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

Cécile BLONDEL^{1*}, Gildas MERCERON¹, John ROWAN², Jérôme SURAULT¹, Jean-Renaud BOISSERIE^{1,3}

¹Laboratoire Paléontologie Évolution Paléoécosystèmes Paléoprimatologie: UMR 7262, Bât. B35 TSA 51106, 6 rue M. Brunet, 86073 Poitiers Cedex9, France. Email: cecile.blondel@univ-poitiers.fr; gildas.merceron@univ-poitiers.fr; jerome.surault@univ-poitiers.fr

²Department of Anthropology, University at Albany, 1400 Washington Avenue, Albany, NY 12222 USA. Email: jrowan@albany.edu

³Centre Français des Études Éthiopiennes, USR 3137 (CNRS & MAEDI, Ambassade de France en Éthiopie) P. O. Box 5554, Addis Ababa, Ethiopia. Email: jean.renaud.boisserie@univ-poitiers.fr.

*Corresponding author: cecile.blondel@univ-poitiers.fr (C. Blondel)

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 (Bonafille 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,
10 Bobe and Eck, 2001, Blondel et al., 2018). Extant reduncins are C₄ grazing antelopes (Cerling
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 C₃-C₄ mixed-feeding to C₄-dominated between ~ 3-1 Ma (Negash et
18 al., 2015, 2020), whereas they had C₄-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
22 unlike that of their extant relatives, as Spencer (1997) suggested for *Menelikia*? Were they
23 consuming C₄ grasses as their extant relatives, or C₄ browse, as some dicotyledonous plants
24 (e.g., succulent Amarantacea) have a C₄ metabolic pathways? Indeed, it is possible they could
25 have been C₃ grazers despite the fact that C₃ 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.

29 The objectives of this paper are two-fold. First, we aim to determine the feeding
30 preferences of reduncins from the Shungura Formation. Second, we aim to use this
31 information to make inferences about Lower Omo Valley environments from 2.9 Ma to 1.8
32 Ma, and to contextualize the Shungura record by drawing comparisons with broader patterns
33 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

51 compared the DMTA and dental mesowear results of Reduncini from the Shungura Formation
52 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 *lyropera*, 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.

88 Because the reduncin dentitions are not always associated with cranial remains, and several
89 taxa have overlapping dental sizes, taxonomic attribution below the tribal level is not possible
90 for most of the specimens (Gentry, 1985). For this reason, we aggregated them at the tribal
91 level for each member. In total, we analyzed 130 specimens for DMTA and 205 specimens
92 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 ruminant 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 C₄ grazers (Estes, 1991;
106 Cerling et al., 2003). Buffalo and reedbucks 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
109 bushbuck (*Tragelaphus scriptus*, n=19) and the reedbuck (*Litocranius walleri*, n=12) are C₃
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 reedbuck (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
122 from the dataset published by Fortelius and Solounias (2000). Following their approach, all
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

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

133 We examined fossil teeth preferably on the labial cups of upper second molars and the lingual
134 cusps of lower second molars with light and moderate wear stages (following Fortelius and
135 Solounias, 2000; Kaiser and Fortelius, 2003 and Louys et al., 2011). Fortelius and Solounias
136 (2000) show that wear in ungulates is stable during the lifespan except for the earliest and
137 latest stages. Rivals et al. (2007) indicate that ontogenetic changes are more pronounced for
138 brachydont ungulates, but that mesowear signals are relatively stable for mesodont and
139 hypsodont species, such as for the reduncins studied here.

