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# Dietary ecology of Reduncini (Bovidae) from the Shungura Formation, Lower Omo Valley, Ethiopia

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Abstract:

The Shungura Formation (Lower Omo Valley, Ethiopia) constitutes one of the most complete stratigraphic and paleontological records for the Plio-Pleistocene of eastern Africa and has yielded a large collection of fossil bovids, in which the most abundant tribe is Reduncini (waterbucks, kobs, and relatives). We used a multi-proxy approach to precisely reconstruct the diet and habitat preferences of Shungura reduncins to better understand of the environmental conditions that prevailed during the Plio-Pleistocene in the Lower Omo Valley. We compared the dental microwear texture analyses and the dental mesowear analyses for fossil samples dating to between 3 Ma and 1.7 Ma. We show that reduncins from the Shungura Formation had a diet dominated by browse at around 2.8 Ma, had diets ranging from browsing to mixed feeding from 2.8 Ma to 2.3 Ma, and consumed far more graze around 2.3 Ma and 1.8 Ma. Our study highlight the benefits of a multi-proxy approach to dietary reconstruction and how each dietary proxy can be leveraged to offer a slightly different, complementary perspectives on the ecology of fossil organisms.

Keywords: Africa, Bovidae, Dental mesowear, Dental microwear, Diet, Paleoenvironment, Plio-Pleistocene

#### 1 1. Introduction

2 The specialized dietary and habitat ecology of bovids (antelopes and kin) make them good 3 indicators of environmental change through time (Vrba, 1980, Spencer, 1997). Bovids are 4 common in Plio-Pleistocene fossil assemblages of Africa (Bobe et al., 2007) and especially so 5 in the Shungura Formation of the Lower Omo Valley, Ethiopia (Fig. 1A, B). The Shungura 6 Formation has yielded numerous hominin fossils (Arambourg and Coppens, 1967; Howell 7 and Coppens, 1976; Howell et al., 1987; Daver et al., 2018), stone tools (Bonnefille et al., 8 1970; Delagnes et al., 2011, Maurin et al., 2014), and a large collection of fossil bovids (42 % 9 of the large mammals), in which the most abundant tribe is Reduncini (Fig. 1C, Gentry, 1985, Bobe and Eck, 2001, Blondel et al., 2018). Extant reduncins are C4 grazing antelopes (Cerling 10 11 et al., 2003; Sponheimer et al., 2003) and are strongly water dependent. They live in savanna 12 habitats within the vicinity of water bodies, namely the valley wetlands and savanna 13 floodplains of sub-Saharan Africa (Estes, 1991; Kingdon, 2013). There are two extant African 14 genera, the large-bodied waterbuck and kobs (genus Kobus) and the smaller reedbucks (genus 15 Redunca).

16 Enamel stable carbon isotope data suggest that reduncins from the Shungura Formation 17 had a diet ranging from C<sub>3</sub>-C<sub>4</sub> mixed-feeding to C<sub>4</sub>-dominated between ~ 3-1 Ma (Negash et 18 al., 2015, 2020), whereas they had C<sub>4</sub>-dominated diets at most other Plio-Pleistocene sites of 19 eastern Africa (Bedaso et al., 2013; Wynn et al., 2016). However, isotopic ecology offers one 20 line of dietary evidence—reflecting only photosynthetic pathway—and we do not currently 21 know what types of plants Shungura reduncins fed on. Did they have a dietary behavior unlike that of their extant relatives, as Spencer (1997) suggested for Menelikia? Were they 22 23 consuming C<sub>4</sub> grasses as their extant relatives, or C<sub>4</sub> browse, as some dicotyledonous plants 24 (e.g., succulent Amarantacea) have a C<sub>4</sub> metabolic pathways? Indeed, it is possible they could 25 have been  $C_3$  grazers despite the fact that  $C_3$  grasses are today restricted to high altitudes (>

26 2000 m) in tropical environments. Answering these questions is necessary to better
27 understand evolution of reduncin dietary ecology and environmental conditions through time
28 in the Shungura Formation.

The objectives of this paper are two-fold. First, we aim to determine the feeding preferences of reduncins from the Shungura Formation. Second, we aim to use this information to make inferences about Lower Omo Valley environments from 2.9 Ma to 1.8 Ma, and to contextualize the Shungura record by drawing comparisons with broader patterns of environmental changes during the Plio-Pleistocene of eastern Africa.

34 For the first objective, we used two methods: dental microwear textural analyses (DMTA)

35 combined with dental mesowear analyses. Dental microwear provides a short-term dietary

36 signal of the physical properties (hardness, toughness, and abrasiveness) of the last food items

37 consumed by an individual (Teaford and Oyen, 1989, Teaford et al., 2017, Winkler et al.,

38 2020). DMTA based on the automated quantification of 3D surfaces (a scale-sensitive fractal

39 analysis or surface texture analysis using ISO parameters, see more details in Scott et al.,

40 2006; Schulz et al., 2013; Calandra & Merceron, 2016) is an effective way to discriminate

41 dietary differences between species (Scott, 2012; Winkler et al., 2013) and to detect variations

42 in diet as a seasonal signal of food preference or availability (Merceron et al., 2010; Berlioz et

43 al., 2017). Conversely, dental mesowear has been shown to be an effective way of

44 characterizing the long-term signal of feeding habits for ungulates (e.g., Fortelius and

45 Solounias 2000; Kaiser and Fortelius, 2003; Blondel et al., 2010; Rivals et al., 2018;

46 Ackermans, 2019; Sewell et al., 2019; Ackermans et al., 2020).

47 For the second objective, we combined our results with faunal data (Blondel et al., 2018;

48 Martin et al., 2018), previously published enamel stable carbon isotopic data (Negash et al.,

49 2015, 2020; Levin et al., 2011, Paquette and Drapeau, 2021), and paleovegetation data

50 (Bonnefille and Dechamps, 1983; Bonnefille, 2010) from the Shungura Formation. We also

compared the DMTA and dental mesowear results of Reduncini from the Shungura Formation
to those of Tragelaphini from the same sequence as published in Blondel et al. (2018).

53

54 2. Materials

55 2.1. Fossil data

56 Reduncini are the most abundant bovid tribe in members B, G, and H; they are common 57 but less abundant in members C, E, and F (Fig. 1C; Bobe and Eck 2001; Blondel et al., 2018). 58 Shungura fossil reduncins comprise at least eight medium- to large-sized species (Gentry, 59 1985) with Kobus oricornus being the predominant species in Member B (Fig. 1D), Menelikia 60 leakeyi the common species in Member C, Kobus sigmoidalis the predominant species in 61 Member E. This latter species is also common in Member F and lower G, alongside Menelikia 62 lyrocera, which was the dominant species from upper Member G to Member H. 63 All fossil specimens analyzed here (n = 303) are curated by the Authority for Research and 64 Conservation of Cultural Heritage (ARCCH) in the National Museum of Ethiopia (Addis 65 Ababa). The material in this study largely belongs to the 1967-1976 International Omo 66 Research Expedition (IORE) collections (4,412 specimens of Reduncini, Howell, 1968; 67 Coppens et al., 1976), but also includes new material from the Omo Group Research 68 Expedition (OGRE) collections (656 specimens of Reduncini, Boisserie et al., 2008, 2010) 69 which represents 12 % of the analyzed specimens. 70 Most of the dental remains comprise isolated molars, mandibles, or fragments of maxillae 71 (see Appendix S1) from members B, C, E, F, mostly lower G, and H of the Shungura 72 Formation. Reduncins are rare in Member D and were not analyzed because of low specimen 73 availability. Specimens were discovered in fluvial fossil assemblages deposited by the paleo-74 Omo River or the upper Member G and Member H facies associated with or just after the

