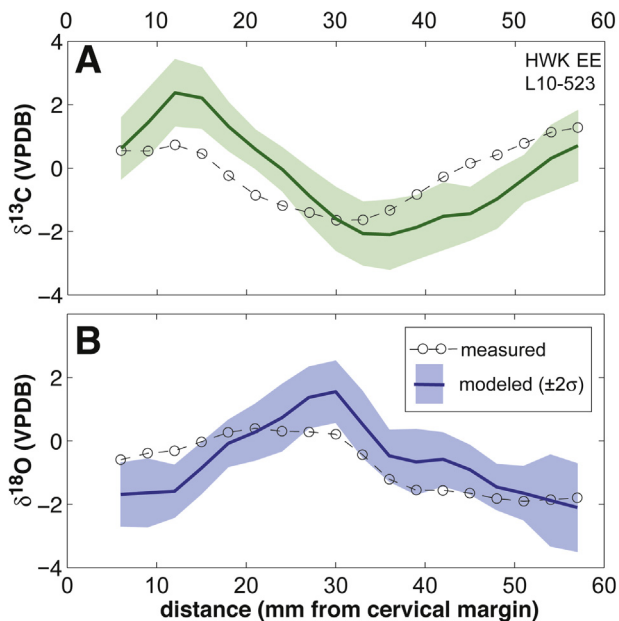
Food resources and habitats of three ungulate clades from the LAS and the Lemuta intervals at HWK EE were investigated through three independent proxies, carbon and oxygen stable isotopes, tooth mesowear, and tooth microwear. Reconstructed diets from the different proxies are summarized in Table 7.

##### 4.1. Food resources and habitats at HWK EE

For the Antilopini, the  $\delta^{13}\text{C}$  values suggest a range of browsing, mixed feeding, and grazing from the six individuals analyzed (three per interval), with a dietary range of 20–99% C<sub>4</sub> vegetation from both intervals. These  $\delta^{13}\text{C}$  values are similar to those observed in the extant mixed-feeding antelope *Eudorcas thomsonii*, whereas other extant species in eastern Africa, *Nanger granti* and *Litocranius walleri*, have C<sub>3</sub>-dominated to mixed C<sub>3</sub>–C<sub>4</sub> and C<sub>3</sub>-dominated diets, respectively (Cerling et al., 2003b; Van der Merwe, 2013). Thus, the limited number of isotope data from the Lemuta and the LAS intervals indicates a wide range of diets, similar to those observed today in extant Antilopini. Tooth wear analyses also indicate a wide range of diets in the Antilopini, tending toward grazing in the Lemuta and toward browsing in the LAS. The tendency for a browsing mesowear signal in extant Antilopini is also reported by Louys et al. (2012), with low mesowear scores for all grazing Antilopini (i.e., values of 0 or 1). Tooth wear data suggest that individuals of cf. *A. recki* were seasonal mixed feeders but died during different seasons through the year, reflecting different diets at the time of death in the Lemuta and the LAS.

Carbon isotope data indicate that Alcelaphini had C<sub>4</sub>-dominated diets (range: 74–100%). Such high values of C<sub>4</sub> vegetation for Alcelaphini in both the Lemuta and the LAS reflect a diet comprising C<sub>4</sub> grasses, similar to the hyper-grazing diet of extant Alcelaphini *Connochaetes taurinus* and *Alcelaphus buselaphus* from northern Tanzania (Van der Merwe, 2013). In contrast to the stable isotope data, tooth mesowear and microwear patterns indicate mixed feeding traits in both the Lemuta and the LAS. *E. oldowayensis* carbon isotope values indicate a grazing diet predominantly composed of C<sub>4</sub> plants (range: 77–95%) in both the Lemuta and LAS. Tooth mesowear also indicates grazing, but microwear suggests mixed feeding at the time of death.

