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Abstract: The well-dated Pleistocene sediments at Olduvai Gorge have yielded an incredibly rich record of hominin fossils, stone tools, and vertebrate faunal remains that taken together, provide insight to hominin behavior and paleoecology. Since 2009, the Olduvai Geochronology and Archeology Project 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 77% of Bed II large mammals analyzed (n=141) had diets comprised of mostly C4 vegetation (> 75% of diet), ~18% had mixed C3C4 diets, and 5% had mostly C3 diets (< 25% C4). Carbon isotope data indicate a decrease in the number of mixed and C3 feeders in interval IIB. Tooth mesowear generally indicate an increase of the abrasiveness of the diet between intervals IIA and IIB, probably related to an increase in grazing. Microwear data indicates more abrasive diets in interval IIA suggesting stronger seasonal differences at the time of death. 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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4 **Large mammal diets and paleoecology across the Oldowan-Acheulean transition at**
5 **Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses**
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49 Key words: intratooth isotope profile, mesowear, microwear, Bed II, paleodiet, herbivore
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54 **Abstract**

55 The well-dated Pleistocene sediments at Olduvai Gorge have yielded an incredibly rich record of
56 hominin fossils, stone tools, and vertebrate faunal remains that taken together, provide insight to
57 hominin behavior and paleoecology. Since 2009, the Olduvai Geochronology and Archeology
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4 Project has undertaken extensive excavations in Bed II that have yielded a large collection of
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6 early Pleistocene stone tools and fossils. The strata of Lower, Middle and Upper Bed II at
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8 Olduvai Gorge capture the critical transition from Oldowan to Acheulean technology and
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10 therefore provide an opportunity to explore the possible role of biotic and abiotic change during
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12 the transition. Here, we analyze newly discovered and existing fossil teeth from Bed II sites
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14 using stable isotope and tooth wear methods to investigate the diets of large mammals. We
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16 reconstruct the dietary ecology of Bed II mammals and evaluate whether vegetation or
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18 hydroclimate shifts are associated with the technological change. Combined isotope and tooth
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20 wear data suggest most mammals were C₄ grazers or mixed feeders. Carbon isotope data from
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22 bulk enamel samples indicate that 77% of Bed II large mammals analyzed (n=141) had diets
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28 C₃ feeders in interval IIB. Tooth mesowear generally indicate an increase of the abrasiveness of
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36 molars which suggest a possible decrease in seasonality across the transition. Neither stable
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38 isotope nor tooth wear analyses indicate major vegetation or hydrological change across the
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40 Oldowan-Acheulean transition.
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53 **1. Introduction**

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55 Olduvai Gorge contains one of the richest early Pleistocene records of stone tools and human-
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57 modified bones in eastern Africa, a record that provides evidence of hominin behavior and their
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59 interactions with other mammals on the landscape. Vertebrate fossils in the gorge were first
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4 studied by Hans Reck's team over 100 years ago, then by Mary and Louis Leakey whose artifact
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6 and hominin fossil discoveries became world-renowned (Leakey, 1959; Leakey et al., 1964;
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8 Leakey, 1971). The pioneering paleoanthropological work by Mary Leakey and colleagues was
9
10 placed in a geological framework by Richard Hay, who defined the stratigraphy of Olduvai
11
12 Gorge (Hay, 1963) based on the original work of Hans Reck (1928, 1951). A more complete
13
14 study of the geology of Olduvai, with a focus on the stratigraphy, was published later by Hay
15
16 (1976). The Bed II stratigraphic framework established by Hay is revised by Stanistreet et al.
17
18 (1976). The Bed II stratigraphic framework established by Hay is revised by Stanistreet et al.
19
20 (this volume). Much effort has gone into determining the ages of the fossils and artifacts from
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22 Bed I and Bed II sites throughout the gorge using combined radiometric dating (Curtis and Hay,
23
24 1972; Deino, 2012; Manega, 1993) and correlation of volcanic tuffs when direct dating is not
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26 possible (Habermann et al., 2016a; McHenry, 2012; McHenry et al., 2016).
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31 One exceptional feature of Olduvai Gorge is that it is one of only a handful of places
32
33 known to date that captures the Oldowan-Acheulean transition (Leakey, 1971). Renewed
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35 excavations at Bed II sites by the Olduvai Geochronology and Archeology Project (OGAP),
36
37 especially at the Henrietta Wilfrida Korongo East East site (HWK EE; Figure 1), has produced
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39 more than 18,000 artifacts and nearly 30,000 fossils (de la Torre, this volume; New excavations
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41 at the HWK EE site) that when combined with other, younger Bed II sites (e.g., EF-HR, MNK,
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43 FC East and FC West, HWK E-Tembo and FLK West), shed new light on the Oldowan-
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45 Acheulean transition, tool use, and hominin-carnivore interactions from ~1.7 to 1.6 Ma (Pante et
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47 al., this volume). Reconstructing the paleoenvironment at Olduvai Gorge is essential to
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49 understanding the role of environmental change during this major archeological transition.
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55 A multitude of approaches to reconstructing paleoenvironments have produced a wealth
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57 of information about the flora and fauna of Olduvai Gorge, especially for Bed I. These include
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59 vertebrate paleontology (e.g., Gentry and Gentry, 1978; Kovarovic et al., 2013; Plummer and
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4 Bishop, 1994)(Bibi et al., this volume), analysis of plant macro- and microfossils (Albert et al.,
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6 2015a; Albert and Bamford, 2012; Bamford, 2012; Bamford et al., 2006; Bamford et al., 2008;
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8 Barboni et al., 2010; Bonnefille, 1984), paleopedology (Ashley et al., 2014), and isotopic studies
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10 of soil carbonates and organic matter (Cerling and Hay, 1986; Sikes, 1994; Sikes and Ashley,
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12 2007), mammalian teeth (Van der Merwe, 2013), and plant biomarkers (Magill et al., 2016;
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14 Magill et al., 2013a, b). Three main conclusions about Olduvai Gorge based on the many
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16 paleoenvironmental studies are that first, the region has long been an arid to semi-arid ecosystem
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18 (Bonnefille, 1984). Second, there is evidence for a highly variable landscape both spatially
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20 (Barboni et al., 2010; Magill et al., 2016) that includes more mesic wetland areas (e.g., lake
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22 margins) and groundwater spring systems and temporally, which has been well documented in
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24 Bed I (Bamford, 2012; Magill et al., 2013b). Third, there is an overall shift towards more arid
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26 conditions between ~1.9 Ma and the present based carbon and oxygen isotope ratios in
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28 pedogenic carbonates (Cerling and Hay, 1986; Sikes and Ashley, 2007) and during Bed II times
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30 based on the avian fossil record (Prassack et al., this volume).
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41 *Figure 1 about here*
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45 Fossil teeth of large herbivores can be used to reconstruct past environments based on
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47 their morphology, microwear texture, and geochemistry. Both stable isotope and tooth wear
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49 methods are commonly used for paleodietary and paleovegetation reconstructions, yet these
50
51 powerful and well-established methods have not yet been applied to Bed II fossil teeth. The
52
53 recent excavation of new fossil teeth by the OGAP team, combined with the existing teeth
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55 collected by Mary Leakey's team in the early 1970's, present an opportunity to reconstruct the
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57 paleoenvironment and mammal diets during the Oldowan-Acheulean transition (see also Rivals
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4 et al., this volume). Here, we use stable isotope analysis and tooth wear methods from Bed II
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6 sites to evaluate diet, vegetation, and hydroclimate during the transition. Results from these
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8 independent approaches for reconstructing diet and vegetation are combined to provide a robust
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10 assessment of the paleoenvironment at the origin of the Acheulean at Olduvai Gorge.
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15 16 **2. Materials and Methods**

17 18 19 **2.1. Teeth analyzed for stable isotopes, mesowear and microwear**

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21 Fossil teeth sampled for stable isotope analysis come from the Leakey and OGAP research
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23 collections. A total of 141 fossil teeth were sampled from the HWK EE, FC East, FC West,
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25 MNK, FLK West, HWK E-Tembo, and EF-HR sites (Figure 1). Teeth represent a wide range of
26
27 mammals, including Proboscidea (Elephantidae, Deinotheriidae), Perissodactyla
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29 (Rhinocerotidae, Equidae), Artiodactyla (Bovidae, Giraffidae, Hippopotamidae, Suidae),
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31 Carnivora (Hyaenidae), and Primates (Cercopithecidae) (see Table 1).
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36 The sampling strategy for stable isotope and tooth wear analyses is designed to include as
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38 many taxa from the faunal assemblage and to capture the full dietary diversity. It is also
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40 designed to reflect relative faunal abundances observed in the faunal assemblage. For example,
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42 abundant taxa such as Alcelaphini and Equidae in Bed II at Olduvai are also the most abundant
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44 taxa in the isotope and tooth wear data sets. Where possible, at least 5 specimens from each
45
46 clade were analyzed to represent the dietary breadth present. This is not always possible for rarer
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48 taxa, such as Deinotheriidae and *Giraffa*. In some cases, analyzed samples for very abundant
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50 taxa are underrepresented (e.g., Alcelaphini), and for rare taxa it is possible for them to be under-
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52 or oversampled with respect to their relative abundance in the faunal assemblage.
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60 *Table 1 about here*
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7 To evaluate whether the specimens sampled for isotope analysis represent the entire
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9 faunal assemblage, we calculate the coefficient of determination between the relative abundance
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11 of the number of individual specimens (NISP) from the OGAP fossil tooth database (Bibi et al.,
12
13 this volume) and that of the isotope data set. If the two datasets are similar, then community
14
15 level interpretations of the isotope data can be applied to the NISP data set.
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19 A second important consideration is fossil provenance. Patterson et al. (2017)
20
21 demonstrate that Pleistocene paleontological and archeological sites have different faunal
22
23 compositions for large mammals in the Turkana Basin. At Olduvai, where the archaeological
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25 deposits are thicker and therefore likely more palimpsest in nature, we consider the Bed II fauna
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27 as a combination of archeological and paleontological in provenance.
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31 Most of the teeth (135 of 141) from these sites can be assigned to two stratigraphic
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33 intervals that span the Bed II subformations (Lower, Middle, and Upper), as defined by Hay
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35 (1976) (see also Stanistreet et al, this volume). The ages of the two intervals, denoted here as
36
37 interval IIA and interval IIB, are based on associated radiometric ages of tephra layers. Sixty-
38
39 three teeth recovered from HWK EE trenches, HWK E-Tembo, Trench 73 at FLK West, and
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41 Trench 36 and the Skull site at MNK are assigned an age of ~1.7 Ma, based on the reported ages
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43 of 1.66 and 1.71 Ma of Tuff IIA by Manega (1993) and Curtis and Hay (1972), respectively. We
44
45 follow the recommendation of Curtis and Hay and use only a single age (1.71 Ma) from Tuff IIA
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47 based on higher K content of that sample (KA 2320) relative to other dated Tuff IIA samples
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49 (Curtis and Hay, 1972). These trenches are all stratigraphically positioned between Tuff IIA and
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51 Tuff IIB, and are here included in what we term interval IIA. Seventy-two teeth come from
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53 between Tuff IIB and IIC, and are grouped within what we term interval IIB. Interval IIB teeth
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55 are assigned an age of ~1.6 Ma based on their proximity to the Bird Print Tuff (BPT), which lies
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4 just above Tuff IIB and has been geochemically correlated by McHenry (this issue) to the
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6 recently dated Tuff FLKWb, with a reported age of 1.664 ± 0.019 Ma (Diez-Martín et al., 2015) .
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8 Interval IIB includes fossil teeth from all FC East and West trenches, the MNK Main and T5
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10 trenches, and HWK E-Tembo. Six teeth come from above Tuff IIC (IIC interval), which include
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12 3 from EF-HR and 3 from FLK Trench 69. Tuff IIC is not dated. Tuff IID is dated around 1.48
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14 Ma (Manega, 1993) or 1.34 Ma in age (Domínguez-Rodrigo et al., 2013).
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19 The material studied for meso- and microwear was selected from all the specimens
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21 available in the collections from HWK EE, FC East, FC West, and MNK. We analyzed large
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23 herbivorous mammals among Proboscidea (Elephantidae, Deinotheriidae), Perissodactyla
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25 (Rhinocerotidae, Equidae), and Artiodactyla (Giraffidae, Hippopotamidae, Suidae, Bovidae). For
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27 Bovidae, where identification of isolated teeth to species level is difficult, we used tribe level:
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29 Alcelaphini, Antilopini, Bovini, Caprini, Hippotragini and Reduncini. For other groups, we used
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31 the lowest level of identification possible (genus or species). All taxonomic assignments follow
32
33 the updated faunal list provided in Bibi et al. (this volume). A total of 298 specimens were
34
35 molded and screened to assess their suitability for microwear and mesowear analyses. After
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37 excluding teeth where both buccal cusps were broken or damaged, 171 specimens were suitable
38
39 for mesowear analysis. After an examination of the epoxy casts under the stereomicroscope,
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41 specimens with taphonomic alterations which damaged the original microwear pattern were
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43 discarded, leaving a total of 248 specimens suitable for microwear analysis.
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51 **2.2. Sampling and analytical methods**

52 *2.2.1. Stable isotopes in vegetation and teeth*

53
54 Stable carbon and oxygen isotope ratios of tooth enamel are determined by an animal's diet and
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56 body water, respectively, and therefore can be used to reconstruct herbivore diets, vegetation,
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58 and local hydroclimate (Kingston and Harrison, 2007; Levin et al., 2006; e.g., Uno et al., 2011;
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4 Van der Merwe, 2013). Tooth enamel carbon isotopes ratios of large herbivores reflect the
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6 proportion of C₃ to C₄ vegetation in their diet during the time in which the tooth formed. Oxygen
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8 isotopes in enamel (or other mammalian bioapatites) are primarily controlled by the isotope ratio
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10 of precipitation but also influenced by food water; plant water; evaporative processes in soils,
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12 plants, and water sources; and animal physiology (Kohn et al., 1996; Levin et al., 2006; Luz et
13
14 al., 1984). Stable carbon and oxygen isotope ratios are reported as delta (δ) values relative to the
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16 Pee Dee Belemnite (PDB) standard using permil (‰) notation where
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$$\delta^{13}\text{C} \text{ (or } \delta^{18}\text{O)} = (R_{\text{sample}}/ R_{\text{standard}} - 1) \times 1000 \quad (1)$$

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21 and R_{sample} and R_{standard} are the ¹³C/¹²C (¹⁸O/¹⁶O) ratios in the sample and in the standard,
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23 respectively, and the δ¹³C and δ¹⁸O values of PDB are defined as 0‰.
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29 Today in eastern Africa nearly all woody vegetation uses the C₃ photosynthetic pathway,
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31 or Calvin cycle, and nearly all low elevation (<1500 m) grasses, some sedges (e.g., *Cyperus*
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33 *papyrus*), and select shrubs (e.g., Amaranthaceae) use the C₄ pathway, or Hatch-Slack cycle
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35 (Cerling and Harris, 1999; Jones and Milburn, 1978; Livingstone and Clayton, 1980; Sage et al.,
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37 2007; Tieszen et al., 1979; Young and Young, 1983). The carbon isotope ratio of C₃ plants is on
38
39 average around -28 ‰ with an observed range of about -36 to -23 ‰. The wide range in δ¹³C
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41 values in C₃ plants is controlled by environmental conditions: more negative values are found in
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43 closed canopy forests whereas xeric conditions—common in lowland eastern Africa—lead to
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45 more positive values (e.g., -26 to -23 ‰). C₄ plants exhibit a narrower range of values, from
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47 about -14 to -10 ‰ in eastern Africa (Cerling et al., 2003a).
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53 To establish the end-member δ¹³C values in tooth enamel (δ¹³C_{enamel}) for C₃ and C₄ diets,
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55 the atmospheric δ¹³C value (δ¹³C_{atm}) and the enrichment in ¹³C between diet and tooth enamel
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57 must be determined. We use the mean value of -6.7 ‰ for the δ¹³C_{atm} based on the high
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59 resolution planktonic foraminifera record from 1.8 to 1.6 Ma from Tipple et al. (2010). We
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4 chose the 1.8 to 1.6 Ma interval because it best matches the age range for Olduvai Bed II ages.
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7 We use the $\delta^{13}\text{C}_{\text{atm}}$ value of -6.7‰ along with biosynthetic fractionation factors for C_3
8
9 and C_4 plants to calculate the $\delta^{13}\text{C}$ values for C_3 and C_4 plants from 1.8 to 1.6 Ma (**Table S1**).
10