75 Lorenyang Lake (Heinzelin, 1983). All specimens included here displayed few indicators of 76 weathering and are well-preserved following careful selection of teeth (see Blondel et al., 77 2018). We excluded all specimens with postmortem damage of cusp tips observable with the 78 naked eye or stereo microscope for dental mesowear analysis and all specimens with a 79 homogeneous pattern of microwear on non-occlusal and occlusal surfaces observed with 80 stereo or confocal microscope for DMTA. The absence of difference between the molar wear 81 surfaces helped to identify altered specimens (Martin et al., 2018; Merceron et al, 2021). The 82 specimens with few taphonomic effects were cleaned (see method 3.2). The only taphonomic 83 study previously conducted (Alemseged, 2003; Alemseged et al., 2007) showed a higher 84 proportion of postcranial elements relative to isolated teeth as depositional environments 85 became more lacustrine. A more in-depth taphonomic study on bone and tooth modification is 86 underway to assess and identify post-mortem alterations for Shungura Formation specimens 87 from both the OGRE and IORE collections.

Because the reduncin dentitions are not always associated with cranial remains, and several taxa have overlapping dental sizes, taxonomic attribution below the tribal level is not possible for most of the specimens (Gentry, 1985). For this reason, we aggregated them at the tribal level for each member. In total, we analyzed 130 specimens for DMTA and 205 specimens for mesowear (S1, S2).

93

94 2.2 Comparative dataset

95 Our comparative dataset represents the main dietary axes in ruminants—grazers, mixed 96 feeders, browsers, and frugivores (Hofmann and Stewart 1972; Hofmann, 1973; Gagnon and 97 Chews, 2000). These broad categories reflect only a portion of ruminant dietary diversity and 98 the full extent of spatiotemporal dietary variation of African bovids (Codron et al., 2007; 99 Louys and Faith 2014). However, our diet reconstruction by proxies at different temporal

100 scales in an individual's lifetime (DMTA, MWS, enamel stable carbon isotopic data) allow us 101 to better detect subtle variability in reduncin dietary ecology through the Shungura Formation. 102 DMTA was applied to 178 wild-shot individuals of ten extant species of ruminants (Table 103 3, S2). The southern savanna buffalo (Syncerus caffer caffer, n=27), the hartebeest 104 (Alcelaphus buselaphus, n=29), the waterbuck (Kobus ellipsiprymnus, n=19), the kob (Kobus 105 *kob*, n=13), and the bohor reedbuck (*Redunca redunca*, n=7) are C<sub>4</sub> grazers (Estes, 1991; 106 Cerling et al., 2003). Buffalo and reduncins are water dependent, whereas hartebeest (tribe 107 Alcelaphini) are adapted to survive in drier grasslands (Kingdon, 2013). Impala (Aepyceros 108 *melampus*, n=10) are mixed feeders. The giraffe (*Giraffa camelopardalis*, n=16), the bushbuck (Tragelaphus scriptus, n=19) and the gerenuk (Litocranius walleri, n=12) are C<sub>3</sub> 109 110 browsers (Leuthold and Leuthold, 1978; Estes, 1991; Cerling et al., 2003). Giraffes consume 111 50 % of their diet from tree and tall shrubs leaves at more than 2m above ground, which are 112 inaccessible to smaller browsers such as gerenuk (Leuthold and Leuthold, 1972). The latter 113 species eats 5 % fruits and 95 % dicots, whereas the bushbuck eats 10 % fruits, 80 % dicots, 114 and 10 % monocots (Gagnon and Chew, 2000). The yellow-backed duiker (Cephalophus 115 *silvicultor*, n=26) has a frugivorous diet supplemented by leaves (Lumpkin and Kranz, 1984). 116 The present-day ruminant specimens we analyzed are housed in collections from the 117 institutions listed in Appendix S2. While we know that these wild specimens come from 118 different regions of Africa, their precise geographic origin is not always indicated in museum 119 collection records except for some specimens (Appendix S2). 120 For dental mesowear analyses, we used the same extant species as described above for the 121 DMTA dataset, with the exception of Kobus kob. Mesowear patterns of extant species derived from the dataset published by Fortelius and Solounias (2000). Following their approach, all 122 123 taxa constituting a comparative dataset should have a reasonable sample size and thus taxa

124 with fewer than 14 individuals sampled are excluded. Our comparative dataset of extant

125 species comprises 439 wild-shot specimens representing nine species (Table 1).

126 3. Methods

127 3.1. Mesowear analysis

Dental mesowear reflects the degree of attritive and abrasive wear on the occlusal molar surface. The former is due to tooth-on-tooth contact resulting in high relief between both cusp(id)s and sharp cusp(id) apices. Abrasive wear is due to the alteration of enamel tissue by food (and/or grit and dust) during mastication. It obliterates dental facets causing lower relief between cusp(id)s and more rounded apices (Fortelius and Solounias, 2000).

We examined fossil teeth preferably on the labial cups of upper second molars and the lingual cuspids of lower second molars with light and moderate wear stages (following Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003 and Louys et al., 2011). Fortelius and Solounias (2000) show that wear in ungulates is stable during the lifespan except for the earliest and latest stages. Rivals et al. (2007) indicate that ontogenetic changes are more pronounced for brachydont ungulates, but that mesowear signals are relatively stable for mesodont and hypsodont species, such as for the reduncins studied here.

Our mesowear sample size was increased by including undetermined lower and upper molars following Blondel et al. (2018). We used a mesowear score (MWS) representing a continuum of mesowear stages from 0 to 4 (Fig. 4), following Kaiser et al. (2009; 2013; see also Blondel et al., 2018). An individual score of 0 is given to high and sharp cusps (HS; expected value for a soft-leaf-eating browsers), 1 to high and rounded cusps (HR), 2 to low and sharp cusps (LS), 3 to low and rounded cusps (LR), and 4 to low and blunt cusps (LB; expected value for the most grazing species). MWS were then averaged for each species (Table 1).

147 3.2. Dental Microwear Textural Analysis

DMTA was analyzed following Blondel et al. (2018). The analysis was performed preferentially on the second upper and lowers molars. When second molars were weathered or unavailable, the isolated third or first molars were selected to maximize the fossil sample size (Schulz et al., 2010; Ramdarshan et al., 2017). The mesiolingual paracone or protocone facets and the distolabial protoconid facets were molded with a silicone polyvinylsiloxane (medium consistency, President Regular Body, Coltène Whaledent).

