

**Cover Page:**

**Title:**

Ruminant mesowear reveals consistently browse-dominated diets throughout the early and middle Miocene of eastern Africa

**Author Information:**

**Abigail S. Hall\***

Department of Anthropology, University of Minnesota, 301 19<sup>th</sup> Avenue South, Minneapolis, Minnesota, 55455, USA. hallx827@umn.edu

**Susanne Cote**

Department of Anthropology and Archaeology, University of Calgary, 2500 University Drive NW, Calgary, Alberta, Canada, T2N 1N4. scote@ucalgary.ca

**\*Corresponding Author**

**Keywords:** *Walangania*; *Dorcatherium*; *Canthumeryx*; hypsodonty; Fort Ternan; Maboko

## **Abstract**

The ecological preferences of ruminant artiodactyls are commonly used to reconstruct the paleoenvironment of Neogene fossil localities throughout Africa. However, comparatively little research has focused on the ecology of ruminant artiodactyls from the Miocene of Africa. Here, we contribute new molar mesowear and hypsodonty data for the ruminant artiodactyls from the early and middle Miocene of Kenya and Uganda. Macroscopic dental characteristics of 608 tragulids, stem pecorans, giraffoids, and bovids dated to between 20 and 13.7 Ma were analyzed. Our hypsodonty results reveal that, whereas tragulids remain brachydont throughout the early and middle Miocene, pecoran ruminants experience an increase in hypsodonty due to the appearance of high-crowned bovids and climacoceratids that migrate into eastern Africa in the middle Miocene. Results from dental mesowear analysis suggest that all tragulids and pecorans were likely browsers, with only one taxon showing mesowear values that overlap with both browsers and mixed feeders in both the upper and lower molars (*Canthumeryx sirtensis*). None of the taxa analyzed had mesowear scores indicative of a grazing diet. Surprisingly, middle Miocene bovids and climacoceratids, despite possessing gross tooth morphologies adapted to abrasive diets, were largely utilizing a browsing diet. Although the early and middle Miocene habitats of eastern Africa were likely very heterogenous, none of the ruminant artiodactyls present in these habitats is interpreted as having incorporated grasses into their diet in significant quantities.

## 1           **1. Introduction**

2           Ruminant artiodactyls are commonly found in Neogene and Quaternary fossil assemblages  
3 throughout Africa and their ecological preferences have been used extensively to broadly  
4 reconstruct paleoenvironments at Plio-Pleistocene hominin-bearing fossil localities (e.g.  
5 Plummer and Bishop, 1994; Sponheimer et al., 1999; DeGusta and Vrba, 2003; Schoeninger et  
6 al., 2003; Schubert et al., 2006; Kingston and Harrison, 2007; Ungar et al., 2007; Faith et al.,  
7 2011; Barr, 2015; Fortelius et al., 2016; Dumouchel and Bobe, 2020; Ungar et al., 2020). To  
8 date, very little research has focused on the Miocene of Africa (but see Solounias and Moelleken,  
9 1993; Cerling et al., 1997; Blondel et al., 2010; Ungar et al., 2012), though ruminant paleodiets  
10 have provided important insights into the paleoenvironments of the North American, South  
11 American and European Miocene (e.g., Janis et al., 2000; Fortelius et al., 2002; Kaiser and  
12 Rössner, 2007; Fraser and Theodor, 2013; Madden, 2014). The lack of data on early and middle  
13 Miocene African ruminant paleoecology is somewhat surprising, as it is during the Miocene that  
14 one might expect ruminant artiodactyls to begin diversifying their diets to include mixed feeding  
15 and grazing, as grasslands and grazing become more common in the late Miocene of Africa (e.g.  
16 Morgan et al., 1994; Uno et al., 2011, 2016; Feakins et al., 2013). Growing evidence suggests  
17 that the appearance of open habitats begins in the early Miocene, with heterogeneous habitats  
18 documented at fossil localities throughout the region (e.g. Lukens et al., 2017; Peppe et al., 2017,  
19 2018, 2020). In addition, African Miocene ruminants become more taxonomically diverse  
20 throughout the Miocene, due to both immigration and *in situ* evolution, suggesting that niche  
21 partitioning may become more important in this clade through time.

22           Numerous methods can be used to reconstruct ruminant paleodiets, including dental  
23 microwear, dental mesowear, hypsodonty, ecomorphology of the cranium and mandible, and

24 stable carbon isotopic analysis. We implement mesowear and hypsodonty because they permit  
25 large numbers of specimens to be analyzed, which is ideal for examining trends across space and  
26 time. In addition, most Miocene ruminant taxa are known from limited cranial material and were  
27 defined largely on the basis of dental characteristics (e.g. Whitworth, 1958). A critical  
28 consideration is that these two methods provide very different information on paleodiet.  
29 Hypsodonty, or increased tooth crown height, is thought to be an adaptive response to increased  
30 dental wear and reflects long-term dietary trends (Janis and Fortelius, 1988). There is a rich  
31 literature on whether hypsodonty is an adaptation to abrasive plants or to increased grit in the  
32 diet, and it often correlates well with the openness of the habitat (Mendoza and Palmqvist, 2007;  
33 Damuth and Janis, 2011; Kaiser et al., 2013; Semprebon et al., 2019). Mesowear, on the other  
34 hand, provides information on the foods that the animal was actually consuming during its  
35 lifetime through an examination of how the teeth are worn (Fortelius and Solounias, 2000;  
36 Ackermans, 2020).

37 Here, we present a mesowear and hypsodonty dataset for ruminant artiodactyls from the  
38 early and middle Miocene of eastern Africa (Kenya and Uganda; Figure 1, Table 1). Our dataset  
39 includes fossil localities dated to between 20 and 13.7 Ma. Our primary questions are (1) what  
40 kinds of diets are these ruminant artiodactyls consuming and how do they shift through space  
41 and time? and (2) does this provide any information on the early occurrence and spread of  
42 grasses and more open habitats in Africa?

43

## 44 **2. Methods**

### 45 ***2.1. Specimens***

46 More than 600 ruminant specimens from the early and middle Miocene collections housed  
47 at the National Museums of Kenya in Nairobi and the Ugandan National Museum in Kampala  
48 were used for this study. All dental specimens assigned to Ruminantia from the early and middle  
49 Miocene sites of Napak, Tinderet (Songhor, Chamtwara, Legetet, Koru, Mteitei Valley, and  
50 Kapurtay), Rusinga, Mfangano, Karungu, Kalodirr, Moruorot, Buluk, Maboko and Fort Ternan  
51 were examined (Table 1; Figure 1). Each locality was assigned to one of three time bins using  
52 radiometric and stratigraphic data from the literature (Table 1). These three time bins correspond  
53 to distinct changes in the composition of ruminant communities in eastern Africa during the early  
54 and middle Miocene.

55 Ruminant artiodactyls in the Miocene of eastern Africa comprise two main groups: (1) the  
56 Tragulidae and (2) early members of the infraorder Pecora. All ruminant artiodactyl lineages in  
57 Miocene Africa appear to be immigrants from Eurasia. In the earliest Miocene sites in eastern  
58 Africa (~ 20 – 19 Ma; time bin #1), tragulids are more diverse than pecorans, though only one  
59 species, *Dorcatherium songhorensis*, is common and widespread (Whitworth, 1958; Pickford,  
60 2002; Geraads, 2010). Pecorans are represented initially by a single taxon, *Walangania*  
61 *africanus*, though a single specimen from Songhor may represent a second taxon, “*Gelocus*”  
62 *whitworthi* (Hamilton, 1973; Cote, 2010). The taxonomic status of *W. africanus* is unclear and it  
63 is probably best considered an undifferentiated stem pecoran (Cote, 2010), though some have  
64 suggested affinities to the Cervoidea (Janis and Scott, 1987; Gentry, 1994); similarities to  
65 *Dremotherium*, which has variably been considered a moschid (Prothero, 2007) or a more basal  
66 member of crown Pecora affiliated to either a bovidomorph or cervoid clade (Sánchez et al.,  
67 2015; Mennecart et al., 2015), are also apparent (Gentry, 1994; Cote, 2010). From roughly 19  
68 Ma onwards, other pecoran taxa begin to immigrate to Africa, including the giraffoid