11
12 Next, we apply the enrichment factor ($\Sigma^*_{\text{enamel-diet}}$) of $14.1 \pm 0.5\text{‰}$ as determined by Cerling and
13
14 Harris (1999) for large ungulates to calculate ${}^{\text{TM}}\delta^{13}\text{C}_{\text{enamel}}$ endmember values of -11.9‰ and +
15
16 2.8‰ for pure C_3 and C_4 diets, respectively (**Table S1**). Note that the application of the
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18 enrichment factor, $\epsilon_{\text{enamel-diet}}^*$, is from rearrangement of the following equation,
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20

$$\epsilon^* = \alpha^* - 1 \quad (2)$$

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22
23
24 from Craig (1954), where alpha (α^*) is the apparent fractionation factor between diet and enamel,
25
26 defined as
27

$$\alpha^* = (1000 + \delta^{13}\text{C}_{\text{enamel}}) / (1000 + \delta^{13}\text{C}_{\text{diet}}) \quad (3)$$

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29
30 We include these equations here as a review of the mathematically correct way to calculate
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32 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‰)
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35 to the $\delta^{13}\text{C}_{\text{diet}}$ values to determine endmember $\delta^{13}\text{C}_{\text{enamel}}$ values.
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42 2.2.1.1. Enamel sampling, pretreatment, and isotope analysis

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45 Sampling of fossil teeth for stable isotopes was done at the Olduvai field station, at University
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47 College London, and at Lamont-Doherty Earth Observatory of Columbia University (LDEO).
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49 Fossil teeth were selected from ten mammalian families, with identification primarily done by
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51 Bibi et al. (this volume), but also by F.R. and M.P. in some cases. Prior to drilling, each tooth
52
53 was inspected, photographed, and a sampling location on the tooth was evaluated.
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57 The sample protocol for bulk sampling involved sampling along broken enamel surfaces
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59 whenever possible, or in some cases a lateral tooth surface, using a Dremel handheld drill with
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4 carbide (Brasseler) or diamond grit impregnated (Lasco) bits at low speed (~1000 RPM). No
5
6 occlusal surfaces were drilled so as to preserve these surfaces for morphological or microwear
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8 studies. The sample surface was prepared by abrading the enamel surface with the drill bit. On
9
10 lateral surfaces, this removed surface adherents and the outermost enamel (*ca.* 100 μ m). If
11
12 present, cementum was drilled away to expose enamel. After visual inspection of the prepared
13
14 surface with a hand lens, a narrow groove about 1mm deep and 1 to 2 mm wide was drilled
15
16 parallel to the growth axis of the tooth. Sample groove lengths varied based on tooth geometry
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18 imposed additional constraints (enamel thickness and crown length), but ideally were 10 to 15
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20 mm long to average out potential seasonal variability in diet and water. Sample masses ranged
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22 from about 3 to 15 mg.
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29 Three equid molars were serially sampled along the growth axis of the tooth to generate
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31 intratooth isotope profiles. Cementum was cleared away using the Dremel to expose a window of
32
33 the fossil enamel. The exposed area was ~5mm wide and ran the length of the tooth crown (50
34
35 to 60 mm). Samples were drilled every 3 mm along the growth axis of the tooth, with sample
36
37 grooves oriented normal to the growth axis. Sample grooves were \leq 1 mm deep, ~1 mm wide,
38
39 and 3 to 6 mm long. Sample masses were about 3-5 mg.
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44 Enamel powders from bulk and intratooth profile samples were pretreated at LDEO prior
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46 to stable isotope analysis with a weak oxidizer followed by buffered acid. Samples were treated
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48 with 3% NaOCl (bleach) for 30 minutes in 1.7 ml centrifuge tubes that were stirred every 10
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50 minutes on a vortex mixer. After the reaction period, samples were centrifuged and the
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52 supernatant was removed. Each sample was then rinsed three times with distilled water. The
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54 rinse procedure involved adding de-ionized (DI) water, stirring on the vortex mixer, then
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56 centrifuging the sample and removing the supernatant. Next, samples were treated with 0.1 M
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58 Na-acetate buffered acetic acid for 30 minutes, as above. Following three distilled water rinses,
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4 they were loosely covered and dried overnight in a fume hood. Approximately 300 to 600 [g of
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6 powdered enamel sample was weighed out into a silver capsules, along with NBS-19 standard
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8 (20-50 [g). Samples and standards were roasted *in vacuo* for 2 hours at 60° C to remove
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10 adsorbed water, then transferred to round bottom, glass reaction vials. A strand of silver wool
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12 was added to each vial to oxidize any SO₂ produced in the reaction. Sample vials were loaded
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14 immediately into a (Thermo) Kiel IV device or transferred into an oven held at 60° C until
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16 analyzed.
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22 Fossil enamel samples were reacted with phosphoric acid at 70° C for 10 minutes *in vacuo*
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24 on a Kiel IV device. Exsolved gases were cryogenically transferred to a microvolume held at
25
26 -170° C, and then transferred to second microvolume with the first held at -70 °C to remove
27
28 water. The purified sample CO₂ was inlet to a dual-inlet Delta V Plus isotope ratio mass
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30 spectrometer. Carbon and oxygen isotope ratios were corrected using international and internal
31
32 standards. The standard deviation of NBS-19 throughout sample runs was ~0.05 ‰ for δ¹³C and
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34 <0.10 ‰ for ¹⁸O. Oxygen isotope values were converted from CO₂ (gas) to fossil enamel
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36 (mineral) values using a fractionation factor of 1.00799, which was calculated using the
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38 temperature dependent equation for fossil enamel (Eq. 4) in Passey et al. (2007).
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44 We calculate the dietary contribution of C₄ vegetation to diet using the C₃ and C₄
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46 endmember enamel values of -11.9 ± 4 ‰ and +2.8 ± 2 ‰, respectively, where uncertainty is
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48 based in observed variability in C₃ and C₄ eastern African plants (e.g., Cerling and Harris, 1999;
49
50 Cerling et al., 2003a). We apply a two-end member mixing model, where the percent of C₄
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52 vegetation in diet is determined as
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54

$$\%C_4 = (\delta^{13}C_{C_3} - \delta^{13}C_{\text{enamel}}) / (\delta^{13}C_{C_3} - \delta^{13}C_{C_4}) \times 100, \quad (4)$$

55
56 where ¹³C_{enamel} is the measured δ¹³C value of the sample and δ¹³C_{C₃} and δ¹³C_{C₄} are the
57
58 calculated C₃ and C₄ endmember values for enamel. We propagate the uncertainty in both the
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4 dietary endmember values and in the analytical procedure ($\pm 0.1 \text{ ‰}$), which results in
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6 uncertainties of 12 to 30 %. We note that uncertainties in the calculated %C₄ in diet are higher
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8 towards the C₄ end of the continuum due to the larger uncertainty of the C₃-endmember value,
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10 which is $\pm 4 \text{ ‰}$. We define C₃-dominated diets as those with $\delta^{13}\text{C}$ values of $\leq -8 \text{ ‰}$ (*ca.* <25%
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12 C₄), mixed C₃-C₄ diets as having values from -8 to -1 ‰ (*ca.* 25-75 %C₄), and C₄-dominated
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We compare 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 correct for the difference in the modern $\delta^{13}\text{C}_{\text{atm}}$ value (-8 ‰) and the calculated early Pleistocene values for Bed II (-6.7 ‰) by adding 1.3 ‰ to all modern $\delta^{13}\text{C}_{\text{enamel}}$ values. In order to compare the modern $\delta^{18}\text{O}$ values to Bed II values, we re-calculate the modern values, originally calculated using the calcite-based acid fractionation factor, using a tooth enamel specific, temperature dependent acid fractionation factor (Eq. 3) from Passey et al. (2007). This is necessary so that the $\delta^{18}\text{O}$ values from both data sets can be directly compared. To do this, we convert the modern $\delta^{18}\text{O}$ values from mineral back to CO₂ gas $\delta^{18}\text{O}$ values using the temperature dependent calcium carbonate acid fractionation factor of Swart et al. (1991). We then apply the tooth enamel acid fractionation factor from Passey et al. (2007). The difference between the originally published and recalculated $\delta^{18}\text{O}$ values for the modern enamel samples is $\sim -0.1 \text{ ‰}$.

Finally, because of their semiaquatic lifestyle, Hippopotamidae are overrepresented in the fluvial and lacustrine sediments of Bed II. To address the overrepresentation of sixteen *H. gorgops* in interval IIB, where they comprise 24% of all samples, our statistical analyses uses only three values from the population, the minimum, median, and maximum values, to represent interval IIB Hippopotamidae.

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4 2.2.1.2. *Intratooth stable isotope profiles and inverse modeling*
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7 Intratooth stable isotope profiles of ungulate tooth enamel provide a time series of the diet and
8
9 body water over the period in which the tooth enamel formed (Fricke and O'Neil, 1996; Sharp et
10 al., 1998). In extant equids, premolars and molars form over 1.5 to 2.8 years, inclusive of crown
11
12 extension and enamel maturation (Hoppe et al., 2004a). The time represented in intratooth
13
14 isotope profiles can therefore be used to evaluate seasonal variability in environmental
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16 precipitation, vegetation, and diet (Metcalf et al., 2011; Nelson, 2005; Sharp et al., 1998).
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19 Amelogenesis, or the process of enamel formation, is a two stage process that starts with a
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21 secretory stage, where the enamel matrix is deposited, followed by a protracted maturation stage,
22
23 where density of the original matrix increases significantly (Suga, 1979). As a result, the isotope
24
25 ratio of a given volume of enamel represents a time integrated signal of the initial period of
26
27 matrix deposition plus the maturation period. Tooth enamel maturation and isotope sampling
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29 methods blur and attenuate the original isotope input signal (Passey & Cerling, 2002; Zazzo et al,
30
31 2005). Here we apply the inverse method developed by Passey et al. (2005) to estimate the
32
33 original input signal for $\delta^{13}\text{C}$ (diet) and $\delta^{18}\text{O}$ (body water) that more closely reflect the actual diet
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35 and body water composition of the equid during the time during in which the tooth formed. The
36
37 inverse model requires input parameters that related to tooth formation, isotope sampling
38
39 geometry, and isotope analysis. Input parameters relevant to tooth enamel formation, or
40
41 amelogenesis, include initial enamel density (f_i), enamel appositional length (l_a) and maturation
42
43 length (l_m) (Passey and Cerling, 2002). We use parameters measured on *Equus ferus przewalskii*
44
45 by (Blumenthal et al., 2014) as estimates for *Equus oldowayensis* molars used here, where $f_i =$
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47 22%, $l_a = 6$ mm, $l_m = 28$ mm. Sample input variables include distance between samples (3 ± 0.5
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49 mm) and depth (0.7 mm \pm 0.2 mm). The final input variables are the measured carbon and
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51 oxygen isotope data and their associated uncertainties, which were smoothed with a 3-point
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4 weighted mean (0.25:0.5:0.25). A measured error term, E_{meas} , is computed from measurement
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6 uncertainties in isotope values and sample measurements. This term ultimately governs model
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8 sensitivity it is used to determine an appropriate damping factor (Σ). The model requires
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10 selection of a damping factor that minimizes the difference between E_{meas} and the prediction
11
12 error (E_{pred}). A detailed description of the these additional model parameters and the
13
14 regularization method is given in Passey et al. (2005). Model code was downloaded and adapted
15
16 from Passey et al. (2005). The inverse model assumes constant growth rate. However, it is
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18 widely accepted that ungulate cheek teeth have non-linear growth rates, particularly towards the
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20 end of crown extension (Bendrey et al., 2015; Zazzo et al., 2012).
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32 *2.2.2. Tooth wear methods*

33 34 35 *2.2.2.1. Mesowear Analysis*

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38 Mesowear analysis is a method of analyzing the gross dental wear of ungulate molars by
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40 evaluating the relief and sharpness of cusp apices which is related to the amounts of attritive and
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42 abrasive dental wear (Fortelius and Solounias, 2000). Mesowear is analyzed macroscopically
43
44 from the buccal side of upper molars, preferably the paracone of M2. Unworn (and marginally
45
46 worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices, are omitted
47
48 from mesowear analysis (Rivals et al., 2007). Mesowear was applied to Rhinocerotidae, Equidae,
49
50 Giraffidae and Bovidae because of their suitable tooth morphology when using the Fortelius and
51
52 Solounias (2000) method. In this study, the standardized method introduced by Mihlbachler et al.
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54 (2011) is employed. The method is based on seven cusp categories, ranging in shape from high
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56 and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the
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4 mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or
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6 MWS (Mihlbachler et al., 2011). For a more detailed description of the method see Rivals et al.
7
8 (this volume).
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10 11 12 2.2.2.2. *Microwear Analysis* 13 14

15 Tooth microwear patterns were examined following the protocol developed by Solounias
16 and Semprebon (2002) and Semprebon et al. (2004). After cleaning, the occlusal surface of each
17 specimen was molded using high-resolution silicone (vinylpolysiloxane) and casts were created
18 using clear epoxy resin. Casts were observed under incident light with a stereomicroscope Zeiss
19 Stemi 2000C at 35× magnification. Microwear scars were quantified in a square area of 0.16
20 mm². We used the classification of features defined by Solounias and Semprebon (2002) and
21 Semprebon et al. (2004) which basically distinguishes pits and scratches. Pits are microwear
22 scars that are circular or sub-circular in outline and are classified as small pits, large pits, or
23 puncture pits. Scratches are elongated microfeatures that have straight and parallel sides.
24
25 Scratches are divided into fine, coarse and hypercoarse scratches. The presence of some other
26 features is recorded qualitatively: cross scratches (scratches with a different orientation than most
27 scratches) and gouges (large features which have ragged, irregular edges and are much larger and
28 deeper than large pits). In addition, scratch textures were assessed using the scratch width score
29 (SWS). For a more detailed description of the method see Rivals et al. (this volume).
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49 In artiodactyls and perissodactyls, scratches and pits were counted in two areas on the
50 paracone of the upper molars and the protoconid of the lower molars. In proboscideans, the area
51 was selected on a loph in the center of the worn part of the occlusal surface. The results were
52 compared with a database constructed from extant ungulate taxa (Rivals et al., 2010; Solounias
53 and Semprebon, 2002). In primates, microwear was counted on the mesio-buccal cusp of upper
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4 molars or on the mesio-lingual cusp of lower molars. The results are compared to the database of
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7 extant primates from Godfrey et al. (2004).