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

147 3.2. Dental Microwear Textural Analysis

148 DMTA was analyzed following Blondel et al. (2018). The analysis was performed
149 preferentially on the second upper and lowers molars. When second molars were weathered or
150 unavailable, the isolated third or first molars were selected to maximize the fossil sample size
151 (Schulz et al., 2010; Ramdarshan et al., 2017). The mesiolingual paracone or protocone facets
152 and the distolabial protoconid facets were molded with a silicone polyvinylsiloxane (medium
153 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 × 200 μm 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 (*HAsfc*_{81-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
180 and Iman, 1981; Sokal and Rohlf, 1969). One-way analysis of variance (ANOVA) for each
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 ($n=205$; $\text{mean}=1.23 \pm 0.07$;
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 ± 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 ($n=29$, $\text{MWS}=0.79$) plot closest to *L. walleri*
194 ($n=69$, $\text{MWS}=0.75$) and significantly differ from the grazer *A. buselaphus* (Table 2B). In
195 Member C, reduncins 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
213 anisotropy ($epLsar = 2 \times 10^{-3}$) and low complexity ($Asfc = 1.67$). The HSD test (Table 4B)
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

220 the LSD test shows that they differ from those in Member F, Member G, and Member H in
221 anisotropy (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
235 LSD test.

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

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

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

292 during the dry season they prefer leaves of shrubs and trees (Estes, 1991, Plumptre and
293 Wronski, 2013). The specimens analyzed here may record this dietary versatility. It is also
294 important to note that several studies have challenged the hypothesis that anisotropy (*epLsar*)
295 reflects only grass consumption. For instance, koalas in Hedberg and DeSantis (2017) and roe
296 deer in Merceron et al. (2010) show that high anisotropy (*epLsar*) on shearing molar facets is
297 not specifically related to grass-eating habits but also tough leaf-eating habits requiring a
298 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 C₄ 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).

314 Indeed, our dental wear studies suggest that Member B reduncins (Fig. 6) were
315 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,
330 2000). Stable carbon isotopes ($\delta^{13}\text{C}$) of tooth enamel for Member B reduncins indicate a
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_3/C_4 browser-grazers, and not exclusively C_4 grazers like their living
333 counterparts (Cerling et al., 2003; Sponheimer et al., 2003).

334 Dental wear analyses suggest that Member C reduncins had a diet ranging from mixed
335 feeding to grazing. DMTA in general suggests mixed feeding like *A. melampus* (Fig. 5),
336 whereas the mesowear score falls similar to grazers like *R. redunca* (obligate grazers, 90 %
337 monocots) and *K. ellipsiprymnus*, variable grazers (Fig. 4, mean=1.29, 1.14, and 1.09
338 respectively). The slight discrepancy between intra-individual microwear and mesowear
339 signals may be linked to differences in temporal resolution and scale of these proxies, such as
340 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 *M. leakeyi* and *K. ancystrocera* 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 *M. leakeyi* (24.4 %) with *K. sigmoidalis* (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 $\delta^{13}\text{C} = -1.5\text{‰}$,
349 Negash et al., 2020) suggest that reduncins from Member C, hence most likely represented by
350 *M. leakeyi* and *K. sigmoidalis*, had mixed C₃/C₄ to C₄ grass-dominated diets. This differs from
351 Member C tragelaphins, represented by *Tragelaphus nakuae*, which were C₃/C₄ mixed
352 feeders preferring C₄ browse, as the presence of succulent C₄ 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*
357 and *S. caffer*. Enamel $\delta^{13}\text{C}$ values of Member E reduncins indicate a pure C₄ diet (n=10,
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 C₄-focused
361 diet ranging from grazing to mixed feeding, whereas *T. nakuae* and *T. gaudryi* were more
362 clearly C₃/C₄ mixed feeders (Blondel et al., 2018).

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

365 6). These results, supplemented with $\delta^{13}\text{C}$ values of tooth enamel (n=10, mean $\delta^{13}\text{C} = -1.3\text{‰}$,
366 Negash et al., 2020), suggest that reduncins from Member F, *K. sigmoidalis* and *M. lyrocer*
367 (51.2 % and 48.8 % respectively), were C₄ grazers. In contrast, *T. nakuae* and *T. gaudryi* were
368 C₃/C₄ 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. lyrocer*
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.
375 However, tooth enamel $\delta^{13}\text{C}$ values (n=11, $\delta^{13}\text{C} = -0.7\text{‰}$, Negash et al, 2020) indicate they
376 consumed slightly more C₄ plants than Member C reduncins ($\delta^{13}\text{C} = -1.5 \text{‰}$). Collectively,
377 these data suggest that Member G reduncins were mixed feeders favoring C₄ grasses.