Various hypotheses could explain these discrepancies. First, they could be due to the fact that each proxy records diet on a different timescale (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016). Stable isotopes of bulk enamel record a dietary average during tooth mineralization (usually the first years

**Figure 7.** Intratooth stable isotope profile from an *Equus oldowayensis* lower first or second molar (L10-523) from the Lemuta interval. Time proceeds from right to left. The open circles and dashed line represent the measured isotope values. The solid line is the mean estimated input signal (shaded region is  $\pm 2\sigma$  uncertainty) from 100 inverse model results for A)  $\delta^{13}\text{C}$  and B)  $\delta^{18}\text{O}$  values. A) Modeled  $\delta^{13}\text{C}$  values indicate seasonal changes in diet ( $-2.1$  to  $+2.3\%$ ) ranging from a C<sub>4</sub>-dominated to pure-C<sub>4</sub> diet over the period in which the tooth formed. B) The  $\delta^{18}\text{O}$  values range from  $-2.1$  to  $+1.6\%$ . The highest dietary input of C<sub>3</sub> vegetation occurs from 45 to 25 mm. This broadly corresponds to, but slightly precedes, the most enriched  $^{18}\text{O}$  values (35–20 mm). VPDB = Vienna Pee Dee Belemnite.



**Table 7**

Summary of the dietary traits interpreted from carbon stable isotopes and tooth wear at HWK EE.<sup>a</sup>

		Dietary proxies		
		Carbon isotopes	Tooth mesowear	Tooth microwear
<i>cf. Antidorcas recki</i>	LAS	MF, G	B	B
	Lemuta	B, MF, G	G-MF	G
Alcelaphini	LAS	G	MF	MF
	Lemuta	G	MF	MF
<i>E. oldowayensis</i>	LAS	G	G	MF
	Lemuta	G	G-MF	MF

<sup>a</sup> B = Browser; G = Grazer; G-MF = Grass-dominated mixed feeder; MF = Mixed feeder. LAS = Lower Aurgitic Sandstone.

of an ungulate's life), while microwear reflects only the last days or weeks of life. A change in diet during the life of the individuals sampled, and especially during the last days or weeks will result in different dietary signals depending on the proxy analyzed. Consequently, the discrepancies observed are likely related to differences in the temporal scale of each proxy, tooth microwear being more sensitive to short term changes than the other two proxies (Davis and Pineda Munoz, 2016).

An alternative hypothesis implicates the characteristics of the vegetation consumed, namely differences between the carbon isotopic composition (C<sub>3</sub> versus C<sub>4</sub>) and the actual wear-inducing characteristics (e.g., phytolith content) of the plants themselves. For example, the low numbers of scratches reported here in taxa with enriched (C<sub>4</sub>) isotopic values could be the result of feeding on C<sub>4</sub> herbs, which have low phytolith numbers (Baker et al., 1959). Several species from the paleobotanical record at Olduvai fit these characteristics. Bonnefille (1984) identified pollen from several C<sub>4</sub> plants in the family Amaranthaceae, which includes the herbaceous dicot *Aerva javanica* at VEK in Lower Bed II and the succulent *Suaeda monoica* at FLK in Bed I. Evidence of Cyperaceae include the C<sub>4</sub> sedge *C. papyrus* (Bamford et al., 2006; Bamford, 2012), though C<sub>3</sub> sedges from wetland areas at FLK in Bed I have also been documented (Magill et al., 2016). Another possible non-grass dietary resource is wetland ferns, which Magill et al. (2016) suggest may have had carbon isotope ratios intermediate between C<sub>3</sub> and C<sub>4</sub> end member values. This suggestion is based on the  $\delta^{13}\text{C}$  values of C30 and C32 diols, which they assume were produced by ferns. In summary, there is evidence for several non-grass C<sub>4</sub> plants, or plants with CAM or intermediate C<sub>3</sub>–C<sub>4</sub> carbon isotope ratios, documented at Olduvai, particularly from Bed I. Most are associated with wetlands, Paleolake Olduvai, or water courses. These plants may have been important resources for some herbivorous mammal species, but there is no evidence yet that they were widespread or were a significant contribution to the diets of large herbivores.

In the case of the discrepancy observed for Alcelaphini and *E. oldowayensis*, where stable carbon isotopes indicate C<sub>4</sub>-dominated (i.e., grazing) diets, while microwear suggests a low abrasive diet (mixed feeding) comprising plants with low phytolith content, one of two hypotheses could explain the discrepancy. First, the animal could have had a grazing diet during most of its life, and later shifted towards more browsing, at least in the last days of life. Second, the diets of the two ungulate taxa could have included C<sub>4</sub> dicots (possibly shrubs) that would impart a browsing signal in the tooth wear metrics and positive  $\delta^{13}\text{C}$  values associated with C<sub>4</sub> vegetation.