8 9 **3. Results**

10 11 **3.1. Stable Isotopes**

12 13 14 15 16 *3.1.1. Comparison of NISP and isotope data sets*

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

39 40 *3.1.2. Bulk samples*

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42 Tooth enamel $\delta^{13}\text{C}$ values ($n=141$) from Bed II at Olduvai span a range of nearly 17 ‰, from
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44 -12.8 to $+4.1$ ‰, with a median value of $+0.7$ ‰. There is a range of 9.4 ‰ in oxygen isotope
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46 data, from -4.3 to $+5.1$ ‰, with a median value of -0.1 ‰. All carbon and oxygen isotope data
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48 are presented in Table S3, which also includes taxonomic data from Bibi et al. (this volume) and
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50 site information. More than 95% of the samples (135 of 141) come from either interval IIA (n
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52 $=63$) or interval IIB ($n=72$). Six additional samples come from Upper Bed II sites EF-HR and
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FLK (Figure 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 main Bed II

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4 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
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6 two main intervals are show in Figure 2. We also include isotope data from 72 extant large
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8 mammals in Tanzania from Van der Merwe (2013), primarily from the Serengeti and Maswa
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10 ecosystems that lie to the west of Olduvai Gorge, to compare extant fauna to the Bed II intervals,
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12 denoted here as IIA and IIB. Histograms of carbon and oxygen isotopes from the modern and
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14 Bed II sample populations are shown in Figure 3.
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21 *Table 2 about here*
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26 The majority of the mammals from the main Bed II intervals have C₄-dominated diets. In
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28 the IIA interval, the ratio of the percentages of taxa with C₄-dominated: mixed: C₃-dominated
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30 diets is 71:21:8. In the interval IIB the ratio is 83:15:2, when corrected for the
31
32 overrepresentation of Hippopotamidae in interval IIB (N = 59; discussed below in section
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34 3.1.1.1). The modern large mammal community is also primarily comprised of mammals with
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36 C₄-dominated diets (57:24:19) but about 15 to 25% less than are present in the Bed II
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38 communities, with considerable increases in the percentages of mammals with mixed and C₃
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40 dominated diets.
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48 *Figure 2 about here*
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53 *Figure 3 about here*
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58 We apply the Mann-Whitney U-test (also called the Wilcoxon test) to compare carbon
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60 and oxygen isotope distributions between time intervals (IIA, IIB, and modern) because there is
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4 no reason to assume the data are normally distributed. Mann-Whitney U-test results indicate no
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6 significant differences between carbon isotope distributions from the three intervals (Table 3).
7
8 Median $\delta^{13}\text{C}$ values are nearly identical between intervals IIA, IIB, and the modern. There are
9
10 however, significant differences ($p < 0.05$) in the oxygen isotope distributions between fossils
11
12 and modern distributions (Table 3). The median $\delta^{18}\text{O}$ values in interval IIA and interval IIB are
13
14 identical (+ 0.2 ‰) when corrected for the overrepresentation of IIB Hippopotamidae. Despite
15
16 their identical median values, interval IIA has a higher maximum $\delta^{18}\text{O}$ value (+ 5.1 vs. + 3.7 ‰),
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18 which may be indicative of more evaporated water and likely, arid conditions during interval IIB
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20 times. The modern median $\delta^{18}\text{O}$ value is 1.8 ‰ more positive than in intervals IIA and IIB.
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29 *Table 3 about here*
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33 The Bed II and modern carbon and oxygen data are shown as box plots for lineages
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35 (family, genus or species) for which there are three or more teeth analyzed for at least on interval
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37 (Figure 4). Elephantidae and Deinotheriidae are excluded from the box plots due to their small
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39 sample size ($N \leq 2$) and lack of continuity across intervals. Although not all groups have robust
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41 sample numbers (e.g., ≥ 5), Hippotragini, Reduncini, Tragelaphini, Equidae, Hippopotamidae,
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43 Hyaenidae and *Theropithecus* all show increases in $\delta^{13}\text{C}$ values between intervals IIA and IIB.
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45 There are no consistent $\delta^{18}\text{O}$ changes across the different lineages between intervals.
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53 *Figure 4 about here*
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58 Finally, we present results of the bulk sampled isotope data by site since the scope of
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60 many archeological studies are focused at that level (Figure S2). Fossil teeth sampled in this
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4 study come primarily from sites HWK EE (n = 61; 59 from interval IIA, 2 from interval IIB), FC
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6 (East and West; n = 52; all from IIB), and MNK (n =20; 3 from IIA, 17 from IIB). FC East and
7
8 FC West are considered together due to their close proximity and same stratigraphic position.
9
10 Six teeth from interval IIC come from sites FLK (Trench 69) and EF-HR; data for these sites are
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12 not presented here but are listed in Table S3. Carbon and oxygen isotopes from each site are
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14 plotted in Figure S2 for HWK EE, MNK, FC East and West, FLK, and EF-HR. All but two
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16 HWK EE samples come from interval IIA. In all sites, C₄-dominated diets are prevalent. At
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18 HWK EE, the ratio of the percentages of taxa with C₄-dominated: mixed: C₃-dominated diets is
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20 71:21:8 (the same as the IIA values). For FC East and FC West, the ratio is 81:17:2 and at MNK
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22 it is 90:10:0. Thus, a higher proportion of mammals sampled from FC East/FC West and MNK
23
24 have C₄-dominated diets and there may have been greater proportions of C₄ vegetation on the
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26 landscape relative to HWK EE. Nevertheless, median $\delta^{13}\text{C}$ values are nearly identical from the
27
28 three sites and median $\delta^{18}\text{O}$ values are only slightly (< 1 ‰) more negative at FC East and West
29
30 and at MNK than at HWK EE (Table S4). U-test results show no statistically significant
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32 differences ($p > 0.05$) between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ distributions at the three sites (Table S5).
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42 3.1.2.1. *Artiodactyls*

43 Bovidae are common in the assemblage, comprising 43% of all Bed II samples in the OGAP and
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45 Leakey collections (Bibi et al., this volume), and box plots of their carbon and oxygen data are
46
47 presented by tribe in Figure 5. There are shifts towards more positive $\delta^{13}\text{C}$ distributions (median
48
49 and/or ranges) between intervals IIA and IIB for Tragelaphini, Reduncini, and Hippotragini.
50
51 Alcelaphini $\delta^{13}\text{C}$ distributions remain unchanged, but their $\delta^{18}\text{O}$ median values increase by ~1 ‰
52
53 between intervals IIA and IIB. We applied the same U-test used to compare distributions in
54
55 intervals IIA and IIB to the Alcelaphini isotope values, one of only two lineages with ≥ 5
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57 specimens analyzed per interval (Table 3). Only $\delta^{18}\text{O}$ values show a significant change between
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4 intervals IIA and IIB. In other bovid tribes, the $\delta^{18}\text{O}$ trends from interval IIA to IIB are mixed,
5
6 probably in part due to small sample sizes. For example, Tragelaphini $\delta^{18}\text{O}$ values increase in
7
8 range and become more positive in interval IIB, while Hippotragini values become more
9
10 negative between IIA and IIB (Figure 5). Among Antilopini, which are only sampled from
11
12 interval IIA, the smaller form, cf. *Antidorcas recki* has a C₄-dominated diet, whereas the larger
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14 form (possibly *Aepyceros*) shows a mixed diet.
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21 *Figure 5 about here*
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26 Bibi et al. (this volume) identified at least 3 species based on tooth size: *Megalotragus*
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28 *isaaci*, Alcelaphini small sp., and Alcelaphini sp. indet. Using the relatively large sample of
29
30 Alcelaphini from Bed II (N=33), we compare $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values among the three types of
31
32 Alcelaphini to explore whether there is isotopic evidence for niche partitioning. The data show
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34 no such evidence (Figure S3).
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38 Other Bed II artiodactyls have C₄-dominated or mixed diets, with the exception of two
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40 *Giraffa stillei*, one from HWK EE (interval IIA) and one from EF-HR (interval above IIC). A
41
42 combined five *Sivatherium* $\delta^{13}\text{C}$ values from the two main intervals indicate C₄-dominated or
43
44 mixed diets; their $\delta^{18}\text{O}$ values are similar between the two intervals.
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48 Eighteen *Hippopotamus gorgops* teeth were sampled, two from interval IIA and sixteen
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50 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
51
52 and -3.6 ‰, the latter of which are the most negative values from all IIA fauna analyzed. In
53
54 interval IIB, the median $\delta^{13}\text{C}$ value for the sixteen *H. gorgops* is -0.1 ‰ (min: -2.8 ‰; max:
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56 $+1.1$ ‰); the median $\delta^{18}\text{O}$ value is -2.6 ‰ (min: -4.3 ‰; max: -1.0 ‰). Hippopotamidae
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4 enamel typically yields the lowest $\delta^{18}\text{O}$ values within a given ecosystem (Bocherens et al., 1996;
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7 Cerling et al., 2008).

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9 Two Suidae genera, *Kolpochoerus* and *Metridiochoerus* both have C_4 -dominate diets (77
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11 to 91 % C_4), with a median $\delta^{13}\text{C}$ value of -0.1 ‰ (min: -0.6 ‰; max: $+1.5$ ‰). *Kolpochoerus*
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13 $\delta^{18}\text{O}$ values are about 1 to 2 ‰ more depleted than coeval *Metridiochoerus* values, suggesting
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16 different diets, water sources, or physiologies.
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19 20 3.1.2.2. *Perissodactyls*

21 Perissodactyls from Bed II include relatively rare Rhinocerotidae and abundant Equidae,
22
23 the latter of which are second only to Alcelaphini in the number of specimens analyzed and
24
25 overall abundance in Bed II. In interval IIA, all five Rhinocerotidae samples analyzed indicate
26
27 C_4 -dominated diets. Three are identified as *Ceratotherium cf. simum* while the others are
28
29 identified only to family (Figure 4; Table S6). In interval IIB, there is one rhino (*Ceratotherium*)
30
31 with a C_4 -dominated diet and one (Rhino indet. ?*Diceros*) with a C_3 -dominated diet, presumably
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33 similar to the extant grazing and browsing rhinos. The median $\delta^{18}\text{O}$ value of the interval IIA
34
35 samples is ~ 1 ‰ more enriched than the interval IIB value.
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40 Equidae teeth analyzed for isotopes are assigned mostly to *Equus oldowayensis* (n=18)
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42 with smaller number coming from *Eurygnathohippus cornelianus* (n=5) and one specimen listed
43
44 as Equidae *gen. et sp. indet.* Equid $\delta^{13}\text{C}$ values indicate C_4 -dominated diets for 21 of 24
45
46 analyzed specimens (Table S3 and Figure 4). Interval IIB equids have a more positive median
47
48 $\delta^{13}\text{C}$ values and smaller interquartile range than in IIA which suggests decreased dietary breadth
49
50 during interval IIB times. The $\delta^{18}\text{O}$ values are slightly more negative in IIB (Figure 4). Despite
51
52 these differences, U-test results comparing interval IIA and IIB Equidae show no significant
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54 differences in either carbon ($p = 0.1754$) or oxygen ($p = 0.3312$) isotope distributions (Table 3).
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4 We compare the $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values between *E. oldowayensis* and *Eu. cornelianus*. The $\delta^{13}\text{C}$
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6 values largely overlap, although the smaller number of *Eu. cornelianus* suggest a diet with a higher
7
8 proportion of C_4 vegetation, whereas *E. oldowayensis* had a broader dietary range (Figure S3C). The
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10 $\delta^{18}\text{O}$ values show no differences between the two equid species (Figure S3D).
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18 3.1.2.3. Proboscideans

19 Proboscidean material is rare from the available dataset of Bed II, with only two
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21 deinotheres and one elephantid specimen analyzed. The deinotheres from interval IIA are the
22
23 most negative $\delta^{13}\text{C}$ values measured from Bed II and functionally define a C_3 endmember diet
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25 (-12.7‰). The $\delta^{18}\text{O}$ values of -1.3 and -1.8‰ are also relatively negative compared to most
26
27 other values from interval IIA (Figure 3). A $\delta^{13}\text{C}$ value of $+1.8\text{‰}$ from a single *Elephas recki*
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29 specimen from IIB puts it on the opposite end of the dietary spectrum ($93\text{‰}\text{C}_4$) from the
30
31 Deinotheriidae.
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37 3.1.2.4. Primates

38 Primates are also rare in Bed II. Four *Theropithecus oswaldi* teeth, one from interval IIA
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40 and three from IIB, have a median $\delta^{13}\text{C}$ value of 0.0‰ , indicating C_4 dominated diets (73 to 94
41
42 $\text{‰}\text{C}_4$). The *T. oswaldi* from interval IIA has more negative median $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values than
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44 those from interval IIB (Figure 4).
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49 3.1.2.5. Carnivores

50 Four hyaenid teeth (*Crocota* sp.) were analyzed from Bed II, one from interval IIA and
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52 three from IIB. The IIA specimen has a $\delta^{13}\text{C}$ value of -4.3‰ and the three from interval IIB
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54 have values ranging from -3.4 to -0.3‰ (Figure 4). Carnivore bioapatite is depleted $\sim 1.3\text{‰}$
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56 with respect to their diet (Fox-Dobbs et al., 2006), so the *Crocota* sp. prey at Olduvai were
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58 herbivores with mixed and C_4 dominated diets. *Crocota* $\delta^{18}\text{O}$ values range from -2.9 to $+0.5\text{‰}$.
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4 The Bed II *Crocuta* stable isotope values are similar to those of modern hyenas from Tanzania
5
6 reported by van der Merwe (2013) and plotted in Figure 4.
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10 11 3.1.3. *Serially sampled equids* 12

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14 The measured and modeled isotope data from the three *Equus oldowayensis* intratooth profiles
15
16 are given in Table S6 and additional model input and output data (E_{meas} , E_{pred} , and ϵ) are
17
18 provided in Table S7. The intratooth profiles are plotted in Figure 6. The modeled $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
19
20 values in the profiles range from -2.3 to $+2.1$ ‰ and -2.1 to $+1.6$ ‰, respectively, which reflect
21
22 the estimated range of dietary input and body water variability, after being corrected for blurring
23
24 due to enamel maturation and sampling (Table S6). The tooth from the Lemuta interval at HWK
25
26 EE (IIA interval, specimen L10-523) shows greater seasonal variability in both isotope ratios
27
28 than the other two profiles, L1-48 (MNK Main) and L62-104 (FC West), that come from interval
29
30 IIB (Figure 6). For example, the estimated diet of the *E. oldowayensis* from IIA ranges from 66
31
32 to 97 %C₄, whereas the diets of the other two range from 74 to 87 %C₄ (specimen L1-48) and
33
34 from 91 to 97 %C₄ (specimen L62-104). All three profiles indicate mostly C₄-dominated diets
35
36 with the exception of some of the samples from tooth L10-523 and one sample from tooth L1-48
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38 indicating seasonally mixed C₃-C₄ diets (Table S6).
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49 *Figure 6 about here*
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54 **3.2. Tooth wear** 55

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57 All the results from the mesowear and microwear analyses are provided in Table 4 for
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59 each site and taxa. Raw data are available in the online supplementary material Table S8. Even if
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61 all teeth available in the collections had been sampled, the sample size for many taxa would still
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4 be very low. The results from taxa with small sample size ($N < 3$) are reported but will not be
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6 used in the interpretations (see section 4. Discussion).
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9 Small samples excluded, mesowear scores range from $MWS = 1.8$ in Reduncini to MWS
10 $= 5.2$ in Equidae (Table 4). This range of values corresponds to those for extant grass-dominated
11 mixed feeders and grazers (Fortelius and Solounias 2000, Mihlbachler et al. 2011). In
12
13 comparison to extant reference samples, the microwear patterns observed correspond to the
14
15 range of extant mixed feeders and grazers (Figure 8; Table 4). The detailed results are reported
16
17 for each taxon, comparing the assemblages from intervals IIA and IIB.
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26 *Table 4 about here*
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29 3.2.1.1. *Artiodactyls*

30 Bovidae are represented by six tribes (Table 4). In general, bovids plot among the extant mixed
31
32 feeders (Figure 8A). Sample size is significant for Alcelaphini, Antilopini, and Reduncini.
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34

35 Alcelaphini provided the largest sample, both at IIA ($N = 45$ for mesowear, $N = 35$ for
36
37 microwear) and IIB ($N = 38$ for mesowear, $N = 40$ for microwear). The two samples show
38
39 mesowear scores similar to extant grass-dominated mixed feeders and grazers. The sample from
40
41 IIB has higher values than in IIA, but the values overlap slightly (Figure 7). The microwear
42
43 pattern with intermediate numbers of scratches is characteristic of mixed feeders (Figure 8A). In
44
45 terms of numbers of pits and scratches, microwear pattern is very similar in the two stratigraphic
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47 units (Table 4). However, some differences are reported with a higher percentage in interval IIA
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49 of large pits and hypercoarse scratches, as well as wider scratches (higher SWS).
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55 The Hippotragini, even with relatively small sample sizes, show mesowear and
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57 microwear values which are very similar to those previously reported for the Alcelaphini
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59 (Figures 7 and 8A). The two samples from intervals IIA and IIB plot among the mixed feeders.
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4 Nevertheless, the sample from interval IIA displays higher percentage of large pits, wider
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6 scratches and presence of hypercoarse scratches than in interval IIB.
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9 The Antilopini only provided data in the interval IIA (N = 13). The mesowear score plots
10 among the mixed feeders, at the limit of the values for extant browsers and grazers (Figure 7).
11
12 The same result is obtained from microwear (Figure 8A). As the Alcelaphini and the
13
14 Hippotragini from interval IIA, the Antilopini show high percentages of large pits (Table 4), but
15
16 here associated with gouges which indicate the presence of large-sized particles of grit on the
17
18 vegetation consumed.
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23 Reduncini show low mesowear scores corresponding to browsing or browse-dominated
24 mixed feeding (Figure 7), but high numbers of scratches indicating grazing (Figure 8A). There is
25
26 a clear discrepancy between the two proxies, especially for the sample from interval IIA (the
27
28 sample size from interval IIB is very small).
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33 Bovini and Tragelaphini are only represented by very small samples. For the two tribes,
34 the specimens from interval IIA show a low mesowear value and low numbers of scratches
35
36 consistent with browsing (Figures 7 and 8A). For the specimens from interval IIB, data from a
37
38 single proxy are available, i.e. microwear for the Bovini and mesowear for the Tragelaphini. For
39
40 the Bovini, microwear shows intermediate values consistent with mixed feeding (Figure 8A). For
41
42 the Tragelaphini, the single mesowear value suggests mixed feeding (Figure 7). However, the
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44 low sample size does not allow definite interpretation.
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50 Caprini are only represented by a single specimen of uncertain stratigraphic provenience
51 (surface find). The low number of scratches would suggest a browsing trend, but sample size is
52
53 too small to allow an interpretation (Figure 8A).
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57 The giraffid *Sivatherium maurusium* shows intermediate mesowear and microwear
58 values. The mesowear values show a tendency toward grazing (MWS > 2), while the microwear
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4 pattern, with low number of scratches (NS < 17), suggests more browsing at the time of death
5
6 (Figure 8B). As previously reported for most of the bovids, the sample from interval IIA shows
7
8 higher percentages of large pits, gouges, hypercoarse scratches, but also cross scratches, than in
9
10 interval IIB (Table 4). Consequently, due to the presence of hypercoarse scratches, the scratches
11
12 are generally also wider in interval IIA. These higher values in interval IIA would suggest the
13
14 presence of high quantities of grit ingested together with the vegetation.
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19 For the hippopotamid *Hippopotamus gorgops*, tooth mesowear indicates grazing (in
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21 interval IIB), while microwear suggests mixed feeding (both in intervals IIA and IIB). The
22
23 microwear pattern is also characterized by a high frequency of cross scratches in intervals IIA
24
25 and IIB, and the presence of coarse and hypercoarse scratches (high SWS) in interval IIB (Table
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27 4).
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31 The suids *Kolpochoerus* sp. and *Metridiochoerus* sp. were analyzed only through
32
33 microwear. The four samples plot in the grazing confidence ellipse or in the grass-dominated
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35 mixed feeders (Figure 8B). All samples have high percentages of cross scratches (from 90 to
36
37 100%) and many samples display large pits, gouges, puncture pits and hypercoarse scratches.
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39 The combination of all these features would suggest these species consumed leaves, grasses,
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41 wood bark, and importantly, might have relied on a rooting diet (Medin et al. 2015).
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49 3.2.1.2. Perissodactyls