378 The combination of the mesowear score and the DMTA suggest that reduncins in
379 Member H, 94.4 % of which represent *M. lyrocer* (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
382 specimens differ from *K. kob*, *K. ellipsiprymnus*, and *L. walleri* in having lower values of
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 *M. lyrocera* 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 $\delta^{13}\text{C}$ values
396 of tooth enamel (n=10, mean $\delta^{13}\text{C} = -1.3\text{‰}$, Negash et al, 2020) suggest that Reduncini from
397 Member H had a C₃/C₄ to pure C₄ diet. Together, data from these proxies indicate that
398 Member H reduncins consumed probably soft C₄ 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 C₃-C₄ browsing to mixed feeding from Member
406 B through Member C. They were much more engaged in C₄ grazing than the tragelaphins
407 from Member E through Member F, and less in lower Member G, and finally they likely fed
408 on tender C₄ grasses in Member H around 1.8 Ma.

409 5.3. Paleoenvironmental implications of reduncin diets

410 All living reduncins, except the mountain reedbuck (*R. fulvorufula*), inhabit wetlands
411 or mesic savannas in the African tropics and never stray far from permanent water bodies
412 (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 C₄ 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. lyroccera* 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 C₄ 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
430 biomass, the $\delta^{13}\text{C}_{\text{ecosystem}}$ (Paquette and Drapeau, 2021), show a gradual opening of the
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. lyroccera*) 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. lyropera* 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 *atopocranium* 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 C₄
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 C₄ 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 C₄
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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492

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783 Figure captions

784 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

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

787 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

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

791

792 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

795 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

799 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.
822 Mesowear score (MWS). C. Enamel carbon stable isotopic composition ($\delta^{13}\text{C} \text{‰ VPDB}$) of
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).

825

826 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 assignment; MWS: mesowear score;
848 DMTA: dental microwear textural analysis.

849 S2. Values for dental microwear texture parameters (DMTA) for living species and Shungura
850 Formation specimens. *Asfc*: complexity; *epLsar*: anisotropy; *HA_{sfc}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.
857