154 All molds were directly scanned at PALEVOPRIM, University of Poitiers, France using a 155 Leica DCM8, white-light confocal surface profilometer equipped with a 100× lens (numerical 156 aperture = 0.90; working distance = 0.9 mm). A 333 x 251 µm area was scanned for each 157 specimen. In contrast to Blondel et al. (2018), a  $200 \times 200 \,\mu\text{m}$  surface was generated from 158 this area, leveled and mirrored in Z using LeicaMap 7.4 (Leica Microsystems) for all studied 159 specimens (Fig. 3 and 4). The few missing points were replaced with a smooth shape 160 calculated from neighboring points. Aberrant peaks were automatically erased (see 161 supplementary material in Merceron et al., 2016 for details). Artifacts such as adhering dust 162 or sediment particles on the enamel surface were removed manually and then replaced with a 163 smooth shape calculated from the neighboring points before proceeding to a final leveling of 164 the surfaces with Mountains software (Blondel et al., 2018). Further analysis to generate 165 DMTA variables was conducted with Toothfrax and Sfrax (Surfract, www.surfract.com) 166 following procedures and settings shown in Scott et al. (2006). Three microwear variables 167 were extracted from each surface (Table 3, S2): Complexity (Asfc or Area-scale fractal 168 complexity) is a measure of the roughness at a given scale, anisotropy (*epLsar* or exact 169 proportion of length-scale anisotropy of relief) measures the orientation concentration of 170 surface roughness, and heterogeneity of complexity (HAsfc or heterogeneity of area-scale 171 fractal complexity) quantifies the variation of complexity observed within each scan. HAsfc is 172 calculated in each sub-surface through 81 cells (HAsfc81-cells). To compare our results with

173 those of Blondel et al. (2018), we ran new analyses on the Shungura tragelaphins after having 174 extracted a  $200 \times 200 \,\mu\text{m}$  surface.

175 3.3. Statistical analysis of dental wear

176 Statistical tests in Statistica v.7 were used to analyze differences in mesowear scores 177 (MWS) and microwear textural parameters between groups (both extant species and tribes 178 from the members of the Shungura Formation). The textural variables were rank-transformed 179 before each analysis to avoid violating normality assumptions for parametric tests (Conover and Iman, 1981; Sokal and Rohlf, 1969). One-way analysis of variance (ANOVA) for each 180 181 parameter was used to test for significant differences. Differences between groups were then 182 highlighted using the combination of the conservative HSD test (Tukey's Honest Significant 183 Differences) together with the less conservative LSD test (Fisher's Least Significant 184 Differences; Tables 2 and 4).

185

186 4. Results

#### 187 4.1. Dental Mesowear Score (MWS) results

188 The average MWS of the entire Shungura reduncin sample (n=205; mean= $1.23 \pm 0.07$ ;

189 Table 1) is close to that of *R. redunca*, an extant fresh grass grazer. The average MWS of the

190 Shungura reduncins is higher than that of the tragelaphins  $(0.68 \pm 0.07, Blondel et al., 2018)$ .

191 HSD tests indicate no significant differences in MWS between Reduncini from different

192 members of the Shungura Formation (Table 2B).

193 Member B (Table 1 and Fig. 4) reduncins (n=29, MWS=0.79) plot closest to L. walleri

194 (n=69, MWS=0.75) and significantly differ from the grazer A. buselaphus (Table 2B). In

195 Member C, reducins differ significantly from A. buselaphus, and from the browsers G.

196 *camelopardalis* and *T. scriptus*, but fall within the range of *R. redunca* (Fig. 4, Table 1 and

197 Table 2B). No significant difference is detected between reduncins from Member E (Table 198 2B) and all extant species in our dataset, whereas reduncins from Member F differ 199 significantly from the mixed feeder A. melampus and the three browsers, but are close to A. 200 buselaphus (Fig. 4, Table 1). In Member G, reduncins show significant differences in MSW 201 with the grazer A. buselaphus and the three browsers, as in Member C (Fig. 4, Table 1 and 202 2B). Reduncins from Member H differ significantly from the grazer A. buselaphus in MWS 203 (Table 2B) but are close to S. caffer and Member B specimens (Fig. 4, Table 1). No 204 significant difference is detected between reduncins and tragelaphins from the same members 205 except in Member F and Member G (HSD test, Table 2C).

206 4.2. Dental Microwear Texture Analysis (DMTA) results

207 DMTA results (Table 3, Fig. 3 and 4) show that Reduncini from the Shungura Formation 208 are close to *A. melampus*, an extant mixed feeder, in complexity and anisotropy, and they 209 differ in all of three texture parameters from the extinct tragelaphins from the Shungura 210 Formation and from extant giraffes.

211 A bivariate plot of complexity and anisotropy (Fig. 5) indicates that reduncins from 212 Member B (Fig. 3A) are close to the leaf-browsing G. camelopardalis in having low anisotropy (*epLsar* =  $2 \times 10^{-3}$ ) and low complexity (*Asfc* = 1.67). The HSD test (Table 4B) 213 214 indicates that Member B reduncins significantly differ from the grazer A. buselaphus, K. kob, 215 and the browser T. scriptus in having lower anisotropy. An LSD test indicates that Member B 216 specimens differ from all extant species in having a lower heterogeneity of complexity. No 217 significant difference (Table 4B, Fig. 6B1, B2, B3) is detected between reduncins and 218 tragelaphins in Member B. HSD tests on three DMTA variables (Table 4B) detect no 219 significant different between reduncins from Member B and those of the upper members, but

the LSD test shows that they differ from those in Member F, Member G, and Member H inanisotropy (Table 4B, Fig. 6B2).

222	Reduncins from Member C (Fig. 3B) are close to mixed feeding A. melampus in
223	complexity and anisotropy (Fig. 5, Table 3). Post hoc tests on the three texture parameters do
224	not show significant difference between reduncins from Member C and A. melampus, G.
225	camelopardalis, L. walleri, and S. caffer (Table 4B). Reduncins and tragelaphins from
226	Member C only differ significantly in anisotropy (epLsar) based on the LSD test. No
227	significant difference is detected between reduncins from Member C and those of the other
228	members based on the three texture parameters (Table 4B, Fig7).
229	Reduncins from Member E are very close to A. melampus in complexity and anisotropy
230	(Fig. 5). Post hoc tests do not show significant difference in the three DMTA parameters
231	between reduncins from Member E and A. melampus, K. ellipiprymnus, K kob, T. scriptus,
232	and S. caffer (Table 4B). No significant difference is detected between reduncins and
233	tragelaphins in Member E for the three texture parameters (Table 4B, Fig.7). Member E
234	specimens differ significantly from reduncins from Member H in complexity based on the

LSD test.

A bivariate plot of complexity versus anisotropy (Fig. 5) shows that reduncins in Member F (Fig. 3C) are close to *T. scriptus* and *S. caffer* in having low complexity (*Asfc*=1.77) and a high anisotropy (*epLsar*= $4.5 \times 10^{-3}$ ). No significant difference is detected between Member F reduncins (Fig.4C) and *A. melampus, K. ellipsiprymnus, K kob, T. scriptus,* and *S. caffer* in the three texture parameters (Table 4B). Reduncins from F significantly differ from tragelaphins in Member F and reduncins in Member B for anisotropy based on the LSD test (Table 4B, Fig. 6B2).

Reduncins in Member G are close to *A. melampus* in anisotropy and complexity like Member C specimens (Fig 6). Post hoc tests on the three texture parameter indicates that they are not significantly different from *A. melampus* and *R. redunca*. No significant difference is detected between reduncins and tragelaphins in Member G for the three texture parameters (Table 4B, Fig. 6).

The low complexity (*Asfc*=1.28) and moderate anisotropy (*epLsar*=4 x  $10^{-3}$ ) of Member H reduncins (Fig. 3D) falls at the limits of *T. scriptus* and *S. caffer* (Fig. 5). No significant difference in anisotropy (Table 4B) exists between Member H reduncins (Fig. 3D) and the cluster of grazers *K. ellipsiprymnus, K. kob, R. redunca, S. caffer*, and browser *T. scriptus*, but they differ significantly from *K. ellipsiprymnus* and *K. kob* in having a lower heterogeneity of complexity (*HAsfc*=0.42). Member H reduncins are not significantly different from those of lower members (Table 4B, Fig.7).