69 *Canthumeryx sirtensis* (Hamilton, 1978; Harris et al., 2010; Cote et al., 2018), which appears in  
70 our time bin #2 (18.5 – 17 Ma). Time bin #2 also contains three tragulid species: *Dorcatherium*  
71 *chappuisi*, *Dorcatherium pigotti*, and *Dorcatherium parvum* (Geraads, 2010; Whitworth, 1958).  
72 Time bin #3 (15 – 13.7 Ma) is demarcated by the arrival of the earliest bovids into the region  
73 (Gentry, 1970, 1994, 2010). The oldest bovids are from Maboko (~ 15Ma; Feibel and Brown,  
74 1991). They are highly fragmentary and taxonomically poorly understood, but likely several taxa  
75 are represented, including a hypsodontine (*Hypsodontus pickfordi*) and an early antilopine  
76 (*Homoiodorcas* sp.; Gentry, 2010). Bovid material from Fort Ternan (13.7 Ma; Pickford et al.,  
77 2006) is much more complete and at least four taxa are represented: *Hypsodontus tanyceras*,  
78 *Kipsigicerus labidotus*, *Gentrytragus thomasi* and a small antilopine (Gentry, 1970, 2010). In  
79 addition, in time bin #3 the giraffoids have diversified into multiple lineages (*Climacoceras*  
80 *gentryi*, *Climacoceras africanus*, *Paleotragus primaevus*; Harris et al., 2010) but tragulids form  
81 a more minor component of the fauna, with possibly only a single species represented at Fort  
82 Ternan *Dorcatherium chappuisi* (Whitworth, 1958; Geraads, 2010).

83 Taxonomic and provenience information is associated with each specimen in both the  
84 National Museums of Kenya in Nairobi and the Ugandan National Museums in Kampala. Most  
85 specimens had been identified previously by other workers. We confirmed and updated specimen  
86 identifications, and new specimens were identified using the most up-to-date published  
87 taxonomic frameworks (Bovidae: Gentry, 2010; Stem Pecorans: Cote, 2010; Giraffoids: Harris et  
88 al., 2010; Tragulids: Geraads, 2010). The Maboko bovids are particularly fragmentary and have  
89 the greatest taxonomic uncertainty. In all analyses, we have treated them simply as indeterminate  
90 bovids.

91 All 608 maxillary and mandibular molar (M1-M3 and m1-m3) specimens from our study  
92 localities were examined to see whether they could be used to calculate a hypsodonty index, be  
93 scored for mesowear, or both. Only individuals with little to moderate wear were used for  
94 mesowear analysis and only specimens with little to no wear were used for hypsodonty,  
95 following standard procedures to ensure meaningful results that reflect both complete tooth  
96 crown height and macrowear (e.g. Janis, 1988, 1990; Fortelius and Solounias, 2000). Both  
97 isolated molars and molars still within the mandible or maxilla were included. Specimens were  
98 examined for completeness of individual teeth by eye and then under a hand lens. Only those  
99 molars which were complete with no breaks were used for hypsodonty. Molars with at least one  
100 intact buccal cusp were scored for mesowear. When a specimen had more than one molar that  
101 could be scored, we chose the second molar, if available. Otherwise, the molar with the least  
102 wear was chosen for both mesowear and hypsodonty. This would give more conservative  
103 mesowear results as sharpness is not an artifact of wear stage, but blunting may be (Fortelius and  
104 Solounias, 2000).

105 The full list of specimens used in this study is available in Supplemental Information  
106 (Table S1). Following preliminary examination of each specimen for its suitability, 608  
107 individuals were measured for hypsodonty and/or scored for mesowear analysis. 282 molars  
108 were used for hypsodonty analysis and 579 for mesowear analysis.

109

110

## 111 **2.2. Methods**

### 112 **2.2.1. Hypsodonty**

113 Hypsodonty was evaluated using the ratio of molar crown height to molar crown length  
114 following the method employed by the NOW Database (Neogene Old World Database;

115 <https://nowdatabase.org/> by The NOW Community / CC BY 4.0.; Fortelius et al., 2002). This  
116 method was used instead of the original method described by Janis (1988) in part because it was  
117 much easier to obtain a repeatable, accurate length measurement than a width measurement from  
118 the ruminant molars in our study. Although the original method developed by Janis (1988) was  
119 based only on mandibular third molars and the method proposed by Fortelius et al. (2002)  
120 includes only second molars, many subsequent studies expanded hypsodonty analysis to include  
121 both first and second lower molars and first, second and third upper molars for ruminant  
122 artiodactyls (e.g., Bibi, 2007; Feranec, 2007; Eronen et al., 2010, 2012; Fraser and Theodor,  
123 2013; Kubo and Yamada, 2014; Strani et al., 2018; Bai et al., 2020). To increase sample size, all  
124 available unworn or slightly worn first, second and third molars from the upper dentition and  
125 first and second molars from the lower dentition were measured. Mandibular molar height was  
126 measured on the lingual side from the base of the crown to the tip of the tallest cusp (metaconid  
127 or entoconid). Maxillary molar height was measured on the buccal side from the base of the  
128 crown to the tip of the tallest cusp (paracone or metacone). Length measurements were taken as  
129 maximum distance between the most mesial margin and most distal margin of the molar. All  
130 measurements were taken using sliding digital calipers and recorded to the nearest tenth of a  
131 centimeter. Measurements were taken by both authors on all specimens and compared. When  
132 measurements differed between observers by more than 0.2 mm the specimen was remeasured  
133 by both authors to ensure an accurate measurement was recorded. These data were then  
134 converted to a ratio of height to mesiodistal length, and the average for each taxonomic grouping  
135 in each time bin was calculated (Table 2). Following the conventions of the NOW Database (e.g.  
136 Fortelius et al., 2002), each taxonomic group was then classified as one of the three classes of



137 hypsodonty: brachydont if the ratio of height to length was less than 0.8, mesodont if the ratio  
138 was between 0.8 and 1.2, or hypsodont if the ratio was greater than 1.2.

139

### 140 **2.2.2. Mesowear**

141 Mesowear incorporates two morphological criteria, cusp shape and occlusal relief, to  
142 estimate the diets of ungulates using a system of visual scoring (Fortelius and Solounias, 2000).

143 Cusp shape reflects the relative contributions of attrition (tooth-on-tooth wear) and abrasion  
144 (food-on-tooth wear). Teeth subjected to more attrition will retain sharp cusps, while those  
145 subjected to increased abrasion will have rounded cusps. Occlusal relief reflects the heights of  
146 the cusp tips relative to the inter-cusp valleys and low occlusal relief is typically seen in taxa  
147 experiencing both attrition and abrasion, such as grazers (Fortelius and Solounais, 2000).

148 Mesowear analysis has been used by many to infer the paleodiet of a variety of taxa, although  
149 most studies examine ungulates (e.g., Kaiser et al., 2000; Franz-Odenaal and Kaiser, 2003;  
150 Kaiser and Solounias, 2003; Rivals and Semprebon, 2006; Semprebon and Rivals, 2007; Blondel  
151 et al., 2010; Semprebon and Rivals, 2010; Fraser and Theodor, 2013; Fraser et al., 2014;  
152 Belmaker and O'Brien, 2017; Dumouchel and Bobe, 2020). Molars at a very early or advanced  
153 wear stage were excluded from the sample as molars in a very early wear stage tend to be  
154 characterized by more sharp cusps whereas those in a very advanced wear stage tend to be  
155 characterized by more blunt cusps (Fortelius and Solounias, 2000). Removing specimens from  
156 these two wear categories was done to prevent our results from being biased by extremes.

157 Originally, mesowear was only scored on the upper second molar (Fortelius and Solounias,  
158 2000), but to increase sample size many studies of fossil specimens have expanded the method to  
159 utilize at least one other molar tooth position and/or the inclusion of lower molars in their sample

160 (e.g., Blondel et al., 2010; Fraser et al., 2014; Yamada et al., 2016; Belmaker and O'Brien, 2017;  
161 van Asperen and Kahlke, 2017; Dumouchel and Bobe, 2020, Xafis et al., 2020).