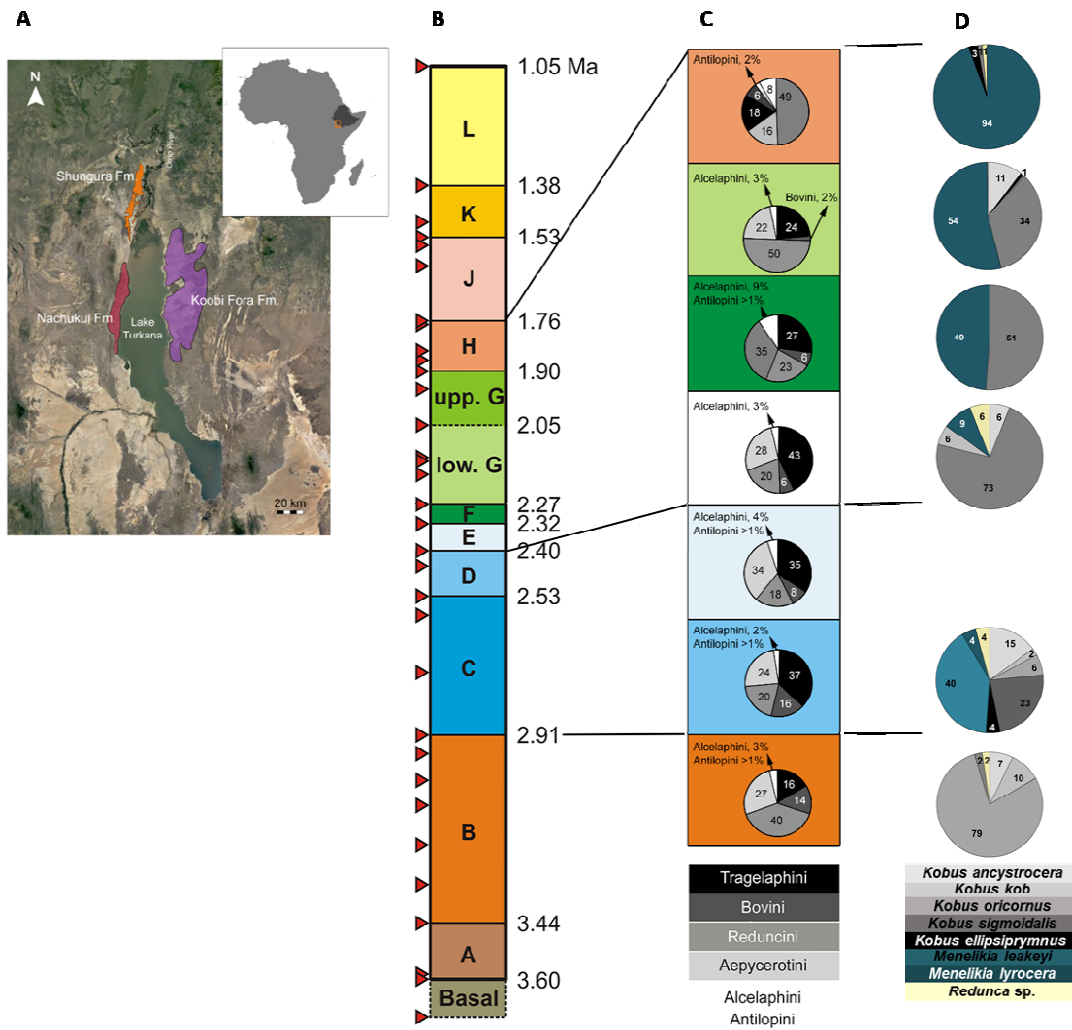


Fig. 1

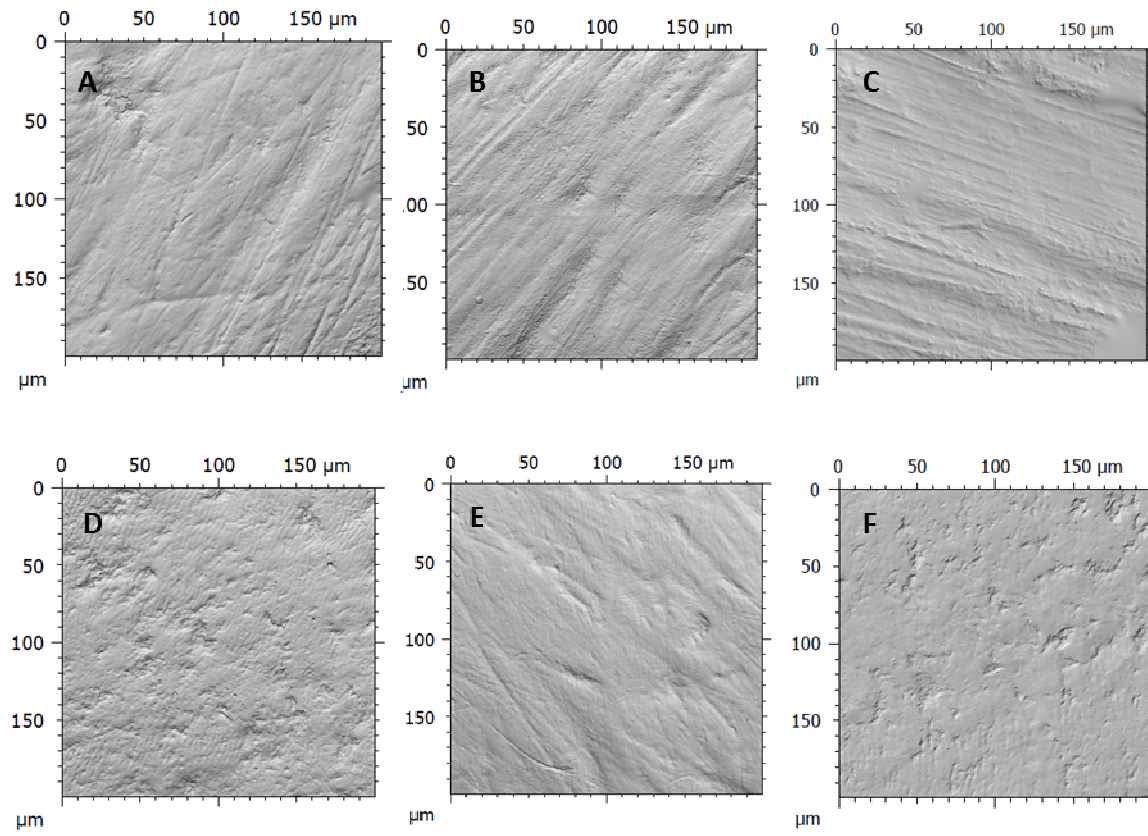


Fig. 2

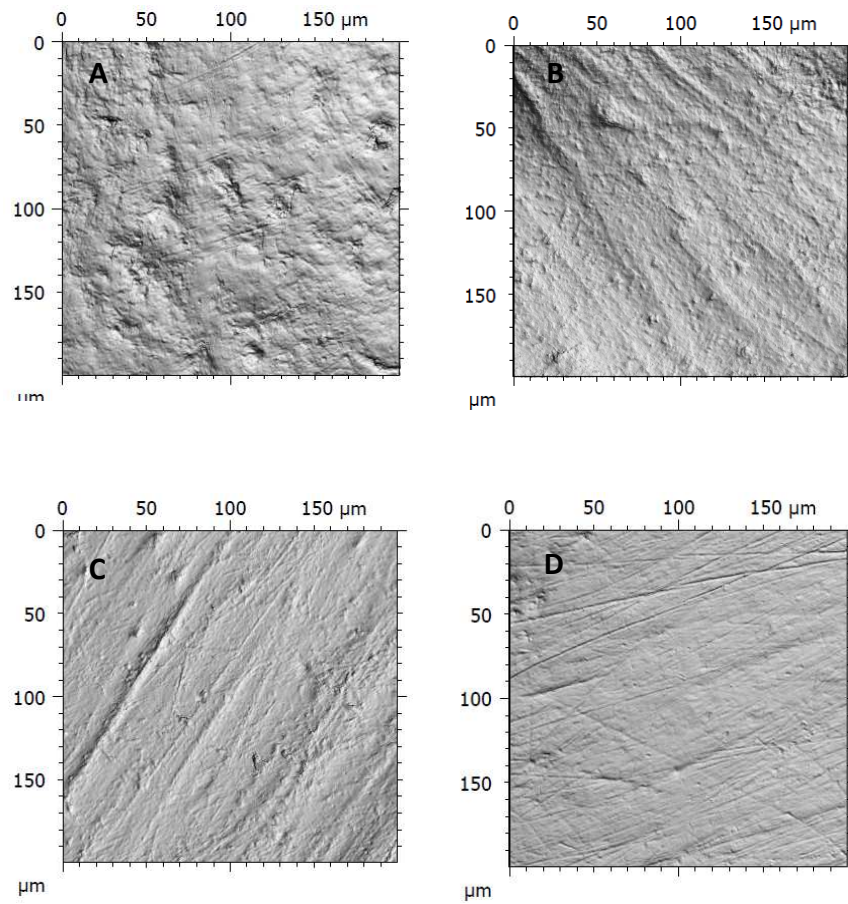


Fig. 3

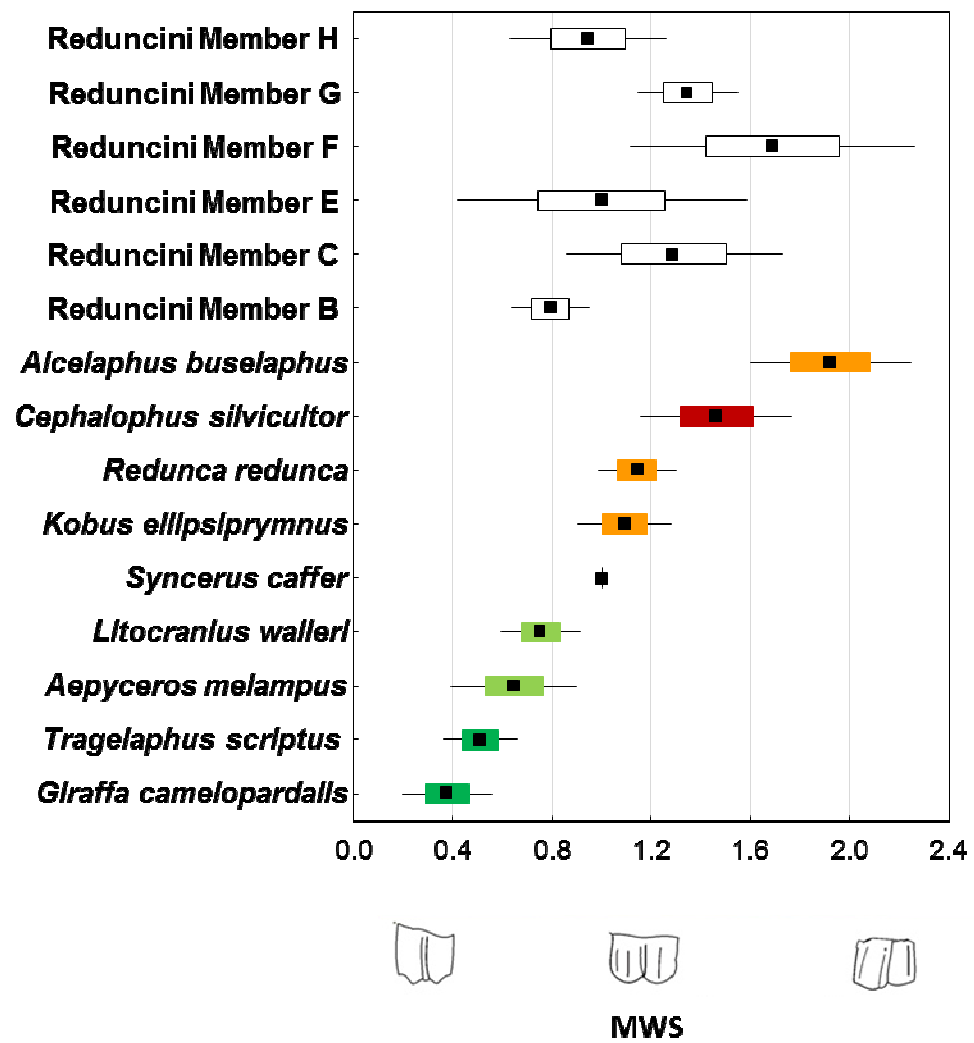


Fig. 4

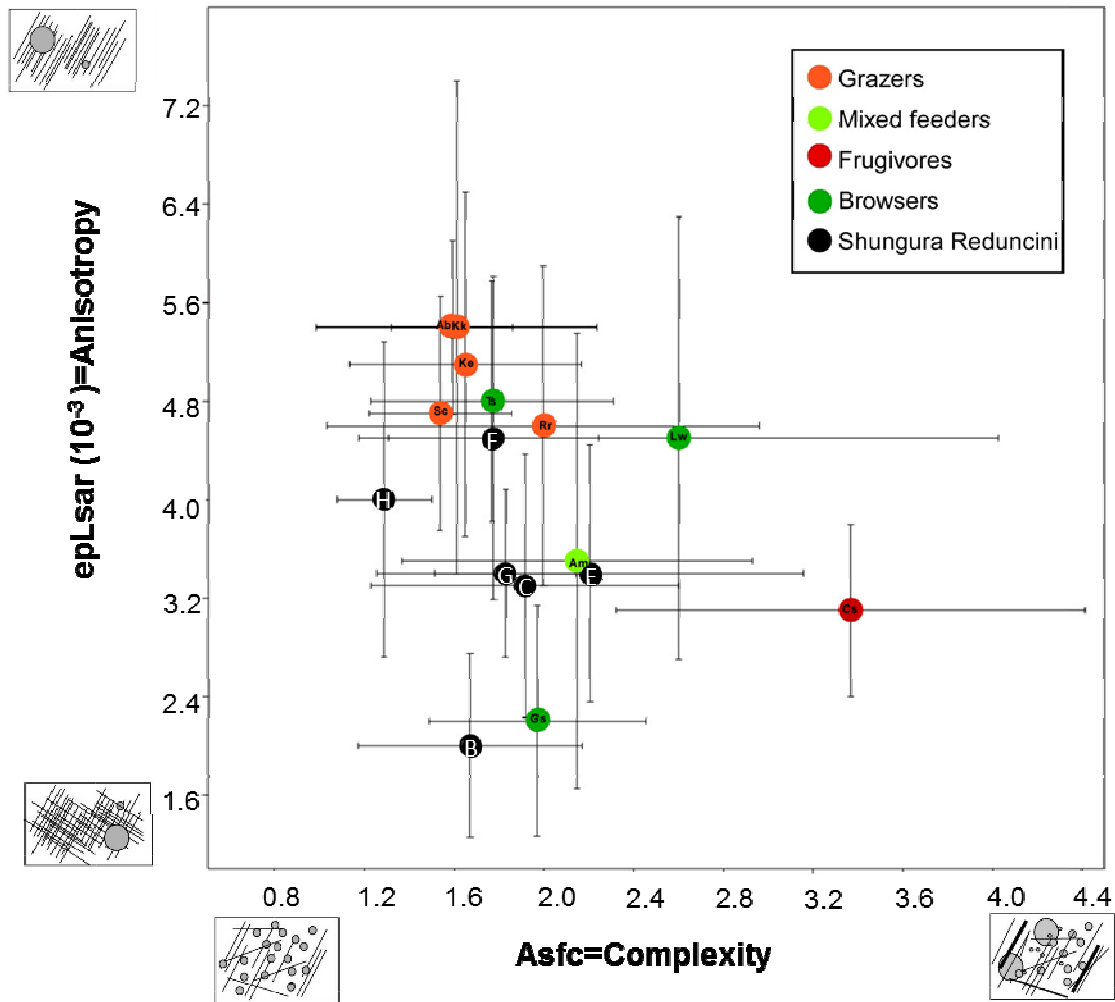


Fig. 5