50 The equids *Equus oldowayensis* and *Eurygnathohippus cornelianus* have high mesowear
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52 values (MWS = 4 to 5.2) which correspond to extant grazers (Figure 7). Mesowear values for the
53
54 two species in interval IIB are higher than those in interval IIA suggesting more abrasive diets in
55
56 the samples from interval IIB. Regarding the microwear pattern, *Equus oldowayensis* shows less
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58 scratches than *Eurygnathohippus cornelianus*, indicating that *Eurygnathohippus cornelianus* was
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4 more of a grazer than *Equus oldowayensis* (Figure 8B). In each assemblage, *Equus oldowayensis*
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6 also has more large pits and gouges than *Eurygnathohippus cornelianus*. It is also significant that
7
8 the samples from interval IIB show a higher number of scratches than those from interval IIA,
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10 indicating more abrasion in interval IIB, as previously reported with mesowear.
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14 For the Rhinocerotidae, *Ceratotherium cf. simum*, the sample from interval IIA (N = 3)
15
16 displays a high number of scratches with values tending towards the extant grazers (Figure 8B).
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18 The absence of large pits and gouges and the presence of mostly fine scratches (low SWS value)
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20 also confirm grass-dominated diets (Table 4).
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26 3.2.1.3. Proboscideans

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28 The elephantid *Elephas recki* is represented by a single specimen showing a microwear
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30 pattern with intermediate number of scratches plotting in between the extant browsers and
31
32 grazers (Table 4 and Figure 8B).
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38 3.2.1.4. Primates

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40 Primates are represented by three specimens attributed to *Theropithecus oswaldi*. In
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42 comparison to extant primates with known diets (Godfrey et al. 2004), the specimens from
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44 intervals IIA and IIB plot among the species which feed on grass such as *Theropithecus gelada*,
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46 *Hapalemur griseus* and *H. simus* (Figure 9).
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53 Mesowear scores are generally higher in the samples from interval IIB compared with
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55 those from interval IIA, with the exception of the small sample of Reduncini (Figure 7). This
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57 would indicate a more abrasive diet for the populations of herbivores from interval IIB.
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4 In terms of tooth microwear, the samples from interval IIA and IIB have the same ranges
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6 of scratches, but the samples from interval IIA tend to have higher numbers of pits than those
7
8 from interval IIB. The samples from interval IIA usually have more large pits and gouges, and
9
10 wider scratches (higher SWS and presence of hypercoarse scratches) than those from interval IIB
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12 (Table 4). All these features would suggest the ingestion of exogenous particles (dust, grit)
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14 related to drier conditions in interval IIA.
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21 4. Discussion

22 4.1. Dietary reconstructions

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24 We find no major shifts in overall dietary ecology across the Oldowan-Acheulean transition,
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26 although there are changes at the tribe or family level. The stable isotope data suggest a decrease
27
28 in the number of mammals with mixed and C₃-dominated diets in interval IIB. However, limited
29
30 sample size for the isotope data set and hominin preference for mammals with C₄-dominated
31
32 diets (e.g., Alcelaphini) may bias the record against browsers (Patterson et al., 2017). Mesowear
33
34 scores generally increase between intervals IIA and IIB, suggesting an increase in grazing.
35
36 Microwear data indicates more abrasive diets in interval IIA based on the higher occurrence of
37
38 scratches. The combination of tooth wear and stable isotope analyses provides two independent
39
40 methods for reconstructing mammalian diets. A combined approach has the potential to yield
41
42 more refined paleodietary and paleovegetation reconstructions. Throughout the ensuing
43
44 discussion of dietary reconstructions based on tooth wear and stable isotopes, it is important to
45
46 keep in mind that each method records diet over different periods of an animal's life. Microwear
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48 analysis represents diet over the previous days or weeks before death; mesowear over months to
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50 years; and stable carbon isotopes record diet during tooth formation, which ranges from ~1-2
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52 years in ungulates and up to a decade or more in proboscideans (Hoppe et al., 2004b; Uno et al.,
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4 2013). Discrepancy in reconstructed diet can occur due to long-term (e.g., ontogenetic) or short
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6 term (i.e., seasonal) differences in diet. Dietary discrepancies are expected to be more frequently
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8 observed among mixed feeders or dietary generalists than in dedicated grazers or browsers.
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10
11 Tooth enamel carbon isotope values indicating C₄-dominated diets in eastern Africa are
12
13 usually assumed to signify grazing taxa, whereas values indicative of C₃-dominated diets are
14
15 usually assumed to represent browsing taxa. This assumption is probably valid for taxa younger
16
17 than ~10 Ma, when carbon isotopes of plant wax biomarkers first show evidence of C₄
18
19 vegetation in eastern Africa (Uno et al., 2016). It is further supported by the earliest record of
20
21 C₄-dominated diets in eastern African from equids at 9.9 Ma (Uno et al., 2011). It is possible
22
23 that there were mixed C₃-C₄ grasslands in eastern Africa in the past, but this would require taxa
24
25 with C₄ dominated diets like equids, which today are C₄ grazers, to have been selective grazers
26
27 based on photosynthetic pathway (or some associated characteristics). It is also possible that
28
29 C₄-dominated diets, present across the orders Artiodactyla, Perissodactyla, and Proboscidea by
30
31 ~7 Ma in Africa, were derived from combination of C₄ grasses and shrubs (e.g., Amaranthaceae).
32
33 Much of this speculation can be addressed through a combined tooth wear and isotope approach
34
35 to test whether a C₃ or C₄ dietary signal, determined from the isotope data, is associated with a
36
37 grazing or browsing diet based on microwear patterns or mesowear scores. This approach was at
38
39 Laetoli, where isotopes and mesowear show C₃-dominated and mixed diets were comprised
40
41 mostly of C₃ browse (Kaiser, 2011; Kingston, 2011), although some of the large mammals were
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43 also exploiting C₃ grasses, which were identified through phytolith analysis (Rossouw and Scott,
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45 2011).
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55 The combined tooth wear and stable isotope data indicate C₄ grass-dominated diets for
56
57 most taxa from Bed II at Olduvai (Figures 2 to 5). Evaluating the two methods independently in
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59 each interval, we find that the tooth wear data show taxa from interval IIA were grass-dominated
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4 mixed feeders and grazers while those from IIB were mostly grazers. The taxa from interval IIB
5
6 tend to show a stronger grazing signal in comparison to their IIA counterparts (Figure 8),
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8 indicating a more abrasive vegetation during interval II B. This could suggest an increase in
9
10 availability of grass or more open habitat in the IIB interval. The carbon isotope data on the
11
12 other hand reveal there were more taxa with C₃-dominated and mixed diets in interval IIA than in
13
14 IIB (Figures 2 and 3). The percentages of mammals with C₄-dominated, mixed, and C₃-
15
16 dominated diets for all Bed II fauna are 77:18:5. Between intervals, the C₄:mixed:C₃ dietary
17
18 ratio shifts from 71:21:8 (IIA) to 82:17:1 (IIB). This approach of using a three-term ratio to
19
20 describe the dietary distribution of an interval is similar to that of Cerling et al. (2015), who used
21
22 carbon isotope data to classify Turkana Basin mammals as C₄-grazers:mixed C₃-C₄ feeders: C₃-
23
24 browsers. Ours differs from theirs in that we take a more conservative approach and maintain
25
26 the vegetation type (C₃ vs C₄) rather than infer feeding habit (browsing vs grazing), because
27
28 tooth wear data suggest that C₃ grasses or C₄ shrubs may have been minor dietary components of
29
30 the Olduvai Bed II mammals.

31 32 33 34 35 36 37 38 39 40 41 *4.1.1. Artiodactyls*

42
43 A more detailed look at different taxonomic groups further illustrates the utility of
44
45 combined tooth wear and isotope data. Among species with a large sample size for tooth wear
46
47 analyses, Alcelaphini show grass-dominated mixed feeding and grazing traits (Figure 8A). This
48
49 is in close but not exact agreement with the carbon isotope data, which indicate C₄-dominated
50
51 diets (Figures 3 and 5). The grass-dominated mixed feeding signal in Alcelaphini comes from a
52
53 low number of scratches (< 20) in the microwear data (Table 4) that results in placement outside
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55 of the 95% confidence centroid for grazers. Their mesowear scores fall within the modern range
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57 of grazers and the upper half of the mixed feeding range (Figure 7). The Hippotragini data are
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4 similar. Carbon data indicate C₄-dominated diets (76 to 100% C₄) and mesowear scores fall in
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6 the lower range of extant grazers and microwear data fall outside of the 95% confidence centroid
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8 for grazers. In both Alcelaphini and Hippotragini, the lack of scratches could possibly be a result
9
10 of browsing on C₄ shrubs, which would reconcile the microwear and carbon isotope data.
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12
13 Bonnefille (1984) identified pollen from a C₄ shrub from the family Amaranthaceae, *Aerva*
14
15 *javanica* (listed as *A. persia* in that publication) in a single sample in Lower Bed II at VEK. This
16
17 does not constitute evidence for widespread C₄ shrubs, but it does document the presence of at
18
19 least one such taxon during Bed II times.
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21

22
23 Both tooth wear and the isotope data for the Antilopini cf. *Antidorcas recki* point to
24
25 predominantly mixed feeding (Figures 5, 7 and 8). The other bovid tribes have sample sizes that
26
27 are too small ($N \leq 4$) to apply these methods, so interpretations are lower confidence. Tooth
28
29 wear from Tragelaphini point towards browsing, whereas isotope data from a relatively small
30
31 sample ($N = 6$) suggest a wide dietary breadth ranging from C₃- to C₄-dominated diets.
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35 Reduncini are deemed C₄ grazers based on the agreement between carbon isotopes and
36
37 microwear, but have somewhat low mesowear scores (mean of 0.5 to 1.80 in IIA and IIB,
38
39 respectively). Extant Reduncini are grazers (Cerling et al., 2003b), but the mesowear
40
41 characteristics of *Redunca redunca* and *Kob ellipsiprymnus* show high relief and rounded cusps,
42
43 two features associated with browsing or mixed feeding (Fortelius and Solounias, 2000). Their
44
45 preference for soft grasses often found in wetlands is one possible explanation for the
46
47 discrepancy between the isotope and mesowear signature. Two Bovini, one from each interval,
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49 are classified as mixed feeders based on their microwear and a single mesowear value, whereas
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51 the isotope value from a single sample in IIA yields a C₄-dominated diet (84 %C₄).
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55 Carbon isotope data from a small number of cf. *Sivatherium* or *Sivatherium maurusium*
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57 ($N = 5$) place their diets on the boundary of C₄-dominated and mixed diets, which is supported
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4 by the mean mesowear scores that suggest mixed to grazing diets in both intervals (Figure 7).
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6 However, the microwear data indicate browse-dominated mixed diets. A seasonal dietary shift
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8 from grazing to browsing could be invoked to reconcile the isotope and microwear data.
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11 Sixteen of eighteen Hippopotamidae analyzed for isotopes come from interval IIB, and
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13 their diets range from mixed to C₄-dominated. Interval IIA hippos have C₄ grass-dominated
14
15 mixed diets based on isotope and microwear data. In interval IIB, carbon isotope values from
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17 MNK are more positive than those from FC East and West (Figure S2), possibly illustrating
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19 habitat variability over very short distances (Figure 1), but collectively indicating mixed and C₄-
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21 dominated diets. Mesowear scores in interval IIB indicate a grazing diet. Microwear data from
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23 IIA indicate a grass-dominated mixed diet whereas in interval IIB it suggests mixed diets (with
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25 more browse relative to IIA specimens).
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31 Two Suidae genera from Bed II, *Metridiochoerus* and *Kolpochoerus*, both have C₄-
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33 dominated diets (Figure 5). Bibi et al. (this volume) have identified multiple species for each
34
35 genus. We analyzed three samples from the *Kolpochoerus limnetes* and *K. paiceae* lineage (the
36
37 latter being synonymous with *K. oldowayensis*) plus one specimen designated *Kolpochoerus* cf.
38
39 *limnetes*, and three from a different lineage, *K. majus*, which is thought to be descended from *K.*
40
41 *phillipi* (Souron et al., 2015). The *K. limnetes/paiceae* lineage has morphological features such
42
43 as increased hypsodonty and length in the third molars and reduced premolars that are interpreted
44
45 as grazing adaptations, whereas the bunolophodont lineage, *K. phillipi/majus*, has a less
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47 specialized dentition and thus possibly had a more diverse and omnivorous diet (Souron et al.,
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49 2015).
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55 From our limited sample size, there does not appear to be any difference in $\delta^{13}\text{C}$ between
56
57 the two *Kolpochoerus* lineages. Three of the *K. limnetes/paiceae* from FC East and FC West
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59 have nearly identical $\delta^{13}\text{C}$ values (-0.5, -0.5 and -0.6 ‰), suggesting a narrow dietary niche.
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4 *K. phillipi/majus* from HWK EE and FC West all have similar $\delta^{13}\text{C}$ values with slightly more
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K. phillipi/majus from HWK EE and FC West all have similar $\delta^{13}\text{C}$ values with slightly more variability than in the *K. limnetes/paiceae* subset of samples (Table S3). Microwear data support the dietary differences posited by Souron et al. (2015), where higher number of scratches in *K. limnetes/paiceae* (avg.: 23.9; range 20.5 to 28; N=9) suggests a diet focused on grasses, whereas *K. majus* has a lower number of scratches (avg.: 19; range 13.5 to 23.5; N=6) and a higher range, indicating more variable diet (more intra-specific variability) that would fit with a more generalist diet. For *Metridiochoerus*, there is not enough data from the different species to evaluate dietary differences. More broadly for the Suidae, the diets of the two genera cannot be differentiated based on carbon isotopes (Figure 5).

In contrast to carbon isotopes, oxygen isotopes and microwear data indicate niche partitioning between the two genera within their C_4 -dominated diet regime. *Kolpochoerus*, which is the more abundant of the two suid genera (Bibi et al., this volume), has more negative $\delta^{18}\text{O}$ values and higher percentages of pits than *Metridiochoerus*. More negative $\delta^{18}\text{O}$ values indicate a greater water dependence for *Kolpochoerus*. This pattern is also present in Turkana Basin Suidae (Harris and Cerling, 2002). There is little to no temporal change in Suidae diet between intervals IIA and IIB. There are no values from modern Suidae from Tanzania to compare the Bed II data to.