162 In this study, we included both upper and lower molars from all three molar positions.  
163 Mesowear was scored on the sharpest buccal cusp on the upper M<sup>1</sup>, M<sup>2</sup>, or M<sup>3</sup> or the sharpest  
164 lingual cuspid on the lower m<sub>1</sub>, m<sub>2</sub>, or m<sub>3</sub>. When multiple teeth were available from the same  
165 mandible or maxilla, we preferentially chose the second molar, if it was well preserved. We  
166 recorded traditional mesowear parameters for cusp shape (sharp, round, blunt) and occlusal relief  
167 (high, low) as outlined by Fortelius and Solounias (2000) and made quantifiable in later  
168 publications (e.g., Rivals and Semperebon, 2006; Rivals et al., 2007, 2009). Numerous modified  
169 mesowear scoring systems have been developed since 2000 (reviewed in Ackermans, 2020) and  
170 we elected to use the scoring system developed by Fraser et al. (2014), defining five mesowear  
171 categories instead of four, and later implemented by Yamada et al. (2016) and van Asperen and  
172 Kahlke (2017). The fifth category effectively separates teeth that are 'high' and 'round'  
173 (Fortelius and Solounias, 2000) into 'high and round' and 'high and really round' (Fraser et al.,  
174 2014). This further division of high occlusal relief teeth into three categories, rather than the  
175 traditional two, seemed most appropriate for our data, which is composed almost exclusively of  
176 high occlusal relief teeth. Furthermore, Fraser et al. (2014) concluded their new method was  
177 better able to discriminate between browsers and mixed feeders when mandibular molars were  
178 included in the sample, as is the case in our study. After scoring tooth relief and cusp shape, each  
179 specimen was assigned a number as follows: 1 for teeth with high relief and sharp cusps, 2 for  
180 teeth with high relief and round cusps, 3 for teeth with high relief and very rounded cusps, 4 for  
181 teeth with low relief and round-blunt cusps, and 5 for teeth with low relief and blunt-flat cusps  
182 (Fraser et al., 2014: Fig. 1). Some mesowear scoring systems have introduced a category for

183 'sharp and low' teeth, often equivalent to a score of 2.5 (Rivals et al., 2009; Louys et al., 2011).  
184 We did not use this category as we did not observe any low relief teeth with sharp cusps in our  
185 sample.

186 Louys et al. (2011) showed convincingly that incorporating third molars into a mesowear  
187 dataset will result in 'sharper' scores, as these teeth will generally be less worn. Our dataset does  
188 include both mandibular and maxillary third molars, but they make up less than one fifth of our  
189 dataset. We also include first molars, which would tend to bias a dataset towards more round or  
190 blunt mesowear profiles. Consequently, we do not think that molar position is greatly impacting  
191 these data and that the relative sharpness or attrition-dominated signal in our sample is valid.

192 Mesowear scoring was done on original specimens with both the naked eye and under a  
193 hand lens. All specimens were assigned a score independently by each author. Scores for each  
194 specimen were then compared between authors and when scores were discrepant the authors  
195 revisited the specimen and came to a consensus about which mesowear category most accurately  
196 reflected the tooth wear displayed by the specimen.

197 Within each time bin, we tested whether tragulid and pecoran mean mesowear scores were  
198 significantly different using a Welch's Two Sample t-test. In all cases maxillary and mandibular  
199 scores were analyzed separately. To explore the relationships between taxa within each time bin,  
200 a Welch's Two Sample t-test was used when two taxa were compared and a single-factor  
201 analysis of variance (ANOVA) followed by a Tukey's multiple comparison test (Tukey's HSD  
202 test) was used when more than two taxa were compared. We also conducted additional inter-bin  
203 and intra-bin analyses, as sample sizes permitted.

204 Additionally, we explored the relationship between mean mesowear score and mean  
205 hypsodonty value for each taxon within our dataset. Maxillary and mandibular samples were

206 separated for each taxon. To determine the strength of the association between mean hypsodonty  
207 index and mean mesowear score within each taxon in our dataset a Pearson Correlation analysis  
208 was performed.

209 Recently, it has been noted in the literature that tooth wear data are often not independent  
210 of phylogeny, and therefore it is important to utilize phylogenetic comparative methods when  
211 possible to discriminate between dietary categories (Belmaker and O'Brien, 2018; Fraser et al.,  
212 2018). The lack of clear phylogenetic relationships for stem pecorans and stem giraffoids, and  
213 even amongst tragulids, makes the use of such methods here problematic.

214

### 215 **3. Results**

#### 216 **3.1 Hypsodonty**

217 Hypsodonty index remains consistent through time in tragulids in both the mandibular and  
218 maxillary molars (Fig. 3). In all three time bins tragulids have brachydont teeth (Table 2), with  
219 no discernable trends or differences in the range of hypsodonty values observed between time  
220 bins or between individual tragulid species.

221 In contrast, pecorans show a clear shift in maximum tooth crown height between the early  
222 and middle Miocene. The increase in hypsodonty in pecorans occurs between time bins #2 and  
223 #3 and is clearly driven by the bovids and the giraffoid *Climacoceras*, which are mesodont (0.8 –  
224 1.2) (Table 2; Fig. 3); all other pecorans in our study are classified as brachydont (height to  
225 length ratios of < 0.8). In both time bin #1 and #2 the taxon *W. africanus* is classified as  
226 brachydont, though our sample size of *W. africanus* in time bin #2 is small (6 maxillary  
227 specimens and 4 mandibular specimens; Table 2). We could only assess hypsodonty for a single  
228 mandibular molar of *Canthumeryx*.

229           These results matched our expectations, since tragulids maintain largely brachydont  
230 dentitions throughout the 6 million years that we sampled. Giraffoids and bovids show more  
231 variation in hypsodonty in general, as is reflected in our dataset. For every genus in our study,  
232 the maxillary molars give a slightly higher mean hypsodonty value than the mandibular molars  
233 (Table 2), but the range of values overlaps (Fig. 3).

234

### 235 **3.2 Mesowear**

236           In mesowear studies, the general perception is the mandibular molars tend to reflect more  
237 of a grazing signal than the maxillary molars (i.e., they are more rounded and thus have higher  
238 scores; Fortelius and Solounias, 2000; Franz-Odenaal and Kaiser, 2003). In contrast, both  
239 Louys et al. (2011) and Fraser et al. (2014) found the opposite pattern - that mandibular molars  
240 tended to have lower mesowear scores than their maxillary counterparts, reflecting more of a  
241 browsing signal. In our data there was a statistically significant difference between the mesowear  
242 scores for maxillary and mandibular molars in both tragulids and pecorans (two-way ANOVA  
243  $p < 0.05$ ), with mandibular molars typically having higher scores than maxillary molars within the  
244 same taxonomic and time bin grouping, following the pattern observed by both Fortelius and  
245 Solounias (2000) and Franz-Odenaal and Kaiser (2003) (Table 2). When the data were explored  
246 further using Two-sample t-tests, however, the only statistically significant difference found  
247 within a single taxonomic group between maxillary and mandibular molar mesowear scores was  
248 for the middle Miocene bovids (time bin #3; Two-sample t-test,  $df = 72.63$   $t = 2.62$ ,  $p = 0.011$ ). In  
249 this group, the mandibular molar mean mesowear score ( $1.63 \pm 0.49$ ) is significantly greater than  
250 the maxillary molar mean mesowear score ( $1.33 \pm 0.62$ ). No other groups showed a significant  
251 difference between mandibular and maxillary molar mesowear scores.

252 Mean mesowear scores for our taxonomic groupings are generally stable throughout the  
253 early and middle Miocene (Table 2; Fig. 4). Most molars in our dataset were assigned a  
254 mesowear score of 1 or 2. Very few specimens were assigned a mesowear score of 3 and just one  
255 bovid specimen from time bin #3 was assigned a mesowear score of 4 (Fig. 4; Table S1). There  
256 was a moderate positive correlation between the mean hypsodonty and mean mesowear score of  
257 each taxon within our dataset, however, this correlation is not statistically significant (Pearson:  $r$   
258  $= +0.31$ ,  $p = 0.24$ ,  $n = 17$ ).