255 5. Discussion

256 5.1 Diets of extant ruminants in our dataset

257 ANOVAs detect significant differences in MWS across the extant ruminant species (Table 258 2). In general, we observe a continuum from browsers to mixed feeders to grazers with 259 frugivores plotting within the range of the latter (Fig. 4, Table 1). The lowest MWS is 260 obtained by G. camelopardalis, a browser that has a diet dominated by leaves (Leuthold and 261 Leuthold, 1978; Estes, 1991), followed by the two others browsing bovids (L. walleri and T. 262 scriptus) and mixed feeding A. melampus. Among mixed feeders, browser-grazer 263 intermediates such as A. melampus focus more on dicot and monocot foliage (30-70 %, 264 Gagnon and Chew, 2000), whereas generalists differ from browser-grazer intermediates by 265 feeding on more fruits and seeds. The MWS of the frugivore C. silvicultor (71 % of diet 266 comprised of fruits, Kingdon, 2013) is as high as those of grazers due to the higher quantity of

267	fiber in fruits than in leaves; as observed by Fortelius and Solounias (2000) and Louys et al.,
268	(2011). The high MWS of K. ellipsiprymnus and R. redunca reflect their grazing preference
269	(Fig.4, Table 1). Waterbuck K. ellipsiprymnus is considered as a variable grazer consuming
270	80 % of grasses but with browsing to boost their protein intake during the dry seasons (Estes,
271	1991; Kaiser et al., 2013; Kingdon and Gentry, 2013; Gagnon and Chew, 2000); R. redunca is
272	an obligate and selective grazer consuming 90 % fresh monocots (Gagnon and Chew 2000,
273	Kingdon and Gentry, 2013). The highest MWS is obtained by A. buselaphus, a grazer that
274	consumes roughage grasses (Gosling and Kingdon, 2013; Estes, 1991; Sponheimer et al.,
275	2003) and classified by Gagnon and Chew (2000) as a variable grazer (60-90 $\%$ monocots).
276	The ANOVAs (Table 4) indicate significant differences in extant ruminants for the three
277	dental microwear texture parameters: complexity (Asfc), anisotropy (epLsar), and
278	heterogeneity of complexity (HAsfc). No significant differences in complexity exist between
279	G. camelopardalis, L. walleri, and T. scriptus but the last two species differ from Giraffa in
280	having higher anisotropy. Moreover, T. scriptus (Fig. 3E) does not differ for the three textural
281	parameters from five grazers A. buselaphus, K. ellipsiprymnus, K. kob, R. redunca (Fig. 3A,
282	B, C), and S. caffer. Thus, DMTA indicates that T. scriptus falls in the cluster of grazers
283	whereas the mesowear score indicates that this species is a browser. The discrepancy between
284	mesowear (long-term dietary signal) and microwear (short-term dietary signal) could indicate
285	that the specimens of <i>T. scriptus</i> in our dataset had a browsing diet during their adult life, but
286	that they fed on grasses or semi-woody plants such as scandent plants during their last few
287	meals or during seasonal changes. Previous studies (Smits, 1986; MacLeod et al., 1996)
288	indicate that bushbucks feed on plants of high nutritive value and can be considered as
289	selective browsers. They have a wide distribution across sub-Saharan Africa, which may be
290	due to their versatile diets that sometimes include grasses in addition to leaves, buds, and
291	fruits (Castello, 2016). During the wet season, bushbucks prefer tender new grasses and

during the dry season they prefer leaves of shrubs and trees (Estes, 1991, Plumptre and
Wronski, 2013). The specimens analyzed here may record this dietary versatility. It is also
important to note that several studies have challenged the hypothesis that anisotropy (*epLsar*)
reflects only grass consumption. For instance, koalas in Hedberg and DeSantis (2017) and roe
deer in Merceron et al. (2010) show that high anisotropy (*epLsar*) on shearing molar facets is
not specifically related to grass-eating habits but also tough leaf-eating habits requiring a
shearing motion during mastication.

299 5.2 Dietary ecology of reduncins from the Shungura Formation

300 Our MWS and DMTA results reveal that the Shungura Formation reduncins were 301 more dedicated to grazing than tragelaphins from the same sequence, differing in their lower 302 values of complexity and heterogeneity of complexity, higher anisotropy, and lower MWS. 303 Shungura reduncins had mixed feeding to grazing preferences throughout most of the 304 sequence. Their average mesowear score is close to that of extant R. redunca, an obligate 305 grazer, whereas the anisotropy and the complexity suggest some mixed feeding like A. 306 melampus, a browser-grazer intermediate (Tables 1 and 3). Thus, the reduncins from the 307 Shungura Formation between 3 Ma and 1.8 Ma most likely had diets more flexible than those 308 of living reduncins, which are all obligate or variable C<sub>4</sub> grazers regardless of where they are 309 distributed in Africa (Kingdon and Gentry, 2013; Cerling et al., 2003, Sponheimer et al., 310 2003). The mesowear signal indicates that they were grazers at the scale of their lifetime, 311 while DMTA indicates that they could adopt a mixed feeding behavior during their last few 312 weeks alive. Thus, they displayed some dietary flexibility as we can observe it from Member 313 B specimens, which mostly belong to the B-10 unit (2.965 Ma).

Indeed, our dental wear studies suggest that Member B reduncins (Fig. 6) were
browser-grazer intermediates. Their average mesowear is close to that of *L. walleri*, a leaf

316 browser, and close to the average MWS of mixed feeders (Blondel et al., 2018). Moreover, 317 their values for anisotropy and complexity are close to those of G. camelopardalis, a leaf-318 dominant browser (Fig. 5), but with an average heterogeneity of complexity lower than that of 319 this species (Table 3). A lower value for heterogeneity of complexity would indicate a diet 320 much more homogeneous in size and nature of the plant items than that of the giraffe (Souron 321 et al., 2015; Ramdarshan et al., 2016, Merceron et al., 2018). Reduncini (Fig. 6B1 and B3) 322 consumed less browse than Tragelaphini in Member B (the bongo-like Tragelaphus rastafari, 323 Blondel et al., 2018) as suggested by their lower values of complexity and heterogeneity of 324 complexity. However, Member B reduncins significantly differ from A. buselaphus, which 325 selectively grazes on tall grass swards (Kingdon, 2013), for MWS, anisotropy, and 326 heterogeneity of complexity. In terms of taxonomy, we consider that most of the Reduncini 327 dental sample from Member B (Fig. 1D) must belong to K. oricornus, the most common 328 species (80.5 %) in this member (Gentry, 1985). They were browser-grazer intermediates that 329 could have consumed of 30-70 % dicots and monocots and 20 % fruits (Gagnon and Chew, 2000). Stable carbon isotopes ( $\delta^{13}$ C) of tooth enamel for Member B reduncins indicate a 330 331 mixed  $C_3/C_4$  to a  $C_4$  pure diet (n=9, mean= -2.8%); Negash et al., 2020). We suggest that they 332 were predominantly C<sub>3</sub>/C<sub>4</sub> browser-grazers, and not exclusively C<sub>4</sub> grazers like their living 333 counterparts (Cerling et al., 2003; Sponheimer et al., 2003).