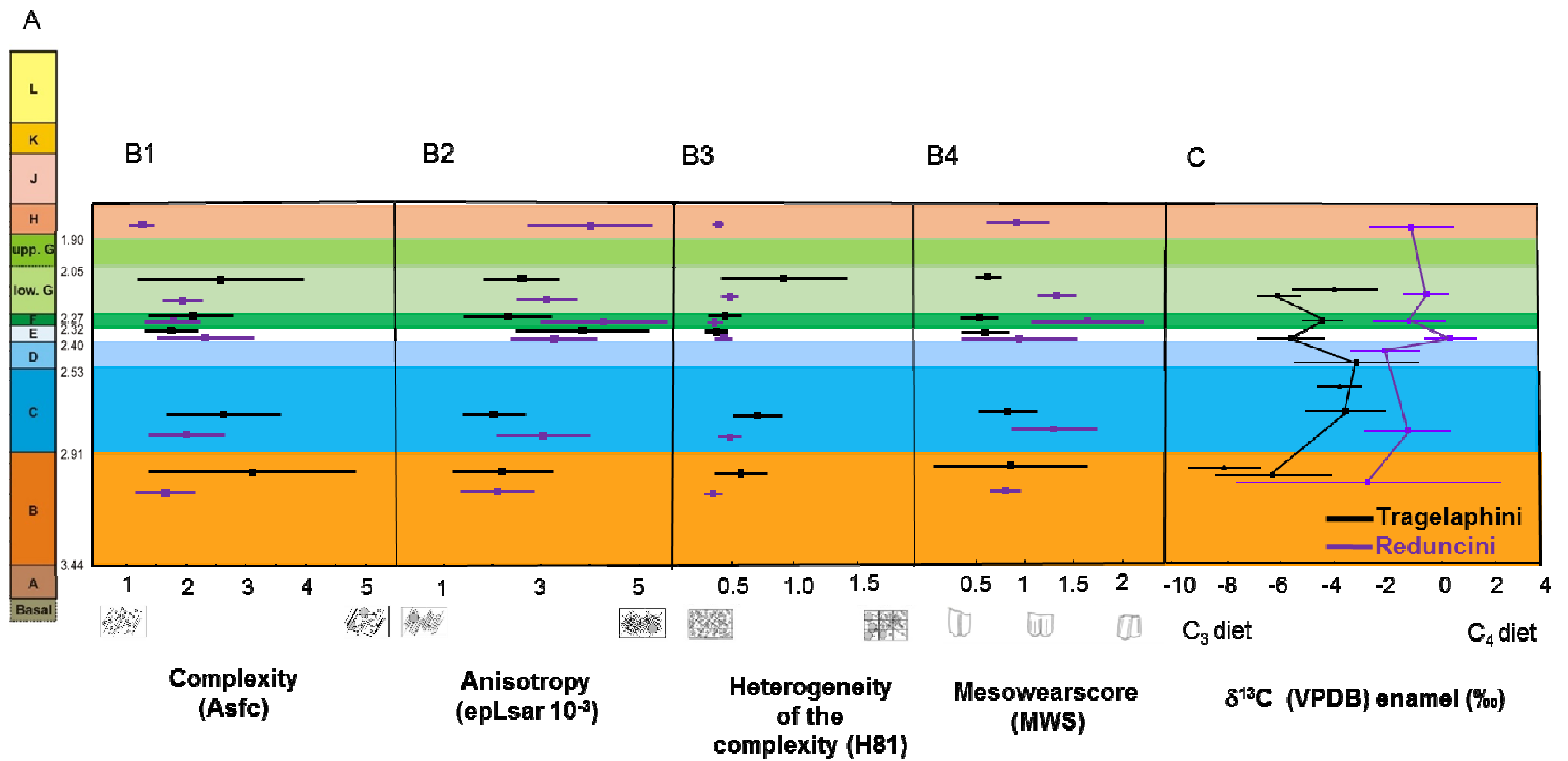


Fig.6

Table 1

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

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

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					epLsar (10^{-3})				Hasfc81cells			
	n	m	med	sd	sem	m	med	sd	sem	m	med	sd	sem
<i>Aepyceros melampus</i> (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
<i>Alcelaphus buselaphus</i> (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
<i>Kobus ellipsiprymnus</i> (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
<i>Kobus kob</i> (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
<i>Litocranius walleri</i> (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
<i>Redunca redunca</i> (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
<i>Syncerus caffer</i> (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
<i>Tragelaphus scriptus</i> (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	p
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		