4.1.2. *Perissodactyls*

Olduvai Equidae were primarily C_4 grazers based on tooth wear and carbon isotope results, all of which comes from large sample sizes (Tables 4 and S3). Mean Equidae mesowear scores range between 4.0 to 5.2, values associated with extant grazers (Figure 7 and Table 4). Microwear results suggest grass-dominated mixed feeding to grazing (Figure 8B). Carbon isotope from bulk and serial sampling indicate primarily C_4 -dominated diets (median = 90 % C_4 ,

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4 range: 47 to 100 %) with seasonal mixed diets (Figures 3, 4 and 6). The minor amounts of C₃
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6 vegetation in their diets may have included some C₃ grasses, although the microwear data
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8 suggests minor browsing (Figure 8B). Modern equids (zebra) from Tanzania have similar δ¹³C
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10 values to Bed II Equidae, whereas modern δ¹⁸O values are about 3 ‰ more positive than Bed II
11
12 values (Figure 4).
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16 We find clear evidence for niche-partitioning between the two Equidae from Bed II. *E.*
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18 *oldowayensis*, the most abundant taxon in the Bed II fossil record, had a mixed to C₄-dominated
19
20 diet that likely included occasional browse, whereas *Eu. cornelianus* had a diet comprised almost
21
22 entirely of C₄-grasses. This is supported by all three proxies: The smaller species, *Eu.*
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24 *cornelianus*, has a higher average mesowear score (5.16; N=6) than *E. oldowayensis* (4.51;
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26 N=53). Carbon isotope ratios of *Eu. cornelianus* are consistently more positive and have a
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28 smaller range of values than those of *E. oldowayensis* (Figure S3C). Finally, microwear results
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30 show higher number of higher scratches for *Eu. cornelianus* (NS=19.8; N=12) than for *Equus*
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32 (NS=17.6 N=50), indicating a higher intake of grass in the former taxon. *Eu. cornelianus* shows
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34 a smaller range in NS values (17.5-23) than *E. oldowayensis* (10.5-25), suggesting a more
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36 variable diet for the latter, although sample size is smaller for *E. oldowayensis*.
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44 Bed II Rhinocerotidae have diets similar to the two extant species, one with a C₃- and the
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46 other with a C₄-dominated diet. Interval IIA specimens have a narrow range of carbon values
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48 indicative of C₄ diets and IIB is represented with one C₃ feeder and one C₄ feeder. Microwear
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50 data from three teeth in IIA are in excellent agreement with the isotope data.
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54 55 56 4.1.3. *Proboscideans* 57

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59 Isotope data from a single *Elephas* molar suggest a C₄-dominated diet while microwear data
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61 indicate a mixed diet (Figures 3 and 8B). With only a single sample, it is difficult to make strong
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4 dietary interpretations, but the reconstructed diet is similar to that of *Elephas* of similar age (1.9
5
6 to 1.55 Ma) from the Turkana Basin, where carbon isotopes (median = -0.2‰) indicate C_4 -
7
8 dominated diets (Cerling et al., 2015). The fossil evidence shows *Elephas* was rare at Olduvai
9
10 (Bibi et al, this volume; (Leakey, 1971). This is intriguing for several reasons. First, C_4
11
12 vegetation and open habitats preferred by *Elephas* were abundant. Second, although Middle Bed
13
14 II exhibits a top-heavy faunal structure (Bibi et al., this volume) relative to the modern Serengeti
15
16 fauna, it seems mega herbivores ($>1,000$ kg) like *Elephas* were much rarer than the macro
17
18 herbivores (100 to 1,000 kg), most of which were grazing Bovidae or Equidae. This could be
19
20 the result of the larger bones of mega herbivores being differentially preserved in the Olduvai
21
22 fossil assemblages due to their lower potential for burial and fossilization (Behrensmeyer and
23
24 Boaz, 1980). However, it must also be considered that the majority of the assemblages analyzed
25
26 here were likely accumulated, at least in part, by hominins. HWK EE and MNK T5 show
27
28 evidence of hominins butchering the bones of Proboscideans, but few skeletal parts of these
29
30 animals are represented at the sites, suggesting some of the fossils that are present in the
31
32 collections were selectively transported from an off-site location where they were likely
33
34 scavenged by hominins (see Pante et al., this volume). The carcasses of macro herbivores are
35
36 more evenly represented and were likely acquired by hominins more often than those of mega
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38 herbivores based on their relative dominance in the collections.
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50 4.1.4. *Primates*

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52 This is the first study to our knowledge to combine microwear ($N = 3$) and stable isotope
53
54 ($N=4$) data from *Theropithecus oswaldi*, and the first isotope and tooth wear data reported from
55
56 Olduvai for this species. Carbon isotope data (median = 0.0‰) indicate a diet of 81% C_4
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58 vegetation, equivalent to the diet of *Paranthropus boisei* from Bed I (van der Merwe et al.,
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4 2008). The microwear data fall within the range of the extant *Theropithecus gelada*, which has
5
6 grass dominated diets (Figure 9). Thus, there is strong consistency from the isotope and tooth
7
8 wear approaches that support C₄ grazing by *T. oswaldi*.
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11 The median $\delta^{13}\text{C}$ value of *T. oswaldi* from Olduvai is 1.0 ‰ more positive than that from
12
13 coeval *T. oswaldi* (median = -1.0 ‰; N = 24) reported from the Turkana Basin from 1.95 to 1.5
14
15 by Cerling et al. (2013). The median $\delta^{18}\text{O}$ values of *T. oswaldi* from the two regions are
16
17 indistinguishable; Bed II is + 1.2 ‰ and Turkana is + 1.1 ‰.
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23 24 **4.2. Paleoenvironmental reconstruction**

25 26 *4.2.1. Vegetation*

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28 We infer a preponderance of C₄ grass on the landscape during the accumulation of Bed II
29
30 sediments based on dietary reconstructions from isotope (N = 141), mesowear (N = 156), and
31
32 microwear (N = 228) analyses of fossil teeth. The data show no evidence for significant
33
34 vegetation change across the Oldowan-Acheulean transition. This view of abundant C₄
35
36 vegetation is consistent with carbon isotope based vegetation reconstructions from lower Bed II
37
38 and Lemuta soil carbonates (Cerling and Hay, 1986; Sikes, 1994). The soil carbonate $\delta^{13}\text{C}$
39
40 values range from -6.8 to -0.6 ‰ with a median of -4.2 ‰. We convert the soil carbonate $\delta^{13}\text{C}$
41
42 values to fraction woody cover (f_{wc}), a more tangible representation of vegetation, following the
43
44 equation developed by Cerling et al. (2011). The f_{wc} from lower Bed II and the Lemuta Beds
45
46 range from 0.42 to 0.03 with a median value of 0.22, where values >0.4 represent bushland or
47
48 shrub land vegetation classifications (N = 1 at Bed II), values from 0.4 to 0.1 represent wooded
49
50 grasslands (N = 14), and f_{wc} values < 0.1 represent grasslands (N = 3). None of the data indicate
51
52 forested or closed canopy conditions (≥ 0.8). The majority of the soil carbonate data fall within
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54 the wooded grassland vegetation classification. A wooded grassland, with heterogeneous
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4 pockets of more and less dense areas of woody cover, fits well with the overall proportion of
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6 grazing mammals recovered from Bed II deposits (Bibi et al. this volume) and from our tooth
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8 wear and isotope data.
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11 In addition to soil carbonate data, carbon isotopes from *n*-alkanes (terrestrial plant waxes)
12
13 have been used to reconstruct vegetation from slightly older (1.9 to 1.8 Ma) Bed I sediments
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15 (Magill et al., 2013a). Plant wax data show precessionally driven vegetation changes that range
16
17 from forest to grassland over the ~100 kyr interval. The Bed I plant wax record suggests there
18
19 were periods with more woody C₃ vegetation (high f_{wc}) on the landscape, especially during
20
21 middle Bed I to lowermost Upper Bed I times, around 1.85 to 1.83 Ma, where *n*-alkanes values
22
23 are 3 to 4 ‰ more negative than other “wet” cycles in the plant wax records. Faunal records
24
25 show a temporary shift towards more humid or wooded conditions during middle Bed I times
26
27 based on an increase in Reduncini and Tragelaphini, taxa associated with humid and wooded
28
29 environments, respectively ((Kappelman, 1984);Figure 9B and C in Bibi et al., this volume).
30
31 Both lines of evidence point to greater water availability and woody vegetation in middle Bed I
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33 compared to Bed II. Bed II faunal distributions (Bibi et al., this volume; Prassack et al., this
34
35 volume), dietary reconstructions presented here and in Rivals et al. (this volume), and previously
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37 published soil carbonate data do not support the presence of widespread, dense woody cover at
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39 any period studied in Bed II.
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48 Paleovegetation in Upper Bed I and Bed II has also been reconstructed from plant remains.
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50 Aside from an early study using pollen (Bonnefille, 1984), most work has focused on the use of
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52 phytoliths (e.g., Albert et al., 2015a; Albert et al., 2009; Barboni et al., 2010) and plant
53
54 macrofossils (Bamford, 2012; Bamford et al., 2006; Bamford et al., 2008; Habermann et al.,
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56 2016b). There is good agreement between the vegetation reconstructions derived from
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58 phytoliths and the tooth wear and enamel isotope data presented from intervals IIA and IIB.
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4 New phytolith assemblages from HWK EE trenches include abundant short rondels produced
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6 by Poaceae (grasses) in nearly all samples. In some samples, elongate and spheroid morphotypes
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8 belonging to the Arecaceae (palms) dominate (de la Torre et al., this volume; New excavations at
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10 HWK EE). Assemblages from Lower Bed II, including the Lemuta member, also include grass
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12 and palm morphotypes, with the latter being more abundant in the Lemuta sandstone. Some
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14 Lemuta samples also yielded short saddle forms ascribed to the C₄ Chloridoideae subfamily of
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16 grasses, as well as bulliform and trichome morphotypes associated with grasses (de la Torre et
17
18 al., this volume; New excavations at HWK EE). The Lemuta sandstones also contains minor
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20 sedge and dicot morphotypes. The most abundant morphotype in the Lower Augitic Sands are
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22 short rondels associated with grasses. There are also abundant dicot morphotypes and some
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24 palms (de la Torre et al., this volume). As with other phytolith studies from Olduvai, there is
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26 high lateral variability among samples.
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33 An incongruous result between the HWK EE phytolith and tooth data is the high abundance
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35 of palm, wood or bark phytoliths, but a relative paucity of C₃ browsing taxa (*Giraffa*,
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37 *Deinotherium*, and ?*Diceros*) that would feed on this woody vegetation (Bibi et al, this volume).
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39 Several studies by Albert, Bamford and colleagues shed light on phytolith production,
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41 preservation, and interpretations. Bamford et al. (2006) found that Serengeti palms (e.g.,
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43 *Hyphaene* and *Phoenix*) produce high numbers of phytoliths, which may result in over
44
45 representation in the fossil record. Palm phytoliths may also be more robust and preserve better
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47 than others, such that a temporal component (rather than just abundance) should be considered
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49 when interpreting phytolith data from ancient sediments (Albert et al., 2015b). Wood and bark
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51 phytoliths are overrepresented in modern soils (Albert et al., 2006). The production and
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53 preservation biases identified in these plant types demonstrate that while their phytoliths'
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4 presence in ancient sediments confirms their presence on the landscape, phytolith abundances
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6 should not be taken at face value to reflect plant abundances in the past (Albert et al., 2006).
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10 11 4.2.2. *Hydroclimate* 12 13

14 Hydroclimate change across the Oldowan-Acheulean transition can be assessed through the bulk
15
16 and the intratooth isotope profile $\delta^{18}\text{O}$ values (Figures 3 and 6). The Mann-Whitney U-test
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18 indicates no significant differences in $\delta^{18}\text{O}$ distributions between intervals IIA and IIB (Table 3).
19
20 However, the maximum and minimum $\delta^{18}\text{O}$ values also decrease between intervals IIA and IIB
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22 by 1.4 and 0.5 ‰. Thus, the oxygen isotope data from bulk sampling of tooth enamel shows no
23
24 evidence of significant change between intervals IIA and IIB.
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28 Previously published $\delta^{18}\text{O}$ data from pedogenic carbonates cannot be split into intervals
29
30 IIA and IIB due to lack of stratigraphic resolution so the data from each interval cannot be
31
32 directly compared. Overall the data show an increase in $\delta^{18}\text{O}$ values in the Lemuta Member with
33
34 respect to Bed I and the lowermost Bed II (Cerling and Hay, 1986; Sikes, 1994). The overall
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36 trend towards more positive $\delta^{18}\text{O}$ values, indicative of increased aridity, continues in Upper Bed
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38 II through Bed IV and into the Masek and Ndutu Formations.
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43 The intratooth isotope profiles from *E. oldowayensis* molars are limited in number, so the
44
45 interpretation of seasonality we draw could change with additional data. Both carbon and
46
47 oxygen isotopes show greater variation in interval IIA than in IIB (Figure 6). It can therefore be
48
49 concluded that seasonality of vegetation and rainfall was likely reduced in the IIB interval
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51 compared to the IIA interval.
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5. Conclusions

Stable isotope and tooth wear analyses of Bed II fauna reveal most large herbivores had C₄-dominated diet, which were likely comprised of grasses based on microwear and phytolith results (de la Torre et al., this volume). Taken together the 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, *Sivatherium maurusium* *Hippopotamus gorgops*, *Kolpochoerus*, *Metridiochoerus*, *Ceratotherium cf. simum*, *Elephas*, and *Theropithecus oswaldi*, were all C₄ grazers or mixed-grazers. The Antilopini cf. *Antidorcas recki* and the Tragelaphini were the only true mixed diet feeders. A limited number of taxa that included *Giraffa stillei*, a Rhinocerotidae (?*Diceros*), and Deinotheriidae had C₃-dominated diets. Hyaenidae prey consisted mostly of grazers and mixed feeders. Combined with the phytolith and large mammal faunal distributions (de la Torre et al., this volume; Bibi et al., this volume), the evidence suggests the abundant C₄ vegetation that was able to support a large and taxonomically diverse guild of grazers and mixed feeders. Yet there was also enough C₃ vegetation, probably associated with wetlands and streams, to support 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, bulk isotope, and intratooth isotope profiles. However, the limited data from three Equidae intratooth profiles suggest decreased seasonality in vegetation and precipitation between intervals IIA and IIB. Thus, it appears local climate and vegetation change did not play a significant role in the advent of Acheulean technology at Olduvai. Future work will be directed at building isotopic records from Bed I and Lowermost Bed II, and integrating these with existing data from this study and from Van der Merwe (2013) to evaluate possible ecosystem change prior to the Oldowan-Acheulean transition.

