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

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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_4 dominated and minor mixed C_3 and C_4 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.

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Korongo East East (HWK EE) by the Olduvai Geochronology Archaeology Project (OGAP) combined with Mary Leakey's original unpublished collections together yield a remarkable assemblage of stone tools and faunal remains that are critical for understanding hominin habitat and behavior during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., submitted; de la Torre and Mora, submitted; Pante et al., submitted, Pante and de la Torre, submitted). 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:

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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-Odendaal et al., 2003; Franz-Odendaal and Solounias, 2004; Kaiser and Franz-Odendaal, 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., submitted; Stanistreet et al., submitted), and is dated to ~1.7 Ma (McHenry et al., 2016; McHenry, submitted) (Fig. 1). Teeth analyzed in this paper include specimens from the Leakey assemblage (Pante and de la Torre, submitted) and from the new excavations at the HWK EE site (de la Torre et al., submitted).

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., submitted), 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., submitted).

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. (submitted). 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 Mihlbachler 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 (Mihlbachler 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 (Mihlbachler 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× 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

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