259 In general, tragulids have low mesowear scores that are stable through time, with most  
260 individuals in our dataset assigned a mesowear score of 1 (Fig. 4; Table 2). For maxillary molars,  
261 tragulid mesowear scores are stable through time, there are no significant differences between  
262 time bins #1, #2, and #3 (Fig. 4; Table 3) and the mean scores are between 1.19 and 1.26. For  
263 mandibular molars, tragulid mesowear scores are only significantly different between time bin  
264 #1 and time bin #3 (Table 3) with the lowest scores in time bin #3 (mean =  $1.15 \pm 0.36$ ) and the  
265 highest scores in time bin #1 (mean =  $1.4 \pm 0.56$ , meaning that tragulid mandibular molar cusps  
266 are actually getting sharper through time. The mandibular molar mean mesowear score for  
267 tragulids in time bin #3 is the lowest of any time bin and additionally shows the lowest standard  
268 deviation amongst tragulids suggesting low within-group variability (Table 2).

269 Tragulids almost always had lower mean mesowear scores than pecorans. Across all three  
270 time bins and in both maxillary and mandibular molars, a higher proportion of tragulids were  
271 assigned a score of 1 compared to pecorans (Fig. 4). In time bin #1, the mean mesowear score of  
272 tragulids and pecorans differed significantly for both mandibular and maxillary molars (Table 3).  
273 In time bin #2 tragulids had lower mean maxillary molar scores than the pecorans, but that  
274 difference was not significant (Table 3), likely due to the small sample sizes of both

275 *Canthumeryx* and *Walangania*; the mean mesowear scores for mandibular molars were  
276 significantly lower for tragulids than for either of the pecoran taxa (Table 3). It is notable that in  
277 time bin #2, *Walangania* had mesowear scores lower than tragulids (mandibular molars) or  
278 almost as low (maxillary molars). In time bin #3 tragulids had lower mean maxillary scores than  
279 bovids and *Climacoceras*, but higher mean maxillary mesowear scores than *Paleotragus* (Table  
280 2), but none of these differences were statistically significant (Table 3). A post hoc Tukey HSD  
281 test revealed that the differences between tragulids and bovids, and between tragulids and  
282 *Climacoceras*, were statistically significant (Table 3).

283 Pecoran ruminants had more variable mesowear scores than tragulids, but they do not  
284 change much through time (Table 2; Fig. 4), which was not the result we expected. Overall,  
285 pecoran mesowear scores are not significantly different between time bins #1, #2, and #3 for  
286 either maxillary or mandibular molars (Table 3). *Canthumeryx* has the highest mesowear scores  
287 of all pecoran taxa and the highest across our entire dataset for both mandibular and maxillary  
288 molars (Table 2). The mean mandibular mesowear score for *Walangania* in time bin #2 is the  
289 lowest of all pecoran taxa and the lowest across our entire dataset, while *Paleotragus* in time bin  
290 #3 had the lowest mean maxillary molar mesowear score (Table 2).

291 Although no statistically significant differences were found when pecoran taxa were  
292 analyzed together between time bin #1, #2, and #3 for either maxillary or mandibular scores,  
293 when pecorans were analyzed at a finer taxonomic level within each time bin statistically  
294 significant results were found. In time bin #2 *Canthumeryx* had higher mean maxillary and  
295 mandibular mesowear scores than *Walangania* (Table 2). The difference between maxillary  
296 mesowear scores was not significantly different (Table 3). In contrast, for the mandibular  
297 dentition, an ANOVA revealed a statistically significant difference between the taxonomic

298 groups within time bin #2 and a post hoc Tukey HSD test showed significant differences in  
299 mandibular mesowear scores between *Walangania* and *Canthumeryx* (Table 3). In time bin #3  
300 *Climacoceras* had the highest mean maxillary mesowear score amongst the pecoran taxa while  
301 *Paleotragus* had the lowest mean maxillary score, but these differences were not found to be  
302 statistically significant (Table 3). Within time bin #3 bovids had the highest mean mandibular  
303 mesowear score amongst the pecoran taxa while *Paleotragus* had the lowest mean mandibular  
304 score (Table 2). According to an ANOVA there was a statistically significant difference in the  
305 mandibular molar mesowear scores in time bin #3, but a post hoc Tukey HSD test revealed these  
306 significant differences were not between the pecoran taxa (Table 3).

307       Where sample sizes allowed, further analyses were used to explore inter-bin and intra-bin  
308 species differences. We compared the mesowear scores of *Walangania africanus* between time  
309 bins #1 and #2. We also tested for differences amongst tragulid species in time bin #2 and  
310 between the two common bovid genera in time bin #3, *Kipsigicerus labidotus* and *Hypsodontus*  
311 *tanycerus* from Fort Ternan. A Two-sample t-test revealed that maxillary mesowear scores were  
312 not significantly different for *Walangania* between time bin #1 and time bin #2 but mandibular  
313 mesowear scores were significantly different (Table 3). For both maxillary and mandibular  
314 molars, the mean mesowear score for *Walangania* was higher in time bin #1 compared to time  
315 bin #2 (Table 2). Average mesowear scores for the two common Fort Ternan bovids *K. labidotus*  
316 (maxillary = 1.33; mandibular = 1.75) and *H. tanycerus* (maxillary = 1.43 and mandibular = 1  
317 .69) are not significantly different for either the mandibular or maxillary molars (Table 3). There  
318 are three tragulid species from Rusinga Island: *D. chappuisi*, *D. pigotti*, and *D. parvum* (Table  
319 1). There are no statistically significant differences among these taxa (Table 3), though the  
320 mandibular mesowear scores for *D. chappuisi* are higher (blunter) than either *D. pigotti* or *D.*



321 *parvum*, which is perhaps as expected in this more bunodont taxon. This pattern is not replicated  
322 in the maxillary molars.

323

## 324 **4. Discussion**

325

### 326 ***4.1 Paleodiets of eastern African early and middle Miocene ruminants***

327 Overall, our results suggest the entire study sample had largely browsing diets. Almost all  
328 of our specimens were scored as 1 or 2 on the scoring system developed by Fraser et al. (2014),  
329 indicating high relief and sharp or round cusps (Fig. 4). These would compare to scores of 0 and  
330 1 in the quantified system developed by Rivals et al. (2007) using the cusp shape and occlusal  
331 relief designations in Fortelius and Solounias (2000). When our values are compared to extant  
332 ruminants with known diets scored using the Fraser et al. (2014) scoring system, our mean scores  
333 for all taxonomic groupings overlap with mesowear scores found exclusively for browsers, and  
334 in some cases with mixed feeders, but never grazers (Fig. 5). Some of our groups show  
335 mandibular mean scores that are actually lower than any of the modern browsing taxa in Fraser  
336 et al.'s (2014) dataset (i.e., *Walangania* and *Dorcatherium* in time bin #2; *Dorcatherium* in time  
337 bin #3; Fig. 5b). Our data for maxillary molars are comparable largely with the sharper-cusped  
338 browsers in Fraser et al. (2014) but do also show some overlap with mixed feeders (Fig. 5a).  
339 That overlap with mixed feeders is being driven by the muntjac (*Muntiacus muntjak*), which has  
340 aberrantly low mesowear values (Fraser et al., 2014: Table 1). If the muntjac were removed from  
341 our dataset, our maxillary molar fossil data would not overlap with mixed feeders at all. We can  
342 also compare our data with the extant dataset of Louys et al. (2011) for African antelopes. They  
343 use the Rivals et al. (2007, 2009) scoring system that is based on Fortelius and Solounias's  
344 (2000) original categories, which begins at 0 instead of 1. Again, our mean mesowear scores for

345 each taxonomic group are comparable to the lowest (e.g. sharpest) scores in the Louys et al.  
346 (2011: Table 4) dataset, overlapping with browsers.