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4 This study demonstrates that a combined approach of stable isotope and tooth wear
5 analyses can yield more detailed and robust dietary reconstructions than a single method alone.
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7 This is most evident for taxa where there are large samples, such as for the Alcelaphini and
8
9 Equidae, which were determined to be predominantly C₄ grazers, with occasional mixed C₃-C₄
10 feeding. It can also help resolve inconsistencies in dietary reconstructions, such for the
11 Reduncini, which yield strong C₄ and grazing signals from the isotopes and mesowear but plot as
12 browsers according to mesowear. Some of the inconsistencies may be highlighting actual dietary
13 breadth (e.g., perhaps seasonal) not detected by the application of a single method alone.
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26
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36 Doherty Earth Observatory contribution #8XXX.
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48 **Figures**

49
50
51 Figure 1. A) Map of Olduvai Gorge with the Bed II sites from which fossil teeth analyzed in this
52 study come from. Interval IIA teeth (~1.7 Ma) are from the HWK EE, FLK West, and MNK
53 Skull sites; Interval IIB (~1.66 Ma) teeth are from the HWK EE, HWK E-Tembo, FC West, FC
54 East, and MNK Main sites; Interval Above IIC includes teeth from the FLK West and EF-HR
55 sites. B) A simplified stratigraphic framework based on Hay (1976) and Stanistreet et al. (this
56 volume), following the proposal to use the top of Lemuta to separate Lower Bed II from Middle
57 Bed II (see Stanistreet et al, this volume). Intervals defined in this study are shown in colored
58 boxes. Sampled sites are listed by interval. Tuffs are marked in orange and their ages are from
59 Curtis and Hay (1972), Deino (2012), and Dominguez-Rodrigo et al. (2013). *Approximate age
60 of Bird Print Tuff (BPT) is derived from dating of a tuff denominated FLKWb by Diez-Martin et
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4 al. (2015), which Uribelarrea et al. (in press) place at ~25cm below the level of the BPT nearby.
5 [color, double column]
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8 Figure 2. Cross plot of tooth enamel carbon and oxygen isotopes from the two main Bed II
9 intervals, A) Interval IIB (1.66 Ma) and B) Interval IIA (~1.7 Ma). Shaded regions indicate C₃-
10 dominated (green, online color version), mixed C₃-C₄ (yellow), and C₄-dominated (orange) diets
11 based on $\delta^{13}\text{C}$ values. Data are plotted at the family level except for bovids, which are plotted by
12 tribe. For giraffids, the *Giraffa* sp. has a C₃-dominated diet and *Sivatherium* sp. a C₄-dominated
13 diet. [color, single column]
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17 Figure 3. Carbon and oxygen isotope data from the two main Bed II intervals and modern taxa
18 from Tanzania (Van der Merwe, 2013). In all three intervals, mammals with C₄-dominated diets
19 are most common with the number of mammals with mixed C₃-C₄ and C₃-dominated diets
20 varying between intervals. Modern $\delta^{18}\text{O}$ values show the broadest range and have a median
21 value that is ~2 ‰ enriched with respect to Bed II median values (Table 2). Interval IIB includes
22 all Hippopotamidae data (N=16), whereas for statistical analyses whereas for statistical analyses
23 only the minimum, maximum and median values are used. [color, single column]
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26
27 Figure 4. Tooth enamel carbon and oxygen isotope box plots by intervals (IIA, IIB, and
28 modern). The vertical gray line in a box is the median, the box ends are the 1st and 3rd quartiles,
29 and lines (whiskers) define the range of data except for outliers. Taxa are divided by the
30 family level or where possible, by genera. In the *Giraffa/Sivatherium* panel, *Giraffa* is in white
31 and *Sivatherium* is in gray. [color, double column]
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35 Figure 5. Tooth enamel carbon and oxygen isotope box plots for Bed II and modern bovid
36 tribes. All Bovidae data are plotted in the uppermost panel for reference. [color, double column]
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40 Figure 6. Intratooth *Equus oldowayensis* isotope profiles from interval IIB (MNK Main L1-48
41 and FC West L62-104; panels A-D) and interval IIA (HWK EE L10-523; panels E & F). Open
42 circles are measured data (smoothed with a 3 pt. weighted mean; see text for details), the thick
43 line is the mean of 100 inverse model solutions for the estimated input signal (i.e., diet or body
44 water), and the shaded area is $\pm 2 \sigma$ of the solutions. The IIA interval profile exhibits greater
45 variability than the two profiles from the IIB interval. [color, double column]
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48 Figure 7. Mesowear scores for the taxa from Bed II intervals IIA and IIB. Sample size is given in
49 parenthesis for each taxon. The data from modern browsers, mixed feeders and grazers are taken
50 from Fortelius and Solounias (2000). [color, double column]
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53 Figure 8. Bivariate plot of the average numbers of pits and scratches for the Bovidae (A) and the
54 other taxa (B). Bars correspond to standard deviations for the fossil samples. Grey areas
55 correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the modern leaf
56 browsers and grazers based on Solounias and Semprebon (2002) and Rivals et al. (2010).
57 [color, single column]
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60 Figure 9. Bivariate plot of the average numbers of pits and scratches for primates (modified from
61 Godfrey et al. 2004) with the three *Theropithecus oswaldi* specimens from Olduvai Bed II
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4 intervals IIA and IIB plotted as red stars. *T. oswaldi* plots among extant primates feeding on
5 grass. [color, single column]
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9 Figure S1. Bar graphs (A, B) and cross plots (C, D) of relative taxonomic abundances of isotope
10 vs. NISP data sets for interval IIA and IIB.
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12 Figure S2. Cross plot of tooth enamel carbon and oxygen isotopes from all sites investigated in
13 this study: A) FLK West, B) EF- HR, C) FC East and West, D) MNK, and E) HWK EE. Shaded
14 regions indicate C₃-dominated (green, online color version), mixed C₃-C₄ (yellow), and C₄-
15 dominated (orange) diets based on $\delta^{13}\text{C}$ values. Data are plotted at the family level except for
16 bovids, which are plotted by tribe.
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20 Figure S3. Histograms of A) $\delta^{13}\text{C}$ and B) $\delta^{18}\text{O}$ for three forms of Alcelaphini (*Megalotragus*
21 *issaci*, Alcelaphini small sp., and Alcelaphini sp. indet) from Bed II. Neither isotope shows
22 niche partitioning among the Alcelaphini. Panels C) and D) show $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for the two
23 Equidae species in Bed II, *Equus oldowayensis* and *Eurygnathohippus cornelianus*. The latter
24 tend to have more positive $\delta^{13}\text{C}$ values that indicate a greater proportion of C₄ vegetation in their
25 diet although sample size is small (N=5). There is no difference in $\delta^{18}\text{O}$ values.
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30 Tables

31 Table 1. Number of teeth analyzed for carbon and oxygen isotope ratios by mammalian family
32 from intervals IIA, IIB, and above IIC. Bovidae are further specified to tribe.
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35 Table 2. Summary statistics of carbon and oxygen stable isotope data for modern and Bed II
36 taxa. Bed II taxa are divided into the intervals IIA, IIB, and above IIC. Interval IIB does not
37 include all Hippopotamidae as they are overrepresented. Modern enamel $\delta^{13}\text{C}$ values are
38 corrected by +1.5 ‰ for recent changes to the $\delta^{13}\text{C}$ value of the atmosphere.
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40

41 Table 3. Mann-Whitney U test results comparing carbon and oxygen isotope distributions
42 between the two main intervals (IIA and IIB) and modern Tanzanian taxa from Van der Merwe
43 (2013). Significant differences in oxygen isotope distributions ($p < 0.05$) are in bold.
44 Hippopotamidae (N=16) are over represented in the IIB interval so their values were removed
45 and replaced with the maximum, mean, and median values to represent the group.
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48 Table 4. Summary of mesowear and microwear data for the fossil assemblages from Olduvai
49 Bed II intervals IIA and IIB. Abbreviations: N = Number of specimens; MWS = Mesowear
50 score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of
51 specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width
52 score; %XS = Percentage of specimens with cross scratches; %HC= Percentage of specimens
53 with hypercoarse scratches; %PP = Percentage of specimens with puncture pits; SD = standard
54 deviation.
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58 Table S1. Calculated $\delta^{13}\text{C}$ values for C₃ and C₄ plants and for tooth enamel based on average
59 C₃ plant and C₄ plant diets. The values are based on estimated $\delta^{13}\text{C}$ values of atmospheric
60 CO₂ ($\delta^{13}\text{C}_{\text{atm}}$) during Bed II and modern times. The Bed II $\delta^{13}\text{C}_{\text{atm}}$ value is calculated from
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4 the mean value from 1.8 to 1.6 Ma from the high resolution planktonic CO₂ δ¹³C record
5 compiled by Tipple et al (2010).
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8 Table S2. Number of specimens and relative abundances (percent) for stable isotope and NISP
9 data sets by interval. NISP values were taken from Bibi et al., this volume.
10

11 Table S3. Stable carbon and oxygen isotope information for all samples analyzed in this study.
12 Other data includes taxonomic information, sample location, %C₄ ($\pm 1 \sigma$) in diet, stratigraphic
13 interval (i.e., IIA), and element sampled.
14

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16 Table S4. Descriptive statistics for stable isotopes and %C₄ in diet for samples from the primary
17 sample sites of HWKEE, FC East and West, and MNK.
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20 Table S5. Mann-Whitney U test results comparing stable isotope values from the primary sample
21 sites of HWKEE, FC East and West, and MNK. None of the comparisons yield significant
22 values.
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25 Table S6. Intratooth stable isotope and estimated %C₄ ($\pm 1 \sigma$) data for Equidae molar profiles.
26 Smoothed data (3 pt., weighted 0.25/0.50/0.25) and inverse model results (estimated input
27 signal) are given with 2 σ uncertainty. Sample locations are given as distance from the occlusal
28 surface. Summary statistics are provided for each intratooth profile. Estimated input signal was
29 calculated using Matlab code modified from "mSolve_1.m" published by Passey et al. (2005).
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33 Table S7. Inverse model error parameters and damping factor (e). The damping factor is
34 determined by matching the predicted error (E_{Pred}) to the measured error (E_{meas}). E_{meas} is slope
35 dependent and was calculated using published Matlab code ($E_{meas}_1.m$) from Passey et al.
36 (2005).
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39 Table S8. Raw tooth wear data. All mesowear and microwear data from Olduvai Bed II fossil
40 teeth analyzed in this study along with taxonomic, sample, and location data. MWS= Mesowear
41 Score (0-6); NP= number of pits; NS = number of scratches, LP= large pits; G= gauges; SWS =
42 scratch width score; XS= cross scratches; PP= puncture pit; HC= hyper coarse scratches.
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Table 1.

Family	Tuff IIA	Tuff IIB	Above Tuff IIC
Bovidae			
Alcelaphini	17	16	--
Antilopini	7	--	1
/Aepycerotini			
Bovini	1	--	--
Hippotragini	4	2	--
Reduncini	3	1	--
Tragelaphini	2	4	--
Indet.	2	--	--
Cercopithecidae	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

Table 2.

Interval	N	%C4			$\delta^{13}\text{C}$				$\delta^{18}\text{O}$			
		median	max	min	median	max	min	range	median	max	min	range
Modern	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	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

Table 3

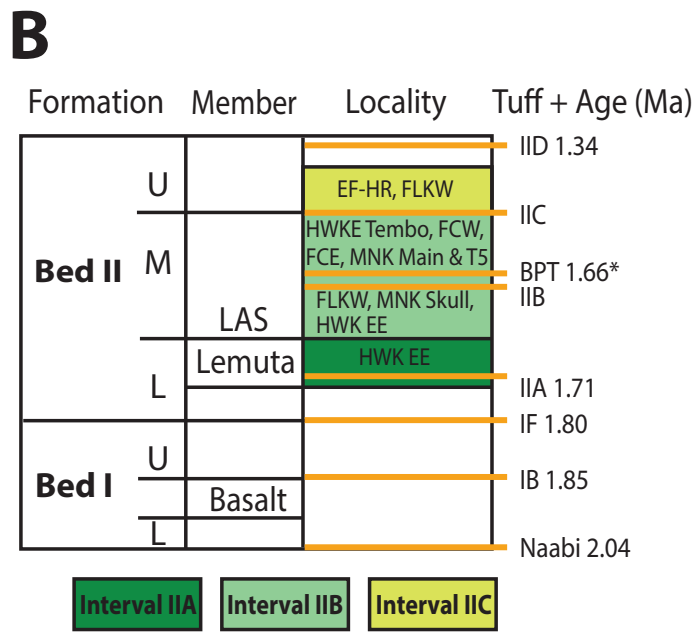
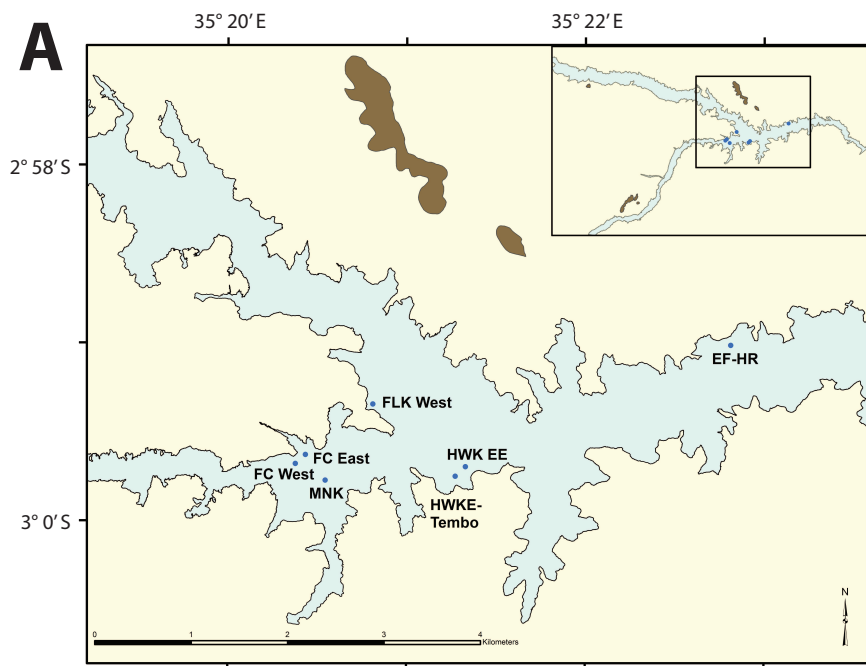
	Intervals IIA and IIB	Interval IIB and Modern	Interval IIA and Modern
All taxa			
Carbon <i>p</i> -value	0.5557	0.6201	0.9613
Oxygen <i>p</i> -value	0.4607	0.0001	0.0015
N	63/59	59/72	63/72
Alcelaphini			
Carbon <i>p</i> -value	0.8451	—	—
Oxygen <i>p</i> -value	0.0445	—	—
N	17/16	—	—
Equidae			
Carbon <i>p</i> -value	0.1754	—	—
Oxygen <i>p</i> -value	0.3312	—	—
N	9/11	—	—

Table 4.

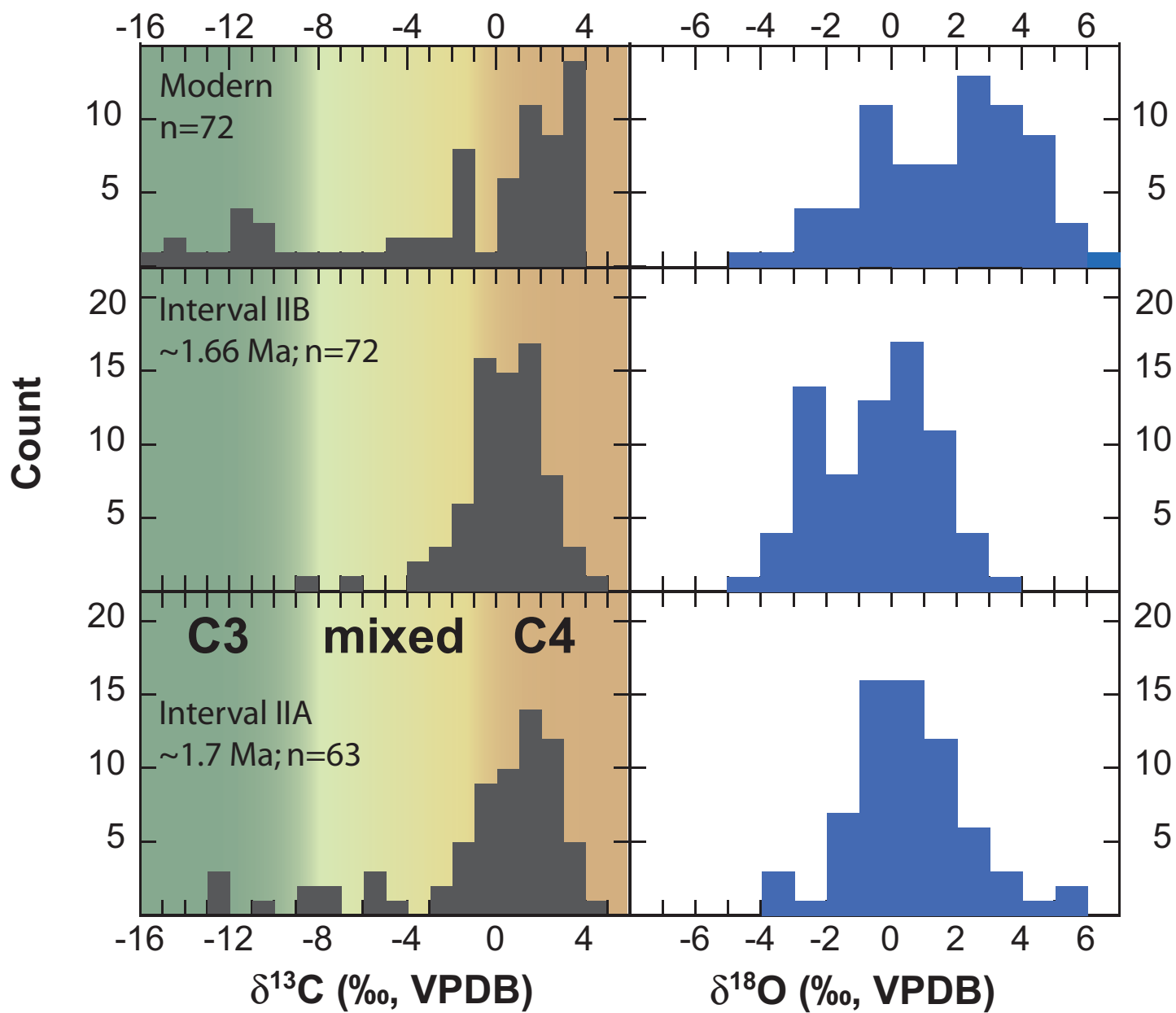
Stratigraphy	Taxa	MESOWEAR			MICROWEAR										
		N	MWS	SD	N	NP	SD (NP)	NS	SD (NS)	%LP	%G	SWS	%XS	%PP	%HC
Interval IIA	Antilopini	13	2.00	1.53	11	22.41	8.43	16.50	5.94	27.27	18.18	1.0	0.00	0.00	0.00
	Bovini	1	1.00		2	17.75		13.75		0.00	0.00	1.0	0.00	0.00	0.00
	Caprini				1	9.00		12.50		0.00	0.00	1.0	0.00	0.00	0.00
	Hippotragini		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
		4													
	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
		2	1.00		1					100.00	0.00		0.00	0.00	0.00
	Tragelaphini					33.00		10.50				1.0			
	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>	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		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		0.00	0.00	0.00
Intervals IIA+IIB	<i>Theropithecus oswaldi</i>				3	14.67		26.00		33.33	0.00	1.3	66.67	0.00	0.00