Stable isotope analyses on the most abundant ungulates at HWK EE show no significant differences in carbon or oxygen isotope values between the Lemuta and LAS (Table 5 and Fig. 5). Dietary behaviors are consistent throughout the sequence, with Alcelaphini

and *E. oldowayensis* exhibiting C<sub>4</sub>-dominated diets and *cf. A. recki* having a broad spectrum of diets. Regarding tooth wear analyses, in the Lemuta the three ungulate taxa analyzed are either grazers (Alcelaphini and *E. oldowayensis*) or mixed feeders (*cf. A. recki*), while in the LAS ungulates are grazing (*E. oldowayensis*), browsing (*cf. A. recki*) and mixed feeding (Alcelaphini). The diet of *E. oldowayensis* appears to be stable, without substantial change throughout the sequence, although the intratooth isotope profile indicates seasonality of diet ranging from mixed C<sub>3</sub>–C<sub>4</sub> to C<sub>4</sub>-dominated vegetation. For the bovids, the two taxa from the Lemuta show mixed feeding or grazing behavior, while those from the LAS show a tendency towards leaf browsing. However, the increase in leaf browsing is only significant for *cf. A. recki*, as it is supported by both mesowear and microwear patterns. These changes are probably related to changes in resource availability (ecological or seasonal changes) such as an increase in the availability of dicots. Interestingly, the Alcelaphini, which are usually the most mobile of the three taxa (Estes, 1991), have mesowear and microwear patterns that do not change from the Lemuta to the LAS. This may reflect the migratory behavior of Alcelaphini populations to access specific (and possibly similar) types of dietary resources through the year. The Lemuta interval, where the microwear pattern tends toward grazing, indicates that the alcelaphines would have been abundant at Olduvai during the wet season when grass would have been more available.

In the Lemuta interval, our results indicating grass consumption are supported by the data on phytoliths, which suggest the presence of areas with trees and C<sub>3</sub> grasses, as well as open areas with C<sub>4</sub> grasses (de la Torre et al., 2018). Nevertheless, tooth microwear does not permit us to differentiate a diet based on C<sub>3</sub> or C<sub>4</sub> grasses, although the phytoliths identified correspond mostly to C<sub>4</sub> chloridoids, which are very short grasses adapted to a dry and warm environment (R.M. Albert, personal communication). Microwear patterns with higher numbers of pits in the specimens from the Lemuta also indicate a dry environment due to the ingestion of grit and dust from the soil and/or exogenous dust on the leaves (Rivals and Semperebon, 2006; Semperebon and Rivals, 2007). In the LAS, the presence of C<sub>3</sub> grass and the overall decline in grass phytoliths (i.e., from ~23% to 16% for the short cell rondel morphotype between the Lemuta and the LAS) supports this conclusion of more forested habitats than in the Lemuta (de la Torre et al., 2018). Moreover, the short cell saddle morphotype, associated with C<sub>4</sub> grasses in the Poaceae subfamily, Chloridoideae, are present in the Lemuta sediments, but were not reported in the LAS sediments (de la Torre et al., 2018). Although the vegetation reconstruction from phytoliths indicates a larger fraction of woody vegetation (mostly palms) than is reflected in the overall dietary signal recorded by isotopes and mesowear, it is important to point out that the foraging areas and migratory ranges of large herbivores may stretch beyond the source area of the phytolith assemblage at HWK EE. In this scenario, the phytolith assemblage would reflect vegetation closely associated with littoral or fluvial margins whereas the diets of large mammals would reflect an integrated vegetation signal from a much larger area. This is in agreement with the fossil plant record from the eastern paleolake margin of Olduvai Gorge, where the paleovegetation included trees, shrubs, grasses, and sedges. The phytolith record also indicates the presence of palms (Albert et al., 2006, 2009; Bamford, 2012) and the pollen record indicates a diversity of dry and mesic trees, shrubs, and forbs (Bonnefille, 1984). The dearth of herbivores with C<sub>3</sub>-dominated diets (both in number of species and abundance) suggests a relatively smaller proportion of C<sub>3</sub> vegetation on the landscape relative to C<sub>4</sub> vegetation in the Lemuta and the LAS intervals.