347 In time bin #1 (20 – 19 Ma), the mean mesowear scores for the tragulid *Dorcatherium*  
348 *songhorensis* are significantly lower than those for *Walangania africanus* but both are  
349 compatible with exclusively browsing diets in the mandibular molars (Fig. 5b). In the maxillary  
350 molars, values for *Walangania* overlap slightly with mixed feeders, driven by the muntjac's low  
351 mesowear values (Fig. 5a). In time bin #2 (18.5 – 17 Ma) there are two pecorans (*Walangania*  
352 *africanus* and *Canthumeryx sirtensis*) and three tragulid species (*D. pigotti*, *D. parvum*, and *D.*  
353 *chappuisi*). Again, the tragulid mesowear scores suggest browsing diets, as do the scores for *W.*  
354 *africanus*. The highest average mesowear scores we have recorded in the entire dataset are for *C.*  
355 *sirtensis*, an early giraffoid found only in time bin #2, but even this taxon would be, at most, a  
356 mixed feeder (Fig. 5). Average scores for both mandibular and maxillary molars of *C. sirtensis*  
357 overlap with some extant browsers (e.g pronghorn (*Antilocapra americana*), gerenuk  
358 (*Litocranius walleri*), and white-tailed deer (*Odocoileus virginianus*)), as well as with the mixed  
359 feeding muntjac (Fraser et al., 2014: Table 1). While the sample size is small, it is intriguing that  
360 mesowear scores for *Walangania* in time bin #2 are lower than those for time bin #1 (Table 2),  
361 though this difference is only statistically significant for the mandibular molars (Table 3). This  
362 could suggest some degree of niche partitioning, with *Canthumeryx* or a non-ruminant pushing  
363 *Walangania* towards an even more browse-dominated diet in the later part of the early Miocene.

364 In time bin #3 (15 – 13.7 Ma), there are tragulids, giraffoids, and bovids. All three groups  
365 have mesowear profiles compatible with browsing diets. This is as expected for the tragulids and  
366 for the giraffoid *Paleotragus*, which is a bunodont giraffoid that has previously been inferred to  
367 be a browser based on microwear (Cerling et al., 1997). In contrast, our results for the bovids and

368 the giraffoid *Climacoceras* are somewhat surprising. Our hypsodonty results show that middle  
369 Miocene bovids and climacoceratids are mesodont (indices between 0.8 and 1.2; Fortelius et al.,  
370 2002). In general, a higher hypsodonty index is associated with increased tooth wear (e.g. Janis  
371 1988, 1990; Janis and Fortelius, 1988; Damuth and Janis, 2011) so one might have expected to  
372 see higher mesowear scores in these mesodont taxa. This does not appear to be the case in our  
373 dataset. Bovid and *Climacoceras* mesowear scores are not higher than pecorans in time bins #1  
374 and #2 (Table 2) and are comfortably aligned with modern browsers (Fig. 5).

375 Ungar et al. (2012) performed dental microwear texture analysis on a small sample of  
376 tragulids from Songhor (time bin #1) and Rusinga (time bin #2). They found evidence for niche  
377 separation within the tragulids and concluded that *D. songhorensis* and *D. chappuisi* were  
378 variable grazers. Our results from mesowear and hypsodonty show no support for this  
379 interpretation and corroborate more conventional thinking that the tragulids of the past were  
380 similar to modern tragulids in occupying largely forest-floor browsing niches (Geraads, 2010;  
381 Dubost, 1978, 1984). Of course, microwear and mesowear are dietary proxies that operate on  
382 different time scales, with mesowear indicating diet over a much longer time period than  
383 microwear, which forms quickly and changes with short-term dietary shifts (reviewed in Davis  
384 and Pineda-Munoz, 2016). Even so, our results do not seem compatible, and further microwear  
385 and stable carbon isotopic analysis of the tragulids would hopefully resolve these discrepant  
386 findings.

387 Regarding frugivory, our quantitative mesowear data show little evidence for fruit  
388 consumption in either the tragulids or pecorans. Fortelius and Solounias (2000) noted that small  
389 frugivores such as the modern African tragulid *Hyaemoschus aequaticus* and duikers showed  
390 unusual mesowear patterns, with more rounded or blunt cusp tips than one would expect in a

391 'browser'. They attributed this to "tip crushing wear" associated with frugivory (Janis, 1990).  
392 Louys et al. (2011) included large numbers of duikers in their study, and found mesowear scores  
393 that overlapped with grazers, owing to the high degree of abrasion caused by hard fruits and  
394 seeds. In theory, frugivores consuming softer fruits should have attrition-driven mesowear  
395 signals that resemble browsers. It is possible that this is some of what we are seeing here, but it is  
396 difficult to tell without corresponding microwear analysis.

397

#### 398 ***4.2 Relationship to eastern African early Miocene paleoenvironments***

399 In the past, eastern African early Miocene paleoenvironments were often reconstructed as  
400 dense forest, perhaps an extension of today's central equatorial tropical forest belt (e.g. Andrews  
401 and Van Couvering, 1975). More recently, it has become clear that there is likely a great deal of  
402 environmental heterogeneity present in Kenya and Uganda during the early Miocene. Lukens et  
403 al. (2017) demonstrate that Karungu (time bin #2) had some very open environments through  
404 analysis of paleosol morphology and geochemistry. In contrast, Michel and colleagues (2014)  
405 demonstrate the existence of a dense and stable forest habitat at a specific Rusinga (time bin #2)  
406 fossil locality (R3). Multiple studies of stable carbon isotopes from most of the same early  
407 Miocene localities in this study (time bins #1 and #2) on the enamel of early Miocene herbivores,  
408 pedogenic carbonate, and paleosol bulk organics have suggested not dense forests, but more of a  
409 mixture of woodland habitats (Garrett et al., 2015; Arney et al., 2017; Butts et al., 2018;  
410 Kingston et al., 2018; Peppe et al., 2017, 2018, 2020). Finally, evidence from phytoliths suggests  
411 that grasses, including C<sub>4</sub> grasses, were indeed present at many of these localities (Kinyanjui et  
412 al., 2017; Novello et al., 2017; Peppe et al., 2020).

413 If more open environments, including grasses and even C<sub>4</sub> grasses, were present in the  
414 early Miocene of eastern Africa, then it is of great interest to determine whether herbivorous

415 mammals had begun widely incorporating these resources into their diets. Our data suggest that  
416 ruminant artiodactyls were not consuming much grass, however. *Canthumeryx sirtensis* is the  
417 only taxon that seems to show some signal for mixed feeding (Fig. 5). It is the largest of the early  
418 Miocene ruminants, so from the perspective of digestive physiology, it makes sense that this  
419 species would be more likely to consume less easily digestible grasses than the much smaller  
420 tragulids or *Walangania*.

421

### 422 ***4.3 The case of Fort Ternan***

423 The paleoenvironment of Fort Ternan (time bin #3) has been particularly controversial,  
424 with reconstructions ranging from dense tropical forest (Pickford, 1985) to ‘Serengeti’-like  
425 grasslands (Retallack, 1992). The bulk of evidence now available, however, seems to favor a  
426 more mosaic-like environment, with standing water surrounded by grasses and sedges, and trees  
427 in the vicinity (e.g. Bonnefille, 1994). Stable carbon isotopes from paleosols and mammalian  
428 enamel indicate the grasses must have been largely C<sub>3</sub> (Cerling et al., 1991, 1997), which is  
429 compatible with the paleofloral evidence (Bonnefille, 1994). There is no clear evidence of  
430 widespread grasslands, and the presence of C<sub>4</sub> grasses is largely equivocal. Furthermore, stable  
431 carbon isotope analysis of each of the common ruminant species at Fort Ternan showed isotopic  
432 values consistent with a C<sub>3</sub> diet (Cerling et al., 1997). Our data on the paleodiets of Fort Ternan  
433 ruminants strongly suggest that grazing was, at most, a minor component of their diets. This is  
434 somewhat contradictory with previous studies on the microwear of the bovids. Shipman et al.  
435 (1981) concluded that *Hypsodontus tanycerus* was a grazer, in contrast with a subsequent  
436 microwear study that classified it as a clear browser (Cerling et al., 1997). *Kipsigicerus labidotus*  
437 was inferred through microwear to be a seasonal mixed feeder in both studies (Shipman et al.,

438 1981; Cerling et al., 1997) supported by the shape of its premaxilla (Solounias and Moelleken,  
439 1993). Finally, Gentry (1970) commented that the dentition of *H. tanycerus* was considerably  
440 more worn than that of *K. labidotus*, suggesting a more abrasive diet for the former. It is unclear  
441 why our results differ so strongly from these former studies. One possibility is that because we  
442 excluded very worn specimens from our analysis, we failed to note an overall difference in the  
443 degree of wear between these two bovid species. In addition, it is possible that *Hypsodontus*  
444 and/or *Kipsigicerus* had a highly seasonal diet, resulting in microwear that differed strongly at  
445 some points in the year. Neither of these scenarios, however, fully explains the overall similarity  
446 in their mesowear scores relative to the drastically different diets inferred by microwear and  
447 gross morphological wear.