Dental wear analyses suggest that Member C reduncins had a diet ranging from mixed feeding to grazing. DMTA in general suggests mixed feeding like *A. melampus* (Fig. 5), whereas the mesowear score falls similar to grazers like *R. redunca* (obligate grazers, 90 % monocots) and *K. ellipsiprymnus*, variable grazers (Fig. 4, mean=1.29, 1.14, and 1.09 respectively). The slight discrepancy between intra-individual microwear and mesowear signals may be linked to differences in temporal resolution and scale of these proxies, such as their ability to record seasonal differences (see 5.1). Indeed, *A. melampus* browse on shrubs,

341	herbs, pods, and seeds during the dry season in the woodlands whereas they become dedicated
342	grazers during the rains while fresh grasses grow again. In Member C, reduncins are more
343	taxonomically diverse than in Member B, with the first presence of Menelikia (Fig. 1D).
344	Gentry (1985) thought that <i>M. leakeyi</i> and <i>K. ancystrocera</i> were the most common reduncins
345	in Member C but the percentages calculated from the updated catalogs of the IORE and
346	OGRE collections suggest that <i>M. leakeyi</i> (24.4 %) with <i>K. sigmoidalis</i> (42.2 %) constitute
347	66.7 % of Reduncini, with K. ancystrocera only represented by 15.6 % of specimens (Fig.
348	1D). Dental wear signals supplemented by carbon isotope data (n=10, median $\delta^{13}C = -1.5\%$ ,
349	Negash et al., 2020) suggest that reduncins from Member C, hence most likely represented by
350	<i>M. leakeyi</i> and <i>K. sigmoidalis</i> , had mixed $C_3/C_4$ to $C_4$ grass-dominated diets. This differs from
351	Member C tragelaphins, represented by Tragelaphus nakuae, which were C <sub>3</sub> /C <sub>4</sub> mixed
352	feeders preferring $C_4$ browse, as the presence of succulent $C_4$ Amaranthaceae was shown by
353	Bonnefille and Dechamps (1983) and dental microwear textures of tragelaphins excluded
354	grazing habits (Blondel et al., 2018).

355 No significant difference for DMTA and MWS is detected between Member E 356 reduncins and A. melampus, a mixed feeder, and variable grazers such as K. ellipsiprymnus and S. caffer. Enamel  $\delta^{13}$ C values of Member E reduncins indicate a pure C<sub>4</sub> diet (n=10, 357 358 mean= 0%; Negash et al., 2020). The diversity in Reduncini from Member E is lower than in 359 Member C (Fig. 1D), with K. sigmoidalis representing 77.4 % of specimens. We suggest that 360 reduncins from Member E (Fig. 6), represented probably by K. sigmoidalis, had a C<sub>4</sub>-focused 361 diet ranging from grazing to mixed feeding, whereas T. nakuae and T. gaudryi were more 362 clearly C<sub>3</sub>/C<sub>4</sub> mixed feeders (Blondel et al., 2018).

The combination of dental mesowear and microwear textural analyses indicates that the reduncins in Member F were variable grazers like *S. caffer* and *A. buselaphus* (Fig. 4 and

6). These results, supplemented with  $\delta^{13}$ C values of tooth enamel (n=10, mean  $\delta^{13}$ C = -1.3‰, Negash et al., 2020), suggest that reduncins from Member F, *K. sigmoidalis* and *M. lyrocera* (51.2 % and 48.8 % respectively), were C<sub>4</sub> grazers. In contrast, *T. nakuae* and *T. gaudryi* were C<sub>3</sub>/C<sub>4</sub> mixed feeders preferring browse (Blondel et al., 2018).

369 The diversity of reduncins in lower Member G is higher than that of Member F (Fig. 370 1D). Member G has yielded a moderate sample of K. sigmoidalis (34.2 %) but M. lyrocera 371 represents more than half of the specimens (53.8 %). Post-hoc tests indicate no significant 372 difference for MWS and DMTA between fossil reduncins and A. melampus, a browser-grazer 373 intermediate, and R. redunca a selective grazer. Thus, the dental wear analyses show that 374 reduncins in lower Member G had a mixed diet dominated by grasses as in Member C. However, tooth enamel  $\delta^{13}$ C values (n=11,  $\delta^{13}$ C = -0.7%, Negash et al, 2020) indicate they 375 consumed slightly more C<sub>4</sub> plants than Member C reduncins ( $\delta^{13}C = -1.5$  %). Collectively, 376 377 these data suggest that Member G reduncins were mixed feeders favoring C<sub>4</sub> grasses.

378 The combination of the mesowear score and the DMTA suggest that reduncins in 379 Member H, 94.4 % of which represent M. lyrocera (Fig.2), were grazers. Indeed, no 380 significant difference in anisotropy and complexity exists between them and the cluster of 381 grazers K. kob, K. ellipsiprymnus, R. redunca, S. caffer (Fig. 5). However, Member H specimens differ from K. kob, K. ellipsiprymnus, and L. walleri in having lower values of 382 383 heterogeneity of complexity. This difference may be attributable to a lower diversity of 384 consumed food items as Souron et al. (2015) suggested for extant suids and Merceron et al. 385 (2021) for alpine ruminants. Reduncins in Member H might have consumed a more 386 homogenous food than K. kob and K. ellipsiprymnus, which consume many species of grasses 387 and even leaves and fruits (Kingdon and Gentry, 2013). Moreover, based on MWS, Member 388 H reduncins significantly differ from the grazer A. buselaphus (Gosling and Kingdon, 2013).

389	The difference in heterogeneity of complexity can also be explained by seasonal variations in
390	diet and also by the quantity of grit and dust in the environment due to climatic conditions,
391	such as drought. After having analyzed the craniodental morphology of M. lyrocera from the
392	KBS Member of the Koobi Fora Formation and from Member H of the Shungura Formation,
393	Spencer (1997) showed that <i>M. lyrocera</i> differed from extant bovids, but falling close to grass
394	and mixed grass feeders. She concluded that this species might have fed on tender and soft
395	vegetation distributed homogeneously in areas with little seasonal variations. The $\delta^{13}C$ values
396	of tooth enamel (n=10, mean $\delta^{13}$ C = -1.3‰, Negash et al, 2020) suggest that Reduncini from
397	Member H had a $C_3/C_4$ to pure $C_4$ diet. Together, data from these proxies indicate that
398	Member H reduncins consumed probably soft C <sub>4</sub> grasses.
399	Recent studies in fossil artiodactyls (Bibi et al, 2013; Souron, et al., 2012), primates
400	(Martin et al., 2018; Wynn et al., 2020), and other herbivorous taxa (Cerling, et al., 2015;
401	Negash et al., 2020) detected two dietary shifts in the eastern African fossil record. The first
402	occurs around 2.8 Ma (between Member B and Member C) and the second around 2.32 Ma
403	(between Member E and Member F). The age of these changes fits well with the findings in
404	the present study. Our results, combined stable carbon isotopes, show that Reduncini of the
405	
	Shungura Formation had a flexible diet from $C_3$ - $C_4$ browsing to mixed feeding from Member
406	Shungura Formation had a flexible diet from C <sub>3</sub> -C <sub>4</sub> browsing to mixed feeding from Member B through Member C. They were much more engaged in C <sub>4</sub> grazing than the tragelaphins
406 407	Shungura Formation had a flexible diet from C <sub>3</sub> -C <sub>4</sub> browsing to mixed feeding from Member B through Member C. They were much more engaged in C <sub>4</sub> grazing than the tragelaphins from Member E through Member F, and less in lower Member G, and finally they likely fed