#### 4.2. Variability in diets among ungulates and seasonality

The multiproxy analysis of the Alcelaphini, cf. *A. recki*, and *E. oldowayensis* in two stratigraphic intervals from HWK EE reveals differences in dietary traits for the most abundant herbivores. The lower range of mesowear values in the Lemuta compared to the LAS suggests diets based on plants of very different abrasiveness in the two intervals. However, in the Lemuta there are significant differences in pits and/or scratches among some taxa, while microwear values in the LAS are not significantly different for the three taxa. Considering that microwear is more sensitive to seasonal variations than mesowear (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016), this opposite trend between the two units could suggest more marked seasonality in the Lemuta than in the LAS. Nonetheless, the palimpsest character of the deposits, which is particularly evident in the LAS (de la Torre et al., 2018), may also help mask potential seasonal episodes in the formation of the assemblage. In the single intratooth isotope profile on the Lemuta equid specimen, carbon isotopes indicate seasonal changes in diet (66–99% C<sub>4</sub>), while the nearly 4‰ range in δ<sup>18</sup>O suggests relatively strong seasonality of precipitation. Based on the growth rates of equid teeth (Hoppe et al., 2004), the seasonal change in the δ<sup>18</sup>O value from the Lemuta equid tooth suggest a single annual rainy season.

In the Lemuta, *E. oldowayensis* and Alcelaphini fed on similar resources, as indicated by similar isotopic and mesowear values. Nevertheless, even if they belonged to the same dietary guild, these animals could eat different suites of grass species. In the LAS, mesowear shows clear differences in dietary traits, suggesting the three taxa were around the HWK EE site during the same season and exploited different vegetal resources.

As the ungulate community is habitat-dependent, the vegetation available must support the various ecological niches for the ungulates adapted to particular vegetal resources. Most of the ungulates from HWK EE are found to be mainly grazers or mixed-feeders (*E. oldowayensis* and Alcelaphini), and few are browsers or browse-dominated mixed feeders (cf. *A. recki* from the LAS). The last was probably feeding on browse if resources available during the LAS time were limited. Alternately, browse was in low supply during Lemuta times, so *A. recki* may have been 'forced' to graze more than. *Equus oldowayensis* and Alcelaphini seem to occupy a grazing niche in both the Lemuta and the LAS, while cf. *A. recki* appears to shift its niche from grazing in the Lemuta to increased browsing in the LAS. Alternately, as stated above, the Lemuta assemblage represents a shorter duration of accumulation time, such as a single season over many years, while the LAS represents a more varied seasonal signal over a longer duration. This would explain the higher variation of the wear data in *A. recki* in the LAS.

Both mesowear and microwear detect differences among species as well as diachronic changes through the HWK EE sequence. Trends reported for the two proxies are consistent in all taxa, i.e., values are shifting in the same direction both for mesowear and microwear (Figs. 2 and 3). However, depending on the taxa, the direction of these shifts, when significant, are different, i.e., shifting toward more grazing or more browsing. For the Alcelaphini, both mesowear and microwear analyses yield consistent results. Tooth mesowear does not show significant change between the two stratigraphic intervals. The microwear pattern shows that Alcelaphini are classified among the extant mixed feeders, and indicate a slight increase in leaf browsing from the Lemuta to the LAS. However, in this case it is not possible to determine whether or not they were seasonal mixed-feeders. The analysis of variability in the microwear pattern does not permit any conclusions to be drawn about the seasonality for the Alcelaphini. Nevertheless, it was

observed that the mesowear signal is stable and only microwear is changing. Considering that microwear is more sensitive to seasonality than is mesowear (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016), it is probable that the difference is due to subtle variations in diet at the time of death.

For cf. *A. recki*, the mesowear and microwear trends are similar to those reported for the Alcelaphini. The two methods indicate highly significant differences in the results i.e., a significant increase in leaf browsing from the Lemuta to the LAS. As observed for the Alcelaphini, the microwear data provide evidence for discrepancies in dietary habits in comparison to mesowear. As reported before, this discrepancy between mesowear and microwear could be linked to seasonal differences (Sánchez-Hernández et al., 2016). Considering that the remains probably accumulated over a long timescale (certainly more than a single season), the results suggest the seasons of accumulation are different (or with a slight overlap) between the two stratigraphic intervals: seasons with diet based on grass in the Lemuta, and seasons with diet mainly based on browse in the LAS.

For the equid *E. oldowayensis*, the mesowear trend is opposite to those evident in cf. *A. recki* and the Alcelaphini. *Equus oldowayensis* is characterized by an increase in the proportion of grass in the diet from the Lemuta to the LAS intervals. However, microwear patterns are not significantly different between the Lemuta and the LAS. Mesowear values clearly indicate grazing, but microwear values trend more toward mixed feeding. This difference could be related to a highly abrasive diet resulting from the presence of grit or dust on the plants, and/or to seasonality and food availability at the time of death. The results of the analysis of variability (Fig. 4), shows that the two samples plot close to each other (i.e., similar CV and SD values), and are located in the area corresponding to seasonal accumulations. Considering that changes in diet indicated by microwear from the Lemuta to the LAS are not significant, this suggests that the *E. oldowayensis* assemblages correspond to the same season(s) in the two stratigraphic intervals.