448 One specimen from Fort Ternan deserves special mention. KNM-FT 675 is a well-  
449 preserved maxilla of *H. tanycerus* that shows considerably different mesowear than any other  
450 specimen in this study (Fig. 2c). Its mesowear score of 4 would equate more with a grazer than a  
451 browser, but it is the only specimen in our sample with a score this high. This suggests some  
452 dietary flexibility in this species, which is deserving of additional study.

453

#### 454 ***4.4 Mesowear in context***

455 Our mesowear results suggest heavily browse-dominated diets for all ruminant taxa from  
456 the early and early-middle Miocene in eastern Africa (20 – 13.7 Ma). Compared to extant data  
457 using the same mesowear quantification system, most of the taxa in this study could be  
458 considered ‘extreme’ in their browsing habits, as their mesowear scores are lower (i.e., sharper or  
459 attrition dominated) than a sample of living ruminant artiodactyls, at least for the mandibular  
460 molars (Fig. 5b). Our results are perhaps unsurprising for the early Miocene, when ruminants are

461 taxonomically less diverse and dominated by small-bodied tragulids. In contrast, our results for  
462 the early middle Miocene ruminants at Maboko and Fort Ternan are surprising. Despite the  
463 diversity of tooth crown heights and body sizes present in these taxa, mesowear provides little  
464 evidence for dietary niche separation. Moderately hypsodont bovids and climacoceratids show  
465 mesowear values that are only modestly higher than tragulids and low-crowned giraffoids  
466 (*Paleotragus*) in time bin #3 and are still comparable to mesowear values for modern browsers.  
467 The correlation between mesowear score and hypsodonty index in our data is weak (see Results),  
468 and in fact the time bin #3 bovids and climacoceratids have lower mesowear scores than earlier  
469 pecorans (*Canthumeryx* and *Walangania* specimens from time bin #1).

470         The Maboko and Fort Ternan bovids and climacoceratids are middle Miocene immigrants  
471 to eastern Africa, as their precursors are not found in the well-sampled early Miocene faunas  
472 from the region. The origins of climacoceratids are unclear, but it does appear to be an entirely  
473 African group (Harris et al., 2010). The origins of bovids are almost as obscure, but at present  
474 the balance of evidence would suggest an origin outside of Africa (Gentry, 1990, 2010; Bibi et  
475 al., 2009). When they appear in eastern Africa, they are already moderately hypsodont,  
476 suggesting a previous adaptation to abrasive diets. Perhaps owing to an abundance of more  
477 digestible browse or a lack of grassy or open habitats, they modified their diets but retained  
478 hypsodont teeth.

479         Our study is not the first to note a mismatch between hypsodonty and mesowear. Damuth  
480 and Janis (2011) note that hypsodonty does not seem to be easily lost once it has evolved in any  
481 particular lineage. The North America pronghorn (*Antilocapridae*) is hypsodont but has an  
482 entirely browsing diet today (Rivals and Semperebon, 2006; Semperebon and Rivals, 2007). Some  
483 studies of Miocene ruminants in Europe have demonstrated that quite brachyodont taxa appear to

484 be consuming grasses (DeMiguel et al., 2008, 2011). Finally, a large number of studies have  
485 concluded that fossil horses consumed a variety of diets, despite their extreme levels of  
486 hypsodonty (Tütken et al., 2013; Marín-Leyva et al., 2016; Semperebon et al., 2016).

487

## 488 **5. Conclusions**

489 This study presents the first mesowear dataset for early and middle Miocene ruminants in  
490 Africa. Our results demonstrate an unequivocal browsing signal for all tragulids and most of the  
491 pecoran ruminants in our dataset, with the possible exception of the larger-bodied *Canthumeryx*  
492 *sirtensis*, which may be a mixed feeder. Ruminant diets from 20-13.7 Ma are surprisingly  
493 homogeneous given the large geographic area and temporal range of our sample, and recent  
494 evidence that the habitats available to these taxa were themselves relatively variable (e.g. Lukens  
495 et al., 2017; Peppe et al., 2020). We find limited evidence for niche partitioning within the  
496 ruminant guild, except for possibly between *Walangania* and *Canthumeryx* at late early Miocene  
497 sites (time bin #2). The middle Miocene bovids and climacoceratids that appear in eastern Africa  
498 after 16 Ma are moderately high crowned, but do not appear to be using this adaptation for  
499 highly abrasive foods; instead, they show unambiguous mesowear signatures for browsing.  
500 These ruminant dietary data could be corroborated by future studies using both microwear and  
501 stable isotopic analyses, and through comparative studies on other mammalian groups from these  
502 localities. Those additional studies could help to better characterize the diets of these ruminant  
503 taxa, particularly with regards to the role of fruit browsing and the role of competition between  
504 ruminant and non-ruminant herbivores.

505

## 506 **Acknowledgements**



507 We thank the National Museums of Kenya (F. Manthi, J. Kibii, R. Mwanja) and Uganda  
508 Museums (A. Mugume, R. Mwanja) for authorizing our research and for access to specimens  
509 under their care. K. McNulty, T. Lehmann, J. Rossie and L. MacLatchy gave us permission to  
510 include newly collected and unpublished ruminant specimens from their field projects. We thank  
511 Kieran McNulty and Christina Barron-Ortiz and two anonymous reviewers for their insights and  
512 helpful comments on the manuscript. In Kenya, this research was conducted with the permission  
513 of the National Commission for Science, Technology and Innovation (Permits  
514 NACOSTI/P/14/9696/679 and NACOSTI/P/17/63582/15023). This research was supported by  
515 grants from the Natural Sciences and Engineering Research Council of Canada (Discovery  
516 Grants Program; Undergraduate Student Research Award) and the University of Calgary's  
517 Program for Undergraduate Research Experience (PURE). This publication is part of the  
518 Research on Early Catarrhine and Hominoid Evolution (REACHE) Project, and this is REACHE  
519 Publication #22.

520

## 521 **References**

522 Ackermans, N.L., 2020. The history of mesowear: a review. PeerJ. 8, e8519.

523 <https://doi.org/10.7717/peerj.8519>.

524 Andrews, P.J., Van Couvering, J.A.H., 1975. Palaeoenvironments in the East African  
525 Miocene, in: Szalay, F. (Ed.), Approaches to Primate Paleobiology. Karger, Basel, pp. 62-103.

526 Arney, I., Cote, S., Fox, D., Kingston, J., MacLatchy, L., Manthi, F., Mbua, E., McNulty,  
527 K., Nengo, I., 2017. Stable isotope evidence of paleoenvironments at early Miocene localities  
528 from Tinderet, Kenya. J. Vertebr. Paleontol. Abstract, S37, 75.

529 Bai, B., Meng, J., Janis, C.M., Zhang, Z-Q., Wang, Y-Q., 2020. Perissodactyl diversities

530 and responses to climate changes as reflected by dental homogeneity during the Cenozoic in  
531 Asia. *Ecol. Evol.* 10, 6333-6355. <https://doi.org/10.1002/ece3.6363>.

532 Barr, W.A., 2015. Paleoenvironments of the Shungura Formation (Plio-Pleistocene:  
533 Ethiopia) based on ecomorphology of the bovid astragalus. *J. Hum. Evol.* 88, 97-107.  
534 <https://doi:10.1016/j.jhevol.2015.05.002>.

535 Belmaker, M., O'Brien, H.D., 2018. Mesowear study of ungulates from the early  
536 Pleistocene site of 'Ubeidiya (Israel) and the implications for early *Homo* dispersal from Africa.  
537 *Quat. Int.* 480, 66-77. <https://doi.org/10.1016/j.quaint.2017.03.052>.

538 Bibi, F., 2007. Origin, paleoecology, and paleobiology of early Bovini. *Palaeogeogr.*  
539 *Palaeoclimatol. Palaeoecol.* 248, 60-72. <https://doi.org/10.1016/j.palaeo.2006.11.009>.