409 5.3. Paleoenvironmental implications of reduncin diets

All living reduncins, except the mountain reedbuck (*R. fulvorufula*), inhabit wetlands
or mesic savannas in the African tropics and never stray far from permanent water bodies
(Kingdon, 2013). These habitats are situated within the sub-Saharan savanna biome and

413 include elements such as floodplain, swamp, and valley grassland where reduncins graze on 414 C<sub>4</sub> grasses with high protein and low fiber (Cotterill, 2000; Estes, 1991, Sponheimer et al., 415 2003). Our findings show that the reduncins from the Shungura Formation exploited a greater 416 diversity of food than their living relatives. Shungura reduncins were versatile in their dietary 417 preferences through time, reflecting various vegetation resources in their habitat for foraging. 418 They probably inhabited different types of grasslands, which contrasts with extant reduncins 419 that share a preference for floodplain grasslands. Spencer (1997, see 5.2) even suggested that 420 *M. lyrocera* lived in a vegetation environment unlike any known today, which fits with a 421 recent analysis arguing for non-analog ecosystems in the eastern African fossil record (Faith 422 et al., 2019). On the other hand, K. sigmoidalis, adapted to grass feeding, inhabited edaphic 423 grasslands around 2 Ma in the Omo region (Spencer, 1997). The paleobotanical evidence 424 (Bonnefille and Dechamps, 1983) indicates shifting proportions of habitat types ranging from 425 gallery forest to open cover (savanna, shrubs) in each member of the Shungura Formation, 426 with more open environments and drier conditions in Members E, F and J. Carbon stable 427 isotope analyses of pedogenic carbonates (Cerling et al., 2011; Levin et al., 2011) indicate an 428 increase of C<sub>4</sub> vegetation towards the top of upper Member G (around 1.9 Ma) coinciding 429 with the draining of Lorenyang Lake. Values modeling the weighted distribution of C4 biomass, the  $\delta^{13}$ C ecosystem (Paquette and Drapeau, 2021), show a gradual opening of the 430 431 landscape through time. These data are consistent with the ecomorphological analyses of 432 bovid astragali (Barr, 2015; Plummer et al., 2015), which suggest a tendency to occupy more 433 open habitats around 2.5 Ma, 2.36 Ma, and 2 Ma but with a persistence of forest and 434 woodland. Bovid ecomorphology by Plummer et al. (2015) also indicate a limited use of 435 wetlands, the usual habitat of extant reduncins like K. leche or K. megaceros, from Member B 436 to lower Member G, or even the absence of this habitat in upper Member G whereas the 437 relative abundance of Reduncini (dominated by *M. lyrocera*) increase through the upper units

438 of the sequence. This suggests that reduncins of the Shungura Formation inhabited various 439 types of grasslands as our dietary analyses would suggest. The high abundance of Reduncini 440 is also noted at Koobi Fora between 2 Ma and 1.4 Ma by Patterson et al. (2017) who deduce 441 the persistence of well-watered grasslands during this period through the Upper Burgi, KBS, 442 and Okote Members of the Koobi Fora Formation. However, Harris (1991) suggests that the 443 morphological changes in Koobi Fora reduncins, particularly the domed nasal region of 444 specimens of *M. lyrocera* from the Upper Burgi and KBS members, might be related to 445 temperature regulation, and that this species might have inhabited drier grasslands extant 446 reduncins. Although there are several functional interpretations of nasal dome in bovids, this 447 structure could very likely be linked to drier grasslands as O'Brien et al. (2016) suggest. They 448 demonstrated that the nasal dome of wildebeest-like Late Pleistocene bovid *Rusingoryx* 449 atopocranion from Kenya could be used for long-distance vocalization in semi-arid 450 grasslands.

451 In sum, the Reduncini, an abundant and diversified tribe during the Plio-Pleistocene in 452 eastern Africa, lived in various environments and occupied a greater diversity of grasslands 453 than living reduncins today. Patterns of faunal turnover in the Turkana Basin indicate spatial 454 and temporal variations in the faunal assemblage, especially in the abundance of Reduncini 455 from areas of the Shungura Formation (Alemseged et al., 2007, Maurin, 2017), and from the 456 subregions of the Koobi Fora Formation (O'Brien et al., 2020). The variations in the 457 distribution of these bovids may be linked to the evolution of drainage system of the Turkana 458 Basin as Cotterill (2005) showed it in the distribution of the K. leche complex and the palaeo-459 drainage dynamics across the south-central Africa in Plio-Pleistocene. However, this awaits 460 more a comprehensive study. Future work using intra-tooth stable carbon and oxygen isotope 461 analyses might be a means to understand seasonal changes in diet and hydroclimate across the 462 Turkana Basin sequences (Souron et al., 2012; Rivals et al., 2018).

463

#### 464 6. Conclusions

465 To better understand the environmental conditions that prevailed during the Plio-466 Pleistocene of the Lower Omo Valley, Ethiopia, we analyzed dental mesowear and microwear 467 texture of reduncins from the Shungura Formation to reconstruct the diet and habitat 468 preference of these taxa. We show that the Shungura Formation reduncins had diets ranging 469 from browsing to mixed feeding from ~ 3 Ma to 2.5 Ma, but became more engaged in C<sub>4</sub> 470 grazing than tragelaphins around 2.3 Ma and 1.8 Ma. Their diets were considerably more 471 diverse than those of the extant reduncins, which prefer C<sub>4</sub> grasses almost exclusively. The 472 diversity of diets in the Shungura record implies various available vegetation resources 473 through the sequence. Our results provide new evidence that the environment in the Lower 474 Omo Valley was probably composed of a mosaic of habitats ranging from forests to open 475 woodlands between 3.4 and 1.7 Ma marked by a trend towards a greater diversity of C<sub>4</sub> 476 grasslands through time. Our study highlights the importance of a multi-proxy approach to 477 precisely determine herbivore diets and points to how these proxies offer slightly different, 478 complementary perspectives on the ecology of fossil organisms.

479

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783 Figure captions

Figure 1. A, Geographical position of the Shungura, Nachukui, and Koobi Fora formations

785 (southern Ethiopia, East Africa); B, chronostratigraphic sequence of the Shungura Formation

after Heinzelin (1983). Dated horizons are marked by red triangles and dates in Ma provided

at member boundaries after Feibel et al. (1989), McDougall and Brown (2006, 2008), and

788 McDougall et al. (2012). C. Relative abundances of bovid tribes from the Shungura

789 Formation (IORE collection). D. Percentage of representation of the Shungura reduncin

species from the IORE and OGRE collections. *Kobus ellipsiprymnus* from Member C is cf.

791

Figure 2. Examples of photosimulations of dental microwear textures on second molars of

793 modern species generated through the LeicaMap 7.4.: the grazers, *Kobus ellipsiprymnus* (A;

794 ZMB687164), Kobus kob (B;ZMB 68356), and Redunca redunca (C; ZMB502), the mixed

feeder impala Aepyceros melampus (D;ZMB58720), the browsing bushbuck Tragelaphus

796 scriptus (E;NHMB n°2) and the leaf browsing giraffe Giraffa camelopardalis (F; SNG-

797 36628).