Microwear variability indicates the existence of seasonal patterns in the formation of the Lemuta and the LAS assemblages. Considering the palimpsest nature of the deposits at HWK EE (de la Torre et al., 2018; Pante et al., 2018) our results imply that accumulation of ungulates in the two intervals follows a seasonal pattern i.e., probably a succession of events at the same season(s) through the formation of each interval. Seasonality at HWK EE is also supported by the taphonomic analysis of fish assemblages, which indicate variations in lake levels and a mass die-off during the dry season (Bibi et al., 2018). These seasonal fluctuations in lake levels certainly influenced the presence of ungulates in the habitats on the margins of the lake at Olduvai and resulted in the seasonal accumulations of their remains in both the Lemuta and the LAS intervals.

Increases in the browsing signature between the Lemuta and the LAS observed from microwear analyses of the bovids help to contextualize the variations in zooarchaeological data between the intervals (Pante et al., 2018). Higher tooth mark and percussion mark frequencies and lower limb bone epiphyseal:shaft fragment ratios observed for the Lemuta when compared with the LAS (Pante et al., 2018) suggest that carcasses acquired by hominins during the Lemuta interval were processed more extensively by both hominins and carnivores. The results for the LAS, which suggest that bone marrow may not have been exploited to its full potential during this interval, are consistent with carnivore consumption of nutritionally-stressed animals in the modern Serengeti ecosystem where carnivores were shown to incompletely ravage the fat- and grease-depleted bones of these carcasses resulting in lower tooth mark frequencies and more limb bone epiphyses relative to shaft

fragments (Blumenschine and Marean, 1993). Together the feeding trace data, along with the microwear results that show a greater browsing component in the diets of the sampled bovids during the LAS, may indicate that the LAS assemblage accumulated mostly during relatively dry periods at Olduvai when grasses were not as readily available and grazing animals may have been more nutritionally-stressed.

## 5. Conclusions

Tooth wear analyses on the most abundant ungulates from HWK EE reveal differences in dietary traits between the Lemuta and the LAS intervals probably corresponding to seasonal differences in the period of death of these animals in each stratigraphic interval. The lack of change in the distribution of carbon and oxygen isotope distributions between the Lemuta and the LAS indicates that there were no major dietary changes among herbivores or hydroclimatic change during this time. Furthermore, the carbon stable isotope data demonstrate that vegetation during Middle Bed II times was able to support the entire range of C<sub>3</sub> to C<sub>4</sub> diets, but that C<sub>4</sub>-dominated diets were most prevalent among the large herbivores analyzed in this study.

The tooth wear results prove useful for disentangling the palimpsest character of the HWK EE assemblage, with its archaeo-stratigraphic architecture pointing to the existence of multiple accumulation events, which are generally jumbled together within successive archaeological units. As indicated by tooth wear analyses, these multiple accumulation events probably occurred seasonally, mostly during dry periods in the case of the LAS assemblage.

The integration of various proxies that record changes in diets across different timescales permits the reconstruction of dietary traits during the lifetime of individuals but also at the time of death. In many cases it demonstrates strong seasonality during the time of accumulation of the assemblages. The integration of our results with those from the zooarchaeological study of the assemblages suggests that both hominins and carnivores altered their feeding behavior ignoring bone marrow that was likely fat-depleted at the time of death, possibly due to seasonal variations in ungulate food availability. More generally, such studies highlight the importance of detecting long- and short-term environmental changes to understand the context within which hominins evolved in eastern Africa.

## Acknowledgements

Fieldwork at HWK EE by OGAP was authorized by the Commission for Science and Technology, the Department of Antiquities, and the Ngorongoro Conservation Area Authority, Tanzania, and funded by the NSF (BCS-0852292) and the European Research Council-Starting Grants (283366). We are thankful to Merve Gumrukcu for her help in isotope sampling and Angeliki Theodoropoulou for her help in tooth wear sampling. Isotopic and tooth wear analyses were funded by the ERC-Starting Grants (283366), Columbia University's Center for Climate and Life (KTU) and the MINECO grants (HAR2013-48784-C3-1-P and HAR2016-76760-C3-1-P). FB was supported by the German Research Foundation (DFG, grant number BI 1879/1-1). Finally, we would like to thank the three anonymous reviewers who provided valuable comments that improved this paper.