540 Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D.S., and Vrba, E.S.,  
541 2009. The fossil record and evolution of Bovidae: state of the field. *Palaeontol. Electron.* 12, 1-  
542 11.

543 Bishop, W.W., Miller, J.A., Fitch, F.J., 1969. New potassium-argon age determinations  
544 relevant to the Miocene fossil mammal sequence in east Africa. *Am. J. Sci.* 267, 669-699.  
545 <https://doi.org/10.2475/ajs.267.6.669>.

546 Blondel, C., Merceron, G., Andossa, L., Taisso, M.H., Vignaud, P., Brunet, M., 2010.  
547 Dental mesowear analysis of the late Miocene Bovidae from Toros-Menalla (Chad) and early  
548 hominid habitats in Central Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 292, 184-191.  
549 <https://doi.org/10.1016/j.palaeo.2010.03.042>.

550 Bonnefille, R., 1994. Palynology and palaeoenvironment of East African Hominid sites, in:  
551 Corruccini, R.S., Ciochon, R.L. (Eds.), *Integrative Paths to the Past: Palaeoanthropological*  
552 *Advances in Honor of F. Clark Howell (Advances in Human Evolution Series, 2)*. Prentice Hall,

553 Englewood Cliffs, New Jersey, pp. 415–427.

554       Boschetto, H.B., Brown, F.H., McDougall, I., 1992. Stratigraphy of the Lothidok Range,  
555 northern Kenya, and K/Ar ages of its Miocene primates. *J. Hum. Evol.* 22, 47-71.  
556 [https://doi.org/10.1016/0047-2484\(92\)90029-9](https://doi.org/10.1016/0047-2484(92)90029-9).

557       Butts, C., Cote, S., Kingston, J., 2018. Reconstructing the paleoenvironments of Kalodirr  
558 and Moruorot, Kenya using stable carbon isotopes. *Vertebr. Anat. Morphol. Palaeontol. Abstract*,  
559 5, 12-13.

560       Cerling, T. E., Quade, J., Ambrose, S. H., Sikes, N. E., 1991. Fossil soils from Fort Ternan,  
561 Kenya: grassland or woodland? *J. Hum. Evol.* 21, 295–306. [https://doi.org/10.1016/0047-](https://doi.org/10.1016/0047-2484(91)90110-h)  
562 [2484\(91\)90110-h](https://doi.org/10.1016/0047-2484(91)90110-h).

563       Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V.,  
564 Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary.  
565 *Nature*. 389, 153-158. <https://doi.org/10.1038/38229>.

566       Cote, S., 2010. *Pecora incertae sedis*, in: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic*  
567 *Mammals of Africa*. University of California Press, Berkeley, pp. 561-562.

568       Cote, S., Kingston, J., Deino, A., Winkler, A., Kityo, R., MacLachy, L., 2018. Evidence  
569 for rapid faunal change in the early Miocene of East Africa based on revised biostratigraphic and  
570 radiometric dating of Bukwa, Uganda. *J. Hum. Evol.* 116, 95-107.  
571 <https://doi.org/10.1016/j.jhevol.2017.12.001>.

572       Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding  
573 ecology in ungulate mammals, and its utility in palaeoecology. *Bio. Rev.* 86, 733-758.  
574 <https://doi.org/10.1111/j.1469-185x.2011.00176.x>.

575       Davis, M., Pineda-Munoz, S., 2016. The temporal scale of diet and dietary proxies. *Ecol.*

576 Evol. 6, 1883-1897. <https://doi.org/10.1002/ece3.2054>.

577 DeGusta, D., Vrba, E., 2003. A method for inferring paleohabitats from the functional  
578 morphology of bovid astragali. J. Archaeol. Sci. 30, 1009-1022. [https://doi.org/10.1016/S0305-](https://doi.org/10.1016/S0305-4403(02)00286-8)  
579 [4403\(02\)00286-8](https://doi.org/10.1016/S0305-4403(02)00286-8).

580 DeMiguel, D., Fortelius, M., Azanza, B., Morales, J., 2008. Ancestral feeding state of  
581 ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae.  
582 BMC. Evol. Biol. 8, 13. <https://doi.org/10.1186/1471-2148-8-13>.

583 DeMiguel, D., Azanza, B., Morales, J., 2011. Paleoenvironments and paleoclimate of the  
584 middle Miocene of central Spain: A reconstruction from dental wear of ruminants. Palaeogeogr.  
585 Palaeoclimatol. Palaeoecol. 302, 452-463. <https://doi.org/10.1016/j.palaeo.2011.02.005>.

586 Drake, R.E., Van Couvering, J.A., Pickford, M.H., Curtis, G.H., Harris, J.A., 1988. New  
587 chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. J. Geol. Soc.  
588 London. 145, 479-491. <https://doi.org/10.1144/gsjgs.145.3.0479>.

589 Dubost, G., 1978. Un aperçu sur l'écologie du chevrotain africain *Hyemoschus aquaticus*  
590 Ogolby, Artiodactyle Tragulidé. Mammalia. 42, 1-62.

591 Dubost, G., 1984. Comparisons of the diets of frugivorous forest ruminants of Gabon. J.  
592 Mammal. 65, 298-316.

593 Dumouchel, L., Bobe, R., 2020. Paleoeological implications of dental mesowear and  
594 hypsodonty in fossil ungulates from Kanapoi. J. Hum. Evol. 140, 102548.  
595 <https://doi.org/10.1016/j.jhevol.2018.11.004>.

596 Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C., Fortelius, M.,  
597 2010. Precipitation and large herbivorous mammals II: application to fossil data. Evol. Ecol. Res.  
598 12, 235-248.

599 Eronen, J.T., Fortelius, M., Micheels, A., Portmann, F.T., Puolamäki, K., Janis, C.M.,  
600 2012. Neogene aridification of the Northern Hemisphere. *Geology*. 40, 823-826.  
601 <https://doi.org/10.1130/G33147.1>.

602 Faith, J.T., Choiniere, J.N., Tryon, C.A., Peppe, D.J., Fox, D.L., 2011. Taxonomic status  
603 and paleoecology of *Rusingoryx atopocranion* (Mammalia, Artiodactyla), an extinct Pleistocene  
604 bovid from Rusinga Island, Kenya. *Quat. Res.* 75, 697-707.  
605 <https://doi.org/10.1016/j.yqres.2010.11.006>.

606 Feakins, S.J., Levin, N.E., Liddy, H.M., Sieracki, A., Eglinton, T.I., Bonnefille, R., 2013.  
607 Northeast African vegetation change over 12 m.y. *Geology*. 41, 295-298.  
608 <https://doi.org/10.1130/G33845.1>.

609 Feibel, C.S., Brown, F.H., 1991. Age of the primate-bearing deposits on Maboko Island,  
610 Kenya. *J. Hum. Evol.* 21, 221-225. [https://doi.org/10.1016/0047-2484\(91\)90063-2](https://doi.org/10.1016/0047-2484(91)90063-2).

611 Feranec, R.S., 2007. Ecological generalization during adaptive radiation: evidence from  
612 Neogene mammals. *Ecol. Evol. Res.* 9, 555-577.

613 Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using  
614 the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus.*  
615 *Novit.* 3301, 1-36. [https://doi.org/10.1206/0003-0082\(2000\)301<0001:FCOUMU>2.0.CO;2](https://doi.org/10.1206/0003-0082(2000)301<0001:FCOUMU>2.0.CO;2).

616 Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A.,  
617 Vislobokova, I., Zhang, Z., Zhou, L., 2002. Fossil mammals resolve regional patterns of  
618 Eurasian climate change over 20 million years. *Evol. Ecol. Res.* 4, 1005-1016.

619 Fortelius, M., Žliobaitė, I., Kaya, F., Bibi, F., Bobe, R., Leakey, L., Leakey, M., Patterson,  
620 D., Rannikko, J., Wedelin, L., 2016. An ecometric analysis of the fossil mammal record of the  
621 Turkana Basin. *Phil. Trans. R. Soc. B.* 371, 20150232 <https://doi.org/10.1098/rstb.2015.0232>.