798

Figure 3. Examples of photosimulations of dental microwear textures on molars of extinct

800 reduncins generated through the LeicaMap 7.4.: OMO28-1968-2434 from Member B (A),

801 OMO18-1968-1765 from Member C (B), OMO33-1969-3069 from Member F (C), OMO279-

802 10001 from Member H (D).

803 Figure 4. Box-and-whiskers plots of mesowear scores (MWS) for modern species and 804 Reduncini from Member B, C, E, F, G and H of the Shungura Formation. Boxplots represent 805 the standard deviation and whiskers indicate the confidence interval of the mean at 95 %. 806 Orange: extant grazers; light green: mixed feeders; dark green: extant browsers; red: extant 807 frugivores, white: extinct species. 808 Figure 5. Distribution (mean, 95 % confidence interval of the mean) of the extant species (Ab, 809 Alcelaphus buselaphus; Cs, Cephalophus silvicultor; Gs, Giraffa camelopardalis; Kk, Kobus 810 kob; Ke, Kobus ellipsiprymnus; Rr, Redunca redunca; Sc, Syncerus caffer; Tsc, Tragelaphus 811 scriptus) and the Reduncini of the Members B, C, E, F, G and H (BR, CR, ER, FR, GR, HR) 812 depending on the complexity (Asfc) and anisotropy (epLsar). Orange: extant grazers; light 813 green: mixed feeders; dark green: extant browsers; red: extant frugivores, black: extinct 814 species.

815

816 Figure 6. A. Chronostratigraphic sequence of the Shungura Formation after Heinzelin (1983). 817 Dates in Ma provided at member boundaries after Feibel et al. (1989), McDougall and Brown 818 (2006, 2008), and McDougall et al. (2012). B. Distribution (mean, 95 % confidence interval 819 of the mean) of dental microwear textural and mesowear of Reduncini (in purple) and 820 Tragelaphini (in black) for each member of the Shungura Formation. B1. mean complexity 821 (Asfc); B2. mean anisotropy (epLsar); B3. mean heterogeneity of the complexity (H81). B4. Mesowear score (MWS). C. Enamel carbon stable isotopic composition ( $\delta^{13}$ C % VPDB) of 822 823 tragelaphins in black triangle after Bibi et al. (2013), in black circle after Negash et al. (2020), 824 and reduncins in purple square after Negash et al. (2020).

820	Table	captions

827	Table 1. Mesowear score (MWS) of extant and extinct specimens: n, specimen number; m,
828	mean; sd, standard deviation; sem, standard deviation of the mean. For modern species,
829	Fortelius and Solounias (2000).
830	Table 2. A. ANOVA comparison of extant species and Reduncini in each member. B. Results
831	of pairwise comparisons of extant species and Reduncini in each member. C. Results of
832	pairwise comparisons of Reduncini and Tragelaphini in each member (df, degrees of freedom;
833	SS, sum of square; MS, mean square; F, Fisher value; P, P-value). Significance at p<0.05 is
834	indicated in normal black for Fisher's LSD and in bold for both Tukey's HSD and Fisher's
835	LSD tests.
836	
837	Table 3. Descriptive statistics (m, mean; med, median; sd, standard deviation and sem,
838	standard deviation of the mean) of dental microwear texture parameters for extant species and
839	extinct taxa.
840	Table 4. A. ANOVA comparison of extant species and Reduncini in each member. B. Results
841	of pairwise comparisons of extant species, Reduncini and Tragelaphini in each member.
842	Significance at p<0.05 is indicated in normal black for Fisher's LSD and in bold for both
843	Tukey's HSD and Fisher's LSD tests. A= Asfc, complexity; E=epLsar, anisotropy; H=,
844	HAsfc81, heterogeneity of the complexity.
845	Appendix captions
846	S1. List of fossil material including specimen number, tooth position: U, upper; L, lower; M,

847 molar; Mb: Shungura Formation member; taxonomic assignation; MWS: mesowear score;

848 DMTA: dental microwear textural analysis.

849	S2. Values	for dental	microwear	texture	parameters	(DMTA)	) for li	iving s	species	and S	Shungura
						· /		<u> </u>			<u> </u>

- 850 Formation specimens. *Asfc*: complexity; *epLsar*: anisotropy; *HAsfc*81: Heterogeneity of the
- 851 complexity. PALEVOPRIM: Laboratoire Paléontologie Évolution Paléoécosystèmes
- 852 Paléoprimatologie Poitiers, France; KNM: National Museums of Kenya; MNHN: Museum
- 853 national d'Histoire Naturelle, Paris, France; NHMB: Naturhistorisches Museum Basel,
- 854 Swizerland; SNG: Naturmuseum Senckenberg, Frankfurt; SMNK: Staatliches Museum für
- 855 Naturkunde, Karlsruhe; SMNS: Staatliches Museum für Naturkunde, Stuttgart. ZMB:
- 856 Zoologisches Museum Berlin, Germany.



Fig. 1



Fig. 2















Fig.6

Table	1
Table	T

Samples		MWS	5	
	n	m	sd	sem
Aepyceros melampus (MF)	17	0.65	0.49	0.12
Alcelaphus buselaphus (Gr)	76	1.92	1.41	0.16
Cephalophus silvicultor (Fr)	39	1.46	0.94	0.15
Giraffa camelopardalis (Br)	61	0.38	0.71	0.09
Kobus ellipsiprymnus (Gr)	22	1.09	0.43	0.09
Litocranius walleri (Br)	69	0.75	0.67	0.08
Redunca redunca (Gr)	77	1.14	0.70	0.08
Syncerus caffer (Gr)	31	1.00	0.00	0.00
Tragelaphus scriptus(Br)	47	0.51	0.51	0.07
Fossil taxa				
Reduncini total	205	1.23	0.94	0.07
lower molar	91	0.92	0.73	0.08
upper molar	114	1.48	1.07	0.10
Member B	29	0.79	0.41	0.08
lower molar	21	0.71	0.46	0.10
upper molar	8	1.00	0.00	0.00
Member C	31	1.29	1.19	0.21
lower molar	14	1.21	1.05	0.28
upper molar	17	1.35	1.32	0.32
Member E	10	1.00	0.82	0.26
lower molar	6	1.00	1.10	0.45
upper molar	4	1.00	0.00	0.00
Member F	16	1.69	1.08	0.27
lower molar	5	1.40	0.89	0.40
upper molar	11	1.82	1.17	0.35
Member G	101	1.35	1.01	0.10

	lower molar	36	0.92	0.65	0.11
	upper molar	65	1.58	1.10	0.14
Member H		18	0.94	0.64	0.15
	lower molar	9	0.67	0.50	0.17
	upper molar	9	1.22	0.67	0.22

## Table 2A

### MWS

111110						
ANOVA		df	SS	MS	F	р
Species/Member	Effect	19	157	8	12.0	<0.001
	Error	785	541	1		

## Table 2B

Aepyceros melampus	Am														
Alcelaphus buselaphus	MWS	Ab													
Cephalophus silvicultor	MWS	MWS	Cs												
Giraffa camelopardalis		MWS	MWS	Gc											
Kobus ellipsiprymnus		MWS		MWS	Ke										
Litocranius walleri		MWS	MWS	MWS		Lw									
Redunca redunca	MWS	MWS		MWS		MWS	Rr		_						
Syncerus caffer		MWS	MWS	MWS				Sc							
Tragelaphus scriptus		MWS	MWS		MWS		MWS	MWS	Ts						
Reduncini Member B		MWS	MWS	MWS						RMB					
Reduncini Member C	MWS	MWS		MWS		MWS			MWS	MWS	RMC				
Reduncini Member E		MWS		MWS								RME			
Reduncini Member F	MWS			MWS		MWS	RMF								
Reduncini Member G	MWS	MWS		MWS		MWS		MWS	MWS	MWS				RMG	
Reduncini Member H		MWS	MWS	MWS									MWS		RMH