## Supplementary Online Material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.08.011>.

## References

- Albert, R.M., Bamford, M.K., Cabanes, D., 2006. Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples. *Quaternary International* 148, 78–94.
- Albert, R.M., Bamford, M.K., Cabanes, D., 2009. Palaeoecological significance of palms at Olduvai Gorge, Tanzania, based on phytolith remains. *Quaternary International* 193, 41–48.
- Baker, G., Jones, L.H.P., Wardrop, I.D., 1959. Cause of wear in sheep's teeth. *Nature* 184, 1583–1584.
- Bamford, M.K., 2012. Fossil sedges, macroplants, and roots from Olduvai Gorge, Tanzania. *Journal of Human Evolution* 63, 351–363.
- Bamford, M.K., Albert, R.M., Cabanes, D., 2006. Plio–Pleistocene macroplant fossil remains and phytoliths from Lowermost Bed II in the eastern palaeolake margin of Olduvai Gorge, Tanzania. *Quaternary International* 148, 95–112.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Bendrey, R., Vella, D., Zazzo, A., Balasse, M., Lepetz, S., 2015. Exponentially decreasing tooth growth rate in horse teeth: implications for isotopic analyses. *Archaeometry* 57, 1104–1124.
- Bibi, F., Souron, A., Bocherens, H., Uno, K., Boisserie, J.-R., 2013. Ecological change in the lower Omo Valley around 2.8 Ma. *Biological Letters* 9, 20120890.
- Bibi, F., Pante, M., Souron, A., Stewart, K., Varela, S., Werdelin, L., Boisserie, J.R., Fortelius, M., Hlusko, L., Njau, J., de la Torre, I., 2018. Paleoeecology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania: the mammal and fish evidence. *Journal of Human Evolution* 120, 48–75.
- Blondel, C., Merceron, G., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2010. Dental mesowear analysis of the late Miocene Bovidae from Toros-Menalla (Chad) and early hominid habitats in Central Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292, 184–191.
- Blumenschine, R.J., Marean, C.W., 1993. A carnivore's view of archaeological bone assemblages. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, University of Southern Illinois, Carbondale, pp. 273–300.
- Bocherens, H., Koch, P., Mariotti, A., Geraads, D., Jaeger, J., 1996. Isotopic biogeochemistry (<sup>13</sup>C <sup>18</sup>O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* 11, 306–318.
- Boisserie, J.-R., Merceron, G., 2011. Correlating the success of Hippopotaminae with the C<sub>4</sub> grass expansion in Africa: relationship and diet of early Pliocene hippopotamids from Langebaanweg, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 308, 350–361.
- Bonnefille, R., 1984. Palynological research at Olduvai Gorge. *National Geographic Society Research Reports* 17, 227–243.
- Brown, W., Christofferson, P., Massler, M., Weiss, M., 1960. Postnatal tooth development in cattle. *American Journal of Veterinary Research* 21, 7–34.
- Cerling, T., Harris, J., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347–363.
- Cerling, T., Harris, J., Leakey, M., Mudidid, N., 2003a. Stable isotope ecology of Northern Kenya, with emphasis on the Turkana Basin. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 583–603.
- Cerling, T., Harris, J., Passey, B., 2003b. Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84, 456–470.
- Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E., Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proceedings of the National Academy of Sciences* 112, 11467–11472.
- Davis, M., Pineda Munoz, S., 2016. The temporal scale of diet and dietary proxies. *Ecology and Evolution* 6, 1883–1897.
- de la Torre, I., Mora, R., 2018. Oldowan technological behaviour at HWK EE (Olduvai Gorge, Tanzania). *Journal of Human Evolution* 120, 236–273.
- de la Torre, I., Albert, R.M., Arroyo, A., Macphail, R., McHenry, L.J., Mora, R., Njau, J.K., Pante, M.C., Rivera-Rondón, C.A., Rodríguez-Cintas, A., Stanistreet, I.G., Stollhofen, H., Wehr, K., 2018. New excavations at the HWK EE site: Archaeology, paleoenvironment and site formation processes during late Oldowan times at Olduvai Gorge, Tanzania. *Journal of Human Evolution* 120, 140–202.
- DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B.M., Van Stolk, C.A., Winburn, A.A., Greshko, M.A., O'Hara, M.C., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. *PLOS ONE* 8, e71428.
- Ecker, M., Bocherens, H., Julien, M.-A., Rivals, F., Raynal, J.-P., Moncel, M.-H., 2013. Middle Pleistocene ecology and Neanderthal subsistence: Insights from stable isotope analyses in Payre (Ardèche, southeastern France). *Journal of Human Evolution* 65, 363–373.
- Estes, R.D., 1991. *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates*. University of California Press, Berkeley.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301, 1–36.