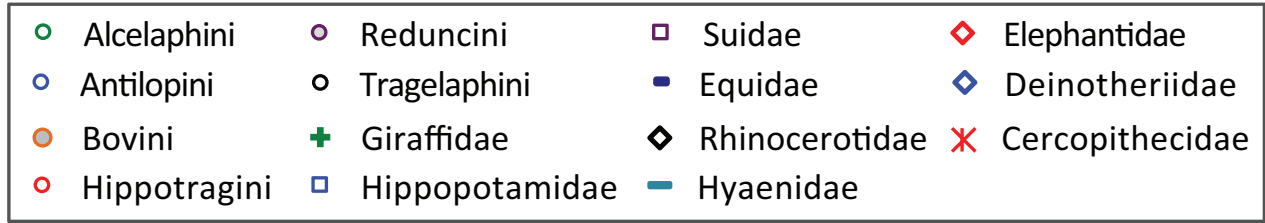
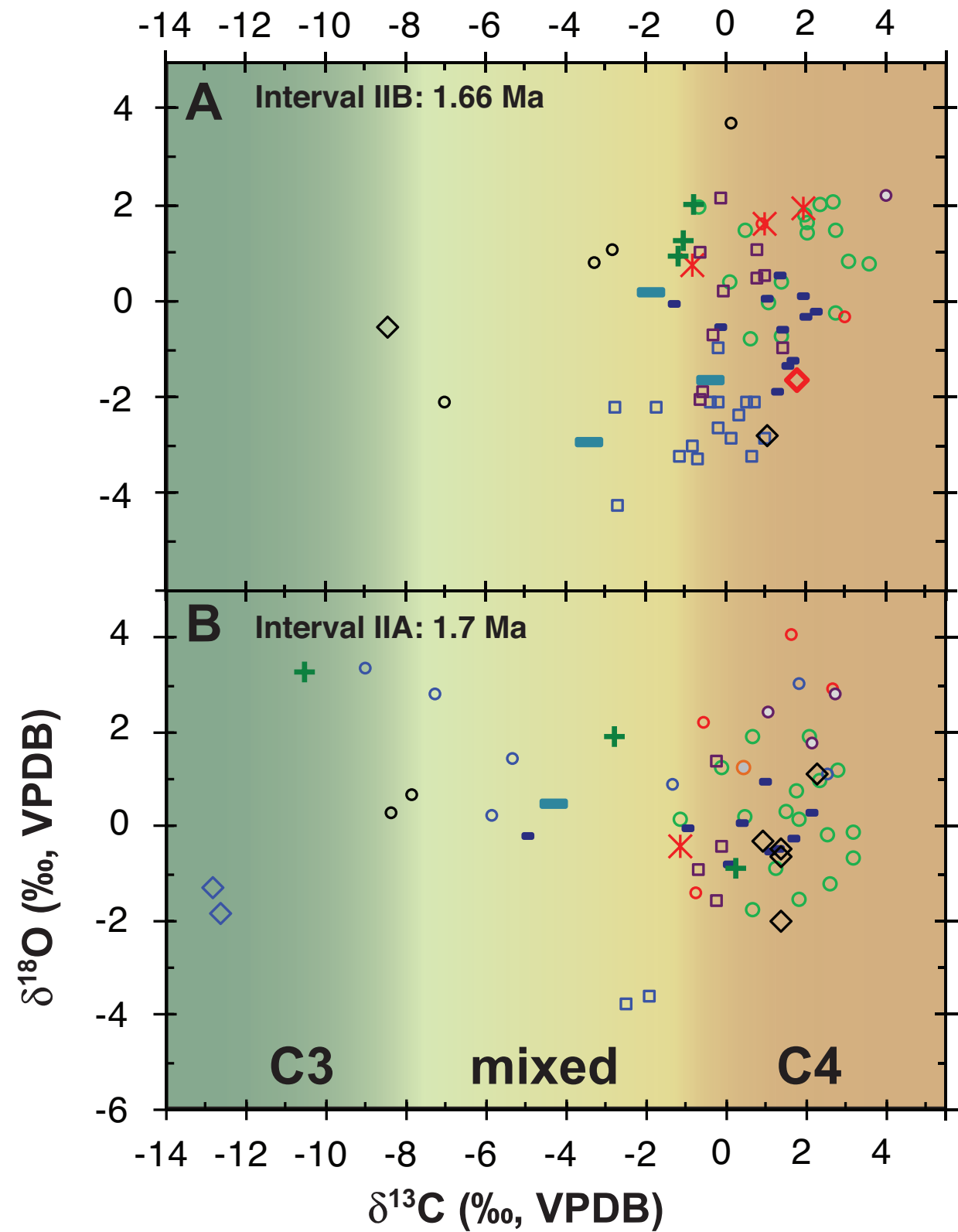
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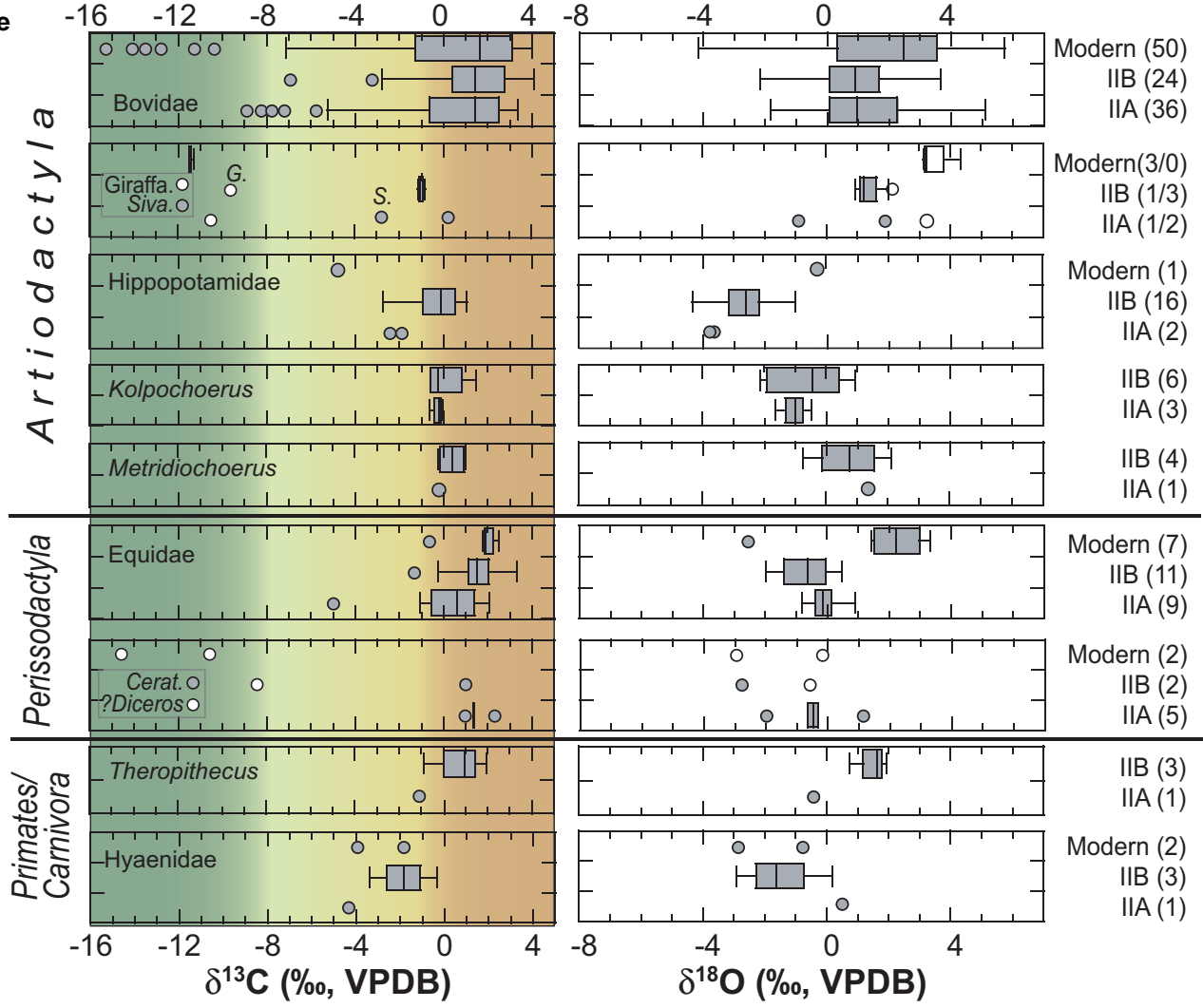
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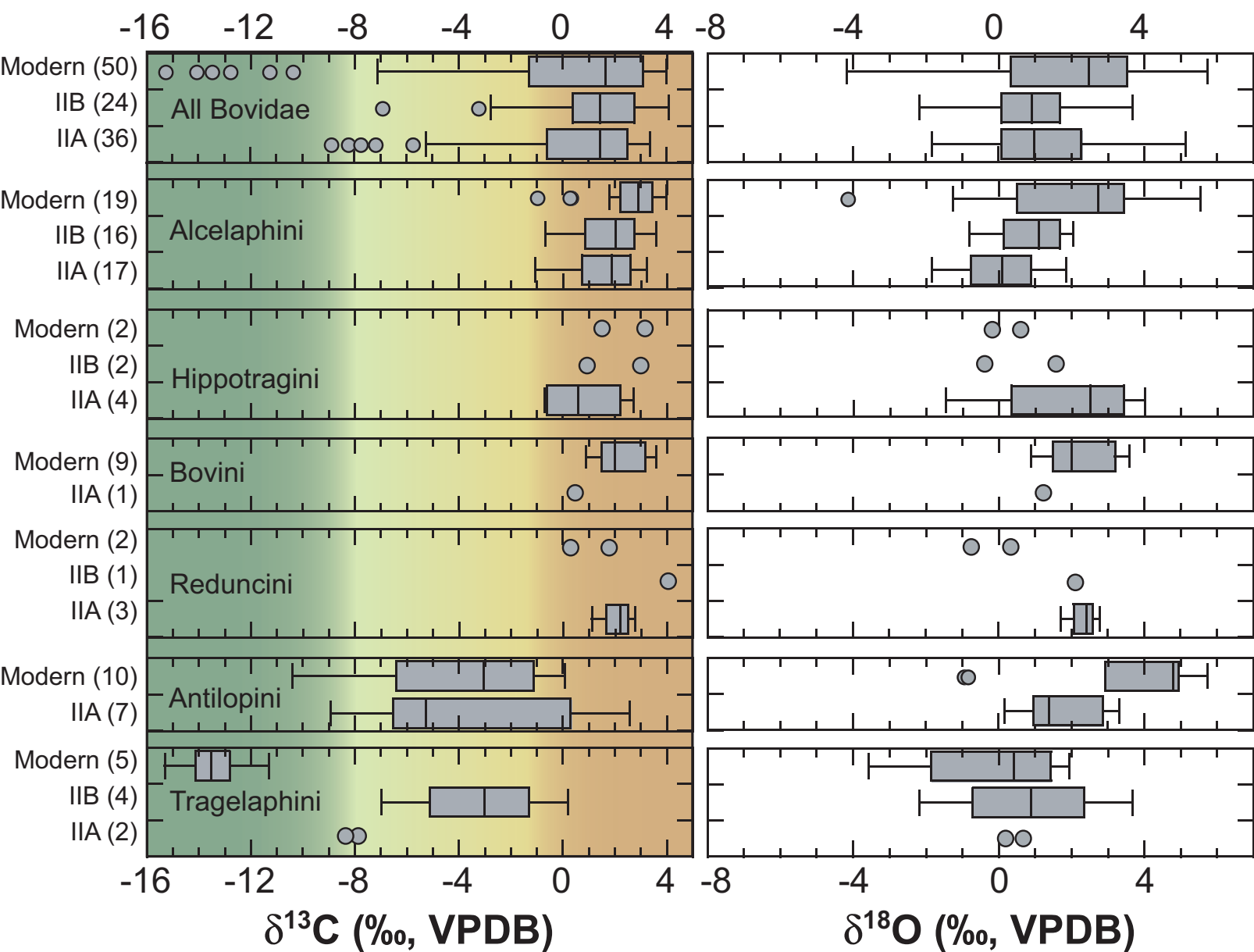
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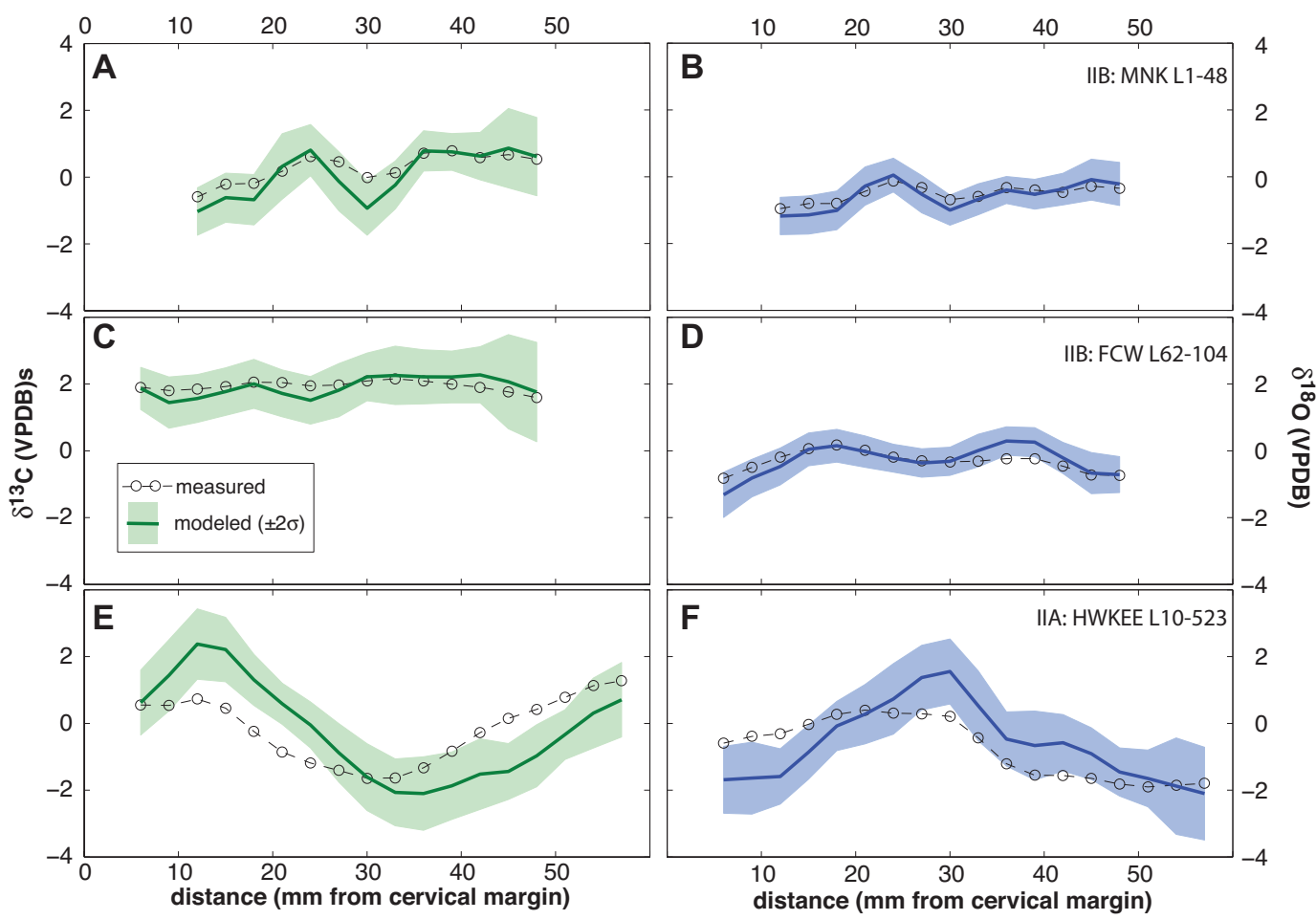