Table 2C

	TMB	TMC	TME	TMF	TMG
Reduncini Member B					
Reduncini Member C		MWS	MWS	MWS	MWS
Reduncini Member E					
Reduncini Member F	MWS	MWS	MWS	MWS	MWS
Reduncini Member G		MWS	MWS	MWS	MWS
Reduncini Member H					

Samples		Asfc				Hasfc81cells							
	n	m	med	sd	sem	m	med	sd	sem	m	med	sd	sem
Aepyceros melampus (MF)	10	2.15	1.91	1.09	0.35	3.5E-03	2.5E-03	2.6E-03	8.2E-04	0.70	0.62	0.45	0.14
Alcelaphus buselaphus (Gr)	29	1.59	1.38	0.71	0.13	5.4E-03	5.9E-03	1.9E-03	3.4E-04	0.60	0.53	0.23	0.04
<i>Cephalophus silvicultor</i> (Fr)	26	3.37	2.39	2.58	0.51	3.1E-03	3.1E-03	1.7E-03	3.3E-04	0.59	0.55	0.19	0.04
<i>Giraffa</i> sp. (Br)	16	1.97	1.92	0.91	0.23	2.2E-03	1.8E-03	1.8E-03	4.4E-04	0.68	0.52	0.49	0.12
Kobus ellipsiprymnus (Gr)	19	1.65	1.28	1.07	0.25	5.1E-03	5.6E-03	2.9E-03	6.6E-04	0.84	0.68	0.66	0.15
Kobus kob (Gr)	13	1.61	1.10	1.03	0.29	5.4E-03	6.4E-03	3.1E-03	8.5E-04	0.84	0.66	0.53	0.15
Litocranius walleri (Br)	12	2.60	1.73	2.24	0.65	4.5E-03	4.4E-03	2.8E-03	8.1E-04	0.87	0.81	0.41	0.12
Redunca redunca (Gr)	7	2.00	1.49	1.04	0.39	4.6E-03	4.6E-03	1.2E-03	4.5E-04	0.66	0.59	0.27	0.10
Syncerus caffer (Gr)	27	1.54	1.36	0.80	0.15	4.7E-03	4.4E-03	2.4E-03	4.5E-04	0.56	0.56	0.23	0.04
Tragelaphus scriptus (Br)	19	1.77	1.39	1.12	0.26	4.8E-03	4.3E-03	2.0E-03	4.6E-04	0.61	0.49	0.42	0.10
Fossil taxa											_		
Reduncini	130	1.77	1.47	1.11	0.10	3.5E-03	3.0E-03	2.4E-03	2.1E-04	0.48	0.44	0.18	0.02
Member B	11	1.67	1.35	0.74	0.22	2.0E-03	1.6E-03	1.1E-03	3.4E-04	0.41	0.38	0.11	0.03
Member C	17	1.91	1.39	1.33	0.32	3.3E-03	2.5E-03	2.1E-03	5.1E-04	0.52	0.51	0.18	0.04
Member E	16	2.21	1.57	1.79	0.45	3.4E-03	3.6E-03	2.0E-03	4.9E-04	0.46	0.46	0.11	0.03
Member F	17	1.77	1.54	0.91	0.22	4.5E-03	4.8E-03	2.5E-03	6.2E-04	0.41	0.39	0.13	0.03
Member G	46	1.83	1.49	1.06	0.16	3.4E-03	2.6E-03	2.3E-03	3.4E-04	0.52	0.46	0.24	0.03
Member H	23	1.29	1.30	0.49	0.10	4.0E-03	3.4E-03	3.0E-03	6.2E-04	0.43	0.42	0.12	0.02
Tragelaphini	83	2.48	1.76	2.15	0.24	2.6E-03	1.9E-03	1.8E-03	2.0E-04	0.67	0.50	0.53	0.06
Member B	15	3.13	2.24	3.13	0.81	2.2E-03	1.7E-03	1.9E-03	4.8E-04	0.62	0.53	3.13	0.81
Member C	21	2.67	2.09	2.09	0.46	2.1E-03	1.5E-03	1.4E-03	3.1E-04	0.77	0.64	0.44	0.10
Member E	16	1.81	1.57	0.87	0.22	3.6E-03	3.1E-03	2.4E-03	6.0E-04	0.45	0.44	0.16	0.04
Member F	15	2.12	1.68	1.28	0.33	2.5E-03	2.0E-03	1.6E-03	4.2E-04	0.49	0.43	0.24	0.06
Member G	16	2.64	1.65	2.62	0.65	2.7E-03	2.3E-03	1.5E-03	3.6E-04	0.94	0.59	0.95	0.24

Table 3

Table 4A

## DMTA

ANOVA Member		df	SS	MS	F	р
Asfc	Effect	20	622088	31104	2.64	<0.001
	Error	370	4359252	11782		
epLsar	Effect	20	1092897	54645	5.20	<0.001
	Error	370	3888440	10509		
Hasfc81	Effect	20	799479	39974	3.54	<0.001
	Error	370	4181860	11302		

## Table 4B

Alcelaphus buselaphus (Gr)	Ab																			
Aepyceros melampus (MF)	E	Am																		
Cephalophus silvicultor (F)	AE		Cs																	
Giraffa sp. (Br)	E		А	Gc																
Kobus ellipsiprymnus (Gr)			AE	Ε	Ke		_													
Kobus kob (Gr)			AE	Ε		Kk		_												
Litocranius walleri (Br)			А	EH			Lw		_											
Redunca redunca (Gr)				Е				Rr		_										
Syncerus caffer (Gr)			AE	Ε			Н		Sc		_									
Tragelaphus scriptus (Br)			AE	Ε			Н			Ts		_								
Tragelaphini Member B	AE				AE	AE	EH	Е	AE	Ε	TMB									
Tragelaphini Member C	AE		Е		AE	AE	Е	Е	AE	AE		TMC		_						
Tragelaphini Member E	EH		AH	Е			Н				Е	EH	TME							
Tragelaphini Member F	EH		AH		E	Е	EH	Е	Е	Е				TMF						
Tragelaphini Member G	Ε		А		E	Е	Е	Е	Е	Е			Η	Η	TMG					
Reduncini Member B	EH	Η	AH	Н	EH	EH	EH	EH	EH	Ε	Н	Н	Η			RMB				
Reduncini Member C	E		А		E	E		Н	Е	E		Е		Η			RMC			
Reduncini Member E	Е		AH	Е			Н	Н			Е	EH			Н		RI	ME		
Reduncini Member F	Η		AH	EH			Н	Н			EH	EH		E	E	Е		F	RMF	
Reduncini Member G	Ε		AH	Е	Е	Е	Η		E	Е	Е	AEH				Е			RM	ИG
Reduncini Member H	EH	AH	AH	AEH	Η	Η	AH	Н	Η		AE	AEH		А	AH	E	A		A	RMH