- Franz-Odenaal, T.A., Kaiser, T.M., Bernor, R.L., 2003. Systematics and dietary evaluation of a fossil equid from South Africa. *South African Journal of Science* 99, 453–459.
- Franz-Odenaal, T.A., Solounias, N., 2004. Comparative dietary evaluations of an extinct giraffid (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) from Langebaanweg, South Africa (early Pliocene). *Geodiversitas* 26, 675–685.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution* 15, 783–822.
- Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 355–365.
- Jorayev, G., Wehr, K., Benito-Calvo, A., Njau, J., de la Torre, I., 2016. Imaging and photogrammetry models of Olduvai Gorge (Tanzania) by Unmanned Aerial Vehicles: A high-resolution digital database for research and conservation of Early Stone Age sites. *Journal of Archaeological Science* 75, 40–56.
- Kaiser, T.M., Franz-Odenaal, T.A., 2004. A mixed-feeding *Equus* species from the Middle Pleistocene of South Africa. *Quaternary Research* 62, 316–323.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *American Journal of Physical Anthropology* 108, 359–373.
- Kingston, J.D., 2011. Stable isotopic analyses of Laetoli fossil herbivores. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context*. Springer, New York, pp. 293–328.
- Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243, 272–306.
- Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. *Reviews in Mineralogy and Geochemistry* 48, 455–488.
- Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta* 60, 3889–3896.
- Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Sciences* 93, 11201–11205.
- Livingstone, D., Clayton, W., 1980. An altitudinal cline in tropical African grass florae and its paleoecological significance. *Quaternary Research* 13, 392–402.
- Loffredo, L.F., DeSantis, L.R.G., 2014. Cautionary lessons from assessing dental mesowear observer variability and integrating paleoecological proxies of an extreme generalist *Cormohipparion emsliei*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 395, 42–52.
- Louys, J., Ditchfield, P., Meloro, C., Elton, S., Bishop, L.C., 2012. Stable isotopes provide independent support for the use of mesowear variables for inferring diets in African antelopes. *Proceedings of the Royal Society B: Biological Sciences* 279, 4441–4446.
- Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. *Geochimica et Cosmochimica Acta* 48, 1689–1693.
- Magill, C.R., Ashley, G.M., Domínguez-Rodrigo, M., Freeman, K.H., 2016. Dietary options and behavior suggested by plant biomarker evidence in an early human habitat. *Proceedings of the National Academy of Sciences* 113, 2874–2879.
- Marín Leyva, A.H., García Zepeda, M.L., Ponce Saavedra, J., Schaaf, P., Arroyo Cabrales, J., Alberdi, M.T., 2013. Inferencias de paleodietas en ungulados y proboscidos: limitaciones conceptuales y técnicas. *Biológicas* 15, 1–10.
- Mayte, G.-B., García-Zepeda, M.L., López-García, R., Arroyo-Cabrales, J., Marín-Leyva, A.H., Meléndez-Herrera, E., Fuentes-Farías, A.L., 2016. Diet and habitat of *Mammuthus columbi* (Falconer, 1857) from two Late Pleistocene localities in central western Mexico. *Quaternary International* 406, 137–146.
- McHenry, L.J., Njau, J.K., de la Torre, I., Pante, M.C., 2016. Geochemical “fingerprints” for Olduvai Gorge Bed II tuffs and implications for the Oldowan–Acheulean transition. *Quaternary Research* 85, 147–158.
- McHenry, L.J., Stanistreet, I.G., 2018. Tephrochronology of Bed II, Olduvai Gorge, Tanzania, and placement of the Oldowan – Acheulean transition. *Journal of Human Evolution* 120, 7–18.
- Merceron, G., Ungar, P., 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. *South African Journal of Science* 101, 365–370.
- Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary change and evolution of horses in North America. *Science* 331, 1178–1181.
- Mihlbachler, M.C., Beatty, B.L., Caldera-Siu, A., Chan, D., Lee, R., 2012. Error rates and observer bias in dental microwear analysis using light microscopy. *Palaeontologia Electronica* 15, 12.
- Pante, M.C., de la Torre, I., 2018. A hidden treasure of the Lower Pleistocene at Olduvai Gorge, Tanzania: the Leakey HWK EE assemblage. *Journal of Human Evolution* 120, 114–139.