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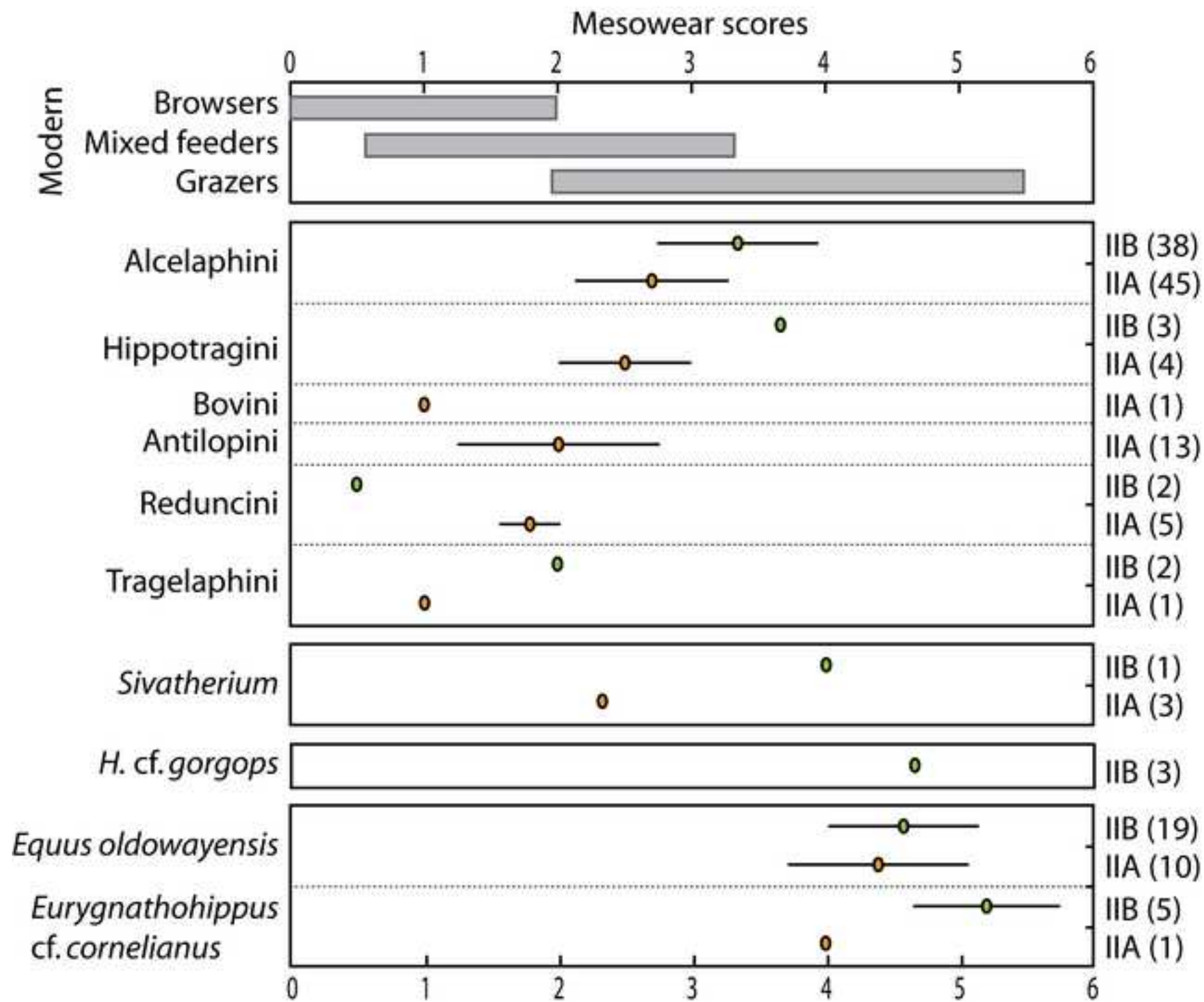
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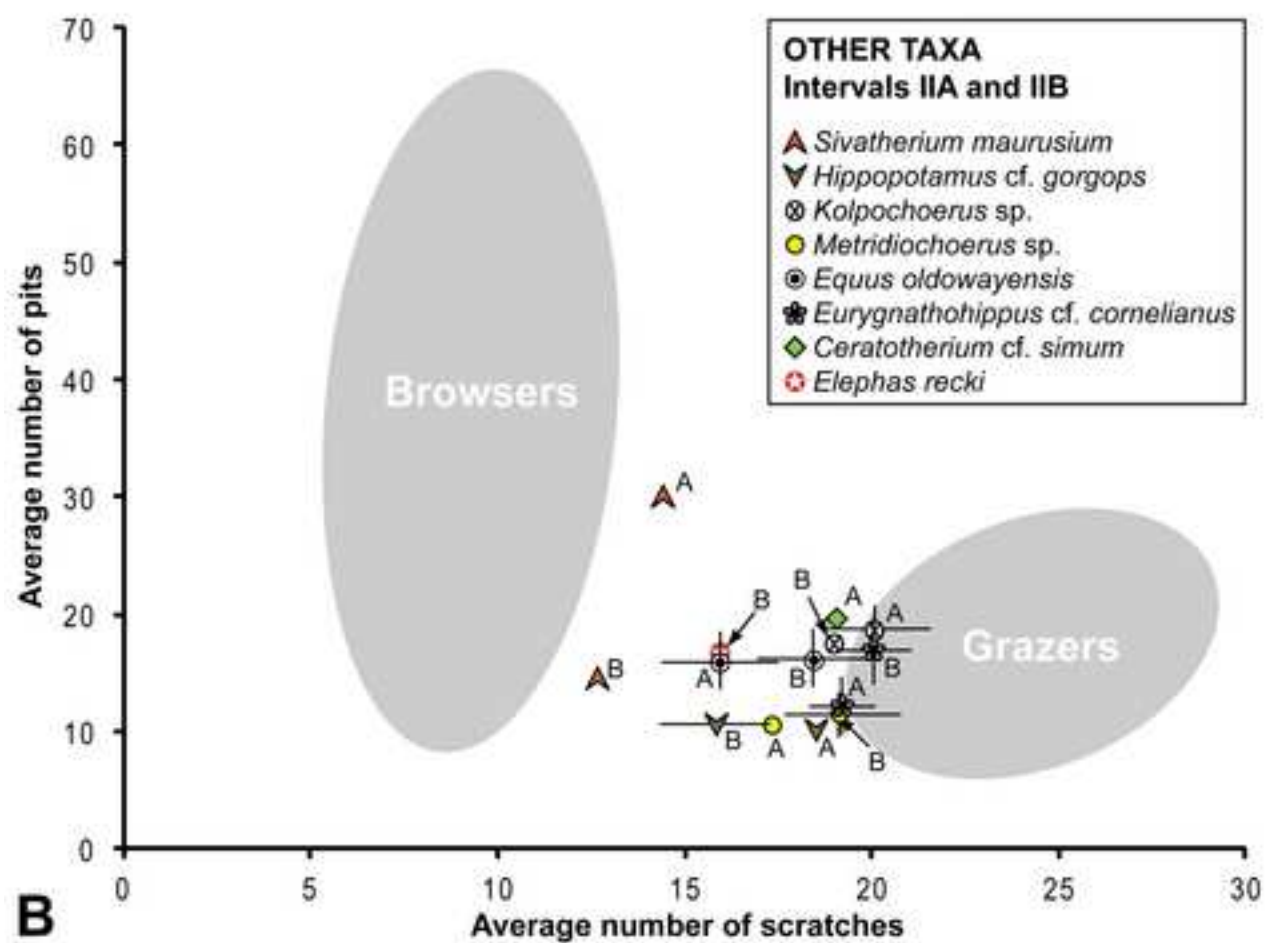
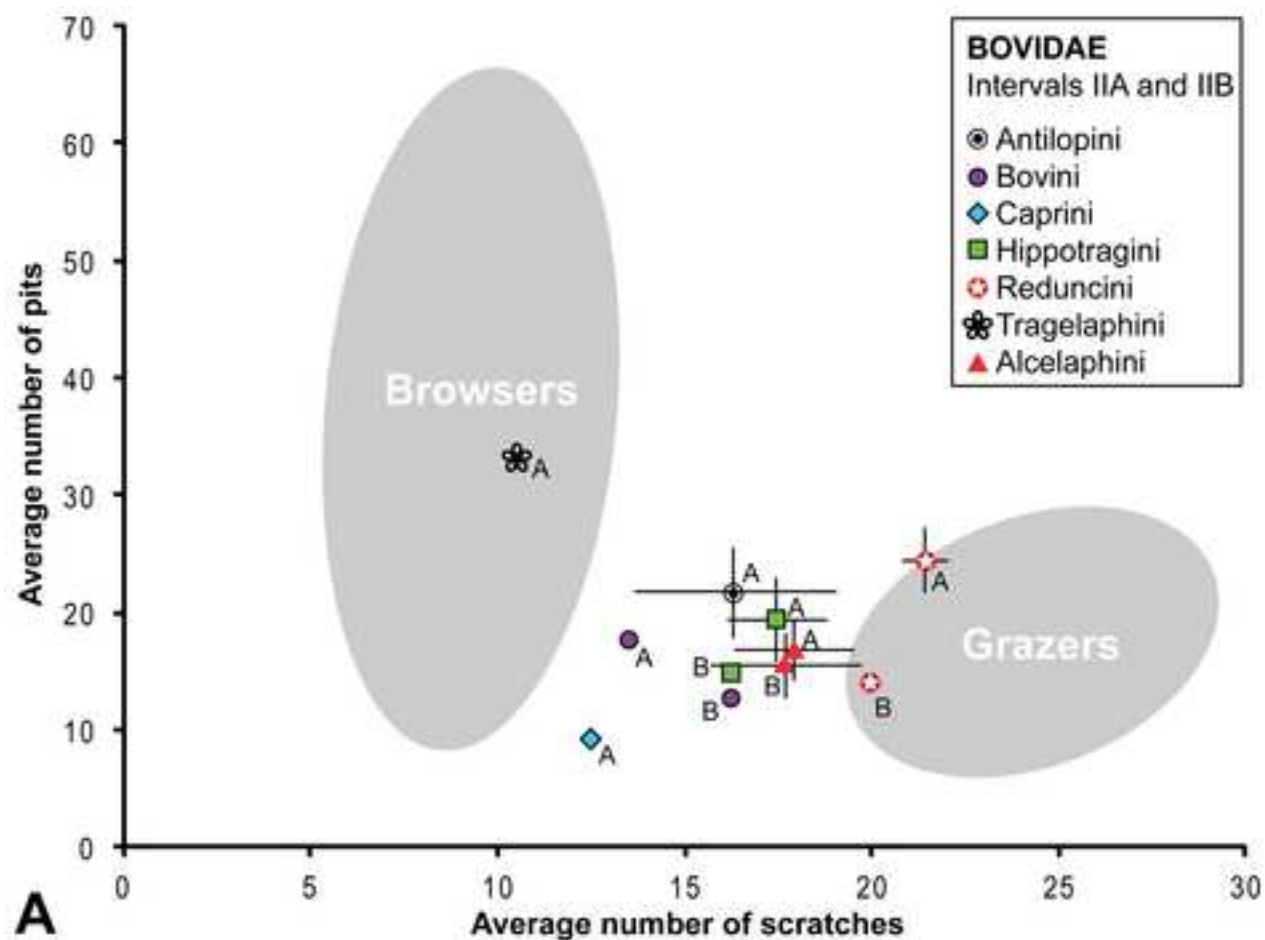
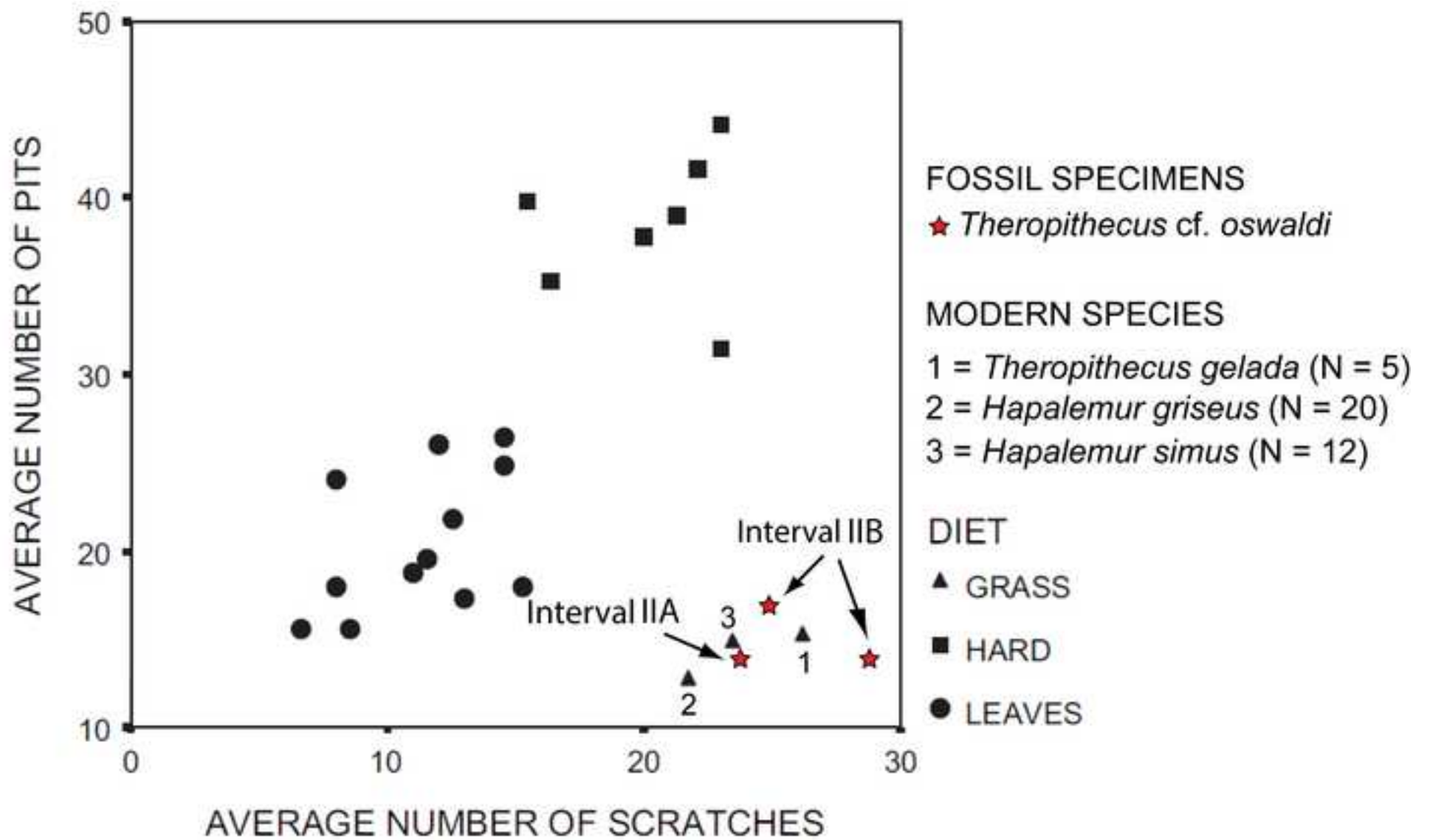


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