- Pante, M.C., Njau, J.K., Hensley-Marschand, B., Keevil, T.L., Martín-Ramos, C., Peters, R.F., de la Torre, I., 2018. The carnivorous feeding behavior of early *Homo* at HWK EE, Bed II, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 120, 215–235.
- Passey, B.H., Cerling, T.E., Schuster, G.T., Robinson, T.F., Roeder, B.L., Krueger, S.K., 2005. Inverse methods for estimating primary input signals from time-averaged isotope profiles. *Geochimica et Cosmochimica Acta* 69, 4101–4116.
- Peter, S.U., Jessica, R.S., Christine, M.S., 2016. Dental microwear differences between eastern and southern African fossil bovids and hominins. *South African Journal of Science* 112, 1–5.
- Rivals, F., Semprebon, G., 2006. A comparison of the dietary habits of a large sample of the Pleistocene pronghorn *Stockoceros onusroagris* from the Papago Springs Cave in Arizona to the modern *Antilocapra americana*. *Journal of Vertebrate Paleontology* 26, 495–500.
- Rivals, F., Mhlabachler, M.C., Solounias, N., 2007. Effect of ontogenetic-age distribution in fossil samples on the interpretation of ungulate paleodiet using the mesowear method. *Journal of Vertebrate Paleontology* 27, 763–767.
- Rivals, F., Prignano, L., Semprebon, G.M., Lozano, S., 2015. A tool for determining duration of mortality events in archaeological assemblages using extant ungulate microwear. *Scientific Reports* 5, 17330.
- Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2016. Tale of two timescales: Combining tooth wear methods with different temporal resolutions to detect seasonality of Palaeolithic hominin occupational patterns. *Journal of Archaeological Science: Reports* 6, 790–797.
- Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 241, 301–319.
- Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to recent Antilocapridae (Mammalia: Artiodactyla). *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 332–347.
- Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *Journal of Human Evolution* 47, 115–144.
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *American Museum Novitates* 3366, 1–49.
- Stanistreet, I.G., McHenry, L.J., Stollhofen, H., de la Torre, I., 2018. Bed II sequence stratigraphic context of EF-HR and HWK EE archaeological sites, and the Oldowan/Acheulean succession at Olduvai Gorge, Tanzania. *Journal of Human Evolution* 120, 19–31.
- Stynder, D.D., 2009. The diets of ungulates from the hominid fossil-bearing site of Elandsfontein, Western Cape, South Africa. *Quaternary Research* 71, 62–70.
- Stynder, D.D., 2011. Fossil bovid diets indicate a scarcity of grass in the Langebaanweg E Quarry (South Africa) late Miocene/early Pliocene environment. *Paleobiology* 37, 126–139.
- Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., Troughton, J.H., 1979. The distribution of C3 and C4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37, 337–350.
- Ungar, P.S., Merceron, G., Scott, R.S., 2007. Dental microwear texture analysis of Variswale bovids and Early Pliocene paleoenvironments of Langebaanweg, Western Cape Province, South Africa. *Journal of Mammalian Evolution* 14, 163–181.
- Uno, K.T., Cerling, T.E., Harris, J.M., Kunimatsu, Y., Leakey, M.G., Nakatsukasa, M., Nakaya, H., 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences* 108, 6509–6514.
- Uno, K., Rivals, F., Bibi, F., Pante, M., Njau, J., de la Torre, I., 2018. Large mammal diets and paleoecology across the Oldowan–Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses. *Journal of Human Evolution* 120, 76–91.
- Van der Merwe, N.J., 2013. Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *South African Journal of Science* 109, 1–14.
- Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 281–289.
- Young, H.J., Young, T.P., 1983. Local distribution of C3 and C4 grasses in sites of overlap on Mount Kenya. *Oecologia* 58, 373–377.
- Zazzo, A., Bendrey, R., Vella, D., Moloney, A.P., Monahan, F.J., Schmidt, O., 2012. A refined sampling strategy for intra-tooth stable isotope analysis of mammalian enamel. *Geochimica et Cosmochimica Acta* 84, 1–13.