622 Franz-Odendaal, T.A., Kaiser, T.M., 2003. Differential mesowear in the maxillary and  
623 mandibular cheek dentition of some ruminants (Artiodactyla). *Ann. Zool. Fennici*. 40, 395-410.

624 Fraser, D., Theodor, J.M., 2013. Ungulate diets reveal patterns of grassland evolution in  
625 North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 369, 409-421.  
626 <https://doi.org/10.1016/j.palaeo.2012.11.006>.

627 Fraser, D., Zybuz, T., Lightner, E., Theodor, J.M., 2014. Ruminant mandibular tooth  
628 mesowear: a new scheme for increasing paleoecological sample sizes. *J. Zool.* 294, 41-49.  
629 <https://doi.org/10.1111/jzo.12149>.

630 Fraser, D., Haupt, R.J., Barr, W.A., 2018. Phylogenetic signal in tooth wear dietary niche  
631 proxies. *Ecol. Evol.* 8, 5355-5368. <https://doi.org/10.1002/ece3.4540>.

632 Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. *J.*  
633 *Mammal.* 81, 490-511. [https://doi.org/10.1644/1545-1542\(2000\)081<0490:DPIEAB>2.0.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0490:DPIEAB>2.0.CO;2).

634 Garrett, N.D., Fox, D.L., McNulty, K.P., Michel, L., Peppe, D.J., 2015. Early Miocene  
635 paleoenvironments of Rusinga Island, Kenya: New data from fossil mammalian tooth enamel  
636 stable isotope communities. *J. Vertebr. Paleontol.* Abstract B35, 130.

637 Gentry, A.W., 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna, in: Leakey,  
638 L.S.B., Savage, R.J.G., *Fossil Vertebrates of Africa Volume 2*, Academic Press, London and  
639 New York, pp. 243-323.

640 Gentry, A., 1990. Evolution and dispersal of Africa Bovidae, in: Bubenik, G., Bubenik,  
641 A.B., *Horns, Pronghorns, and Antlers. Evolution, Morphology, Physiology, and Social*  
642 *Significance*. Springer-Verlag, New York, pp. 195-227.

643 Gentry, A.W., 1994. The Miocene differentiation of old world Pecora (Mammalia). *Hist.*  
644 *Biol.* 7, 115-158. <https://doi.org/10.1080/10292389409380449>.

645 Gentry, A.W., 2010. Bovidae, in: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals*  
646 *of Africa*. University of California Press, Berkley, pp. 747-803.

647 Geraads, D., 2010. Tragulidae, in: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals*  
648 *of Africa*. University of California Press, Berkley, pp. 729-735.

649 Harris, J.M., Solounias, N., Geraads, D., 2010. Giraffoidea, in: Werdelin, L., Sanders, W.J.  
650 (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkley, pp. 797-811.

651 Hamilton, W.R., 1973. The lower Miocene ruminants of Gebel Zelten, Libya. *Bull. br.*  
652 *Mus. nat. Hist. Geol.* 21, 75-150.

653 Hamilton, W.R., 1978. Fossil giraffes from the Miocene of Africa and a revision of the  
654 phylogeny of the Giraffoidea. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 283, 165–229.  
655 <https://doi.org/10.1098/rstb.1978.0019>.

656 Janis, C. M., 1988. An estimation of tooth volume and hypsodonty indices in ungulate  
657 mammals, and the correlation of these factors with dietary preference, in: Russell, D.E., Santoro,  
658 J.P., Sigogneau-Russell, D. (Eds.), *Teeth Revisited*. Proceedings of the VII th International  
659 Symposium on Dental Morphology, Paris, 1986. *Mem. Mus. Natn. Hist. Nat., Paris (serie C)* 53,  
660 367–387.

661 Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals,  
662 and its relationship to the determination of diets of extinct species, in: Boucot, J. (Ed.),  
663 *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, pp. 241-260.

664 Janis, C.M., Scott, K.M., 1987. The interrelationships of higher ruminant families with  
665 special emphasis on the members of the Cervoidea. *Am. Mus. Novit.* 2893, 1-85.

666 Janis, C.M., Fortelius, M., 1988. On the means whereby mammals achieve increased  
667 functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.* 63,

668 197-230. <https://doi.org/10.1111/j.1469-185X.1988.tb00630.x>.

669 Janis, C.M., Damuth, J., Theodor, J.M., 2000, Miocene ungulates and terrestrial primary  
670 productivity: Where have all the browsers gone? PNAS. 97, 7899-7904.  
671 <https://doi.org/10.1073/pnas.97.14.7899>.

672 Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and  
673 extant equids. Geodiversitas. 25, 321-345.

674 Kaiser, T.M., Rössner, G. E., 2007. Dietary resource partitioning in ruminant communities  
675 of Miocene wetland and karst Palaeoenvironments in Southern Germany. Palaeogeogr.  
676 Palaeoclimatol. Palaeoecol. 252, 424-439.

677 Kaiser, T.M., Solounias, N., Fortelius, M., Bernor, R.L., Schrenk, F., 2000. Tooth  
678 mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande  
679 (Germany) – A blind test study. Carolea. 58, 103-114.

680 Kaiser, T.M., Müller, D.W.H., Fortelius, M., Schulz, E., Codron, D., Clauss, M., 2013.  
681 Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates:  
682 implications for understanding tooth wear. Mamm. Rev. 43, 34-46.  
683 <https://doi.org/10.1111/j.1365-2907.2011.00203.x>

684 Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores  
685 at Laetoli: implications for early hominin paleoecology. Palaeogeogr. Palaeoclimatol.  
686 Palaeoecol. 243, 272-306. <https://doi.org/10.1016/j.palaeo.2006.08.002>.

687 Kingston, J., Maclatchy, L., Cote, S., Kinyanjui, R., 2018. Isotopic evidence for habitat  
688 heterogeneity at Bukwa, an early Miocene catarrhine site in Uganda. Am. J. Phys. Anthropol.  
689 Abstract, 165, 139-140.

690 Kinyanjui, R., Peppe, D., MacLatchy, L., Kingston, J., Cote, S., Driese, S.G., Fox, D.L.,



691 Jacobs, B.F., Lehmann, T., Lukens, W.E., Rossie, J.B., McNulty, K.P., 2017. Early Miocene  
692 vegetation across Eastern African as reconstructed from phytolith data. Geol. Soc. Am. Bull.  
693 Abstract, 39-2.

694 Kubo, M.O., Yamada, E., 2014. The Inter-Relationship between dietary and environmental  
695 properties and tooth wear: Comparisons of mesowear, molar wear rate, and hypsodonty index of  
696 extant Sika Deer populations. PLoS ONE. 9, e90745.  
697 <https://doi.org/10.1371/journal.pone.0090745>.

698 Louys, J., Meloro, C., Elton, S., Ditchfield, P., Bishop, L.C., 2011. Mesowear as a means  
699 of determining diets in African antelopes. J. Archaeol. Sci. 38, 1485-1495.  
700 <https://doi.org/10.1016/j.jas.2011.02.011>.

701 Lukens, W.E., Lehmann, T., Peppe, D.J., Fox, D.L., Driese, S.G., McNulty, K.P., 2017.  
702 The early Miocene critical zone at Karungu, western Kenya: An equatorial, open habitat with  
703 few primate remains. Front. Earth. Sci. 5, 1-21. <https://doi.org/10.3389/feart.2017.00087>.

704 MacLatchy, L., Deino, A., Kingston, J., 2006. An updated chronology for the early  
705 Miocene of NE Uganda. J. Vertebr. Paleontol. Abstract, 26(3), 93A.

706 Madden, R.H., 2014. Crown height and tooth wear on islands, in: Madden, R.H. (Ed.),  
707 Hypsodonty in mammals: evolution, geomorphology, and the role of earth surface processes.  
708 Cambridge University Press, Cambridge, UK, pp. 154-190.

709 Marín-Leyva, A.H., DeMiguel, D., García-Zepeda, M.L., Ponce-Saavedra, J., Arroyo-  
710 Cabrales, J., Schaaf, P., Alberdi, M.T., 2016. Dietary adaptability of Late Pleistocene *Equus*  
711 from West Central Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 441, 748-757.  
712 <https://doi.org/10.1016/j.palaeo.2015.10.019>.

713 McDougall, I., Watkins, R. T., 1985. Age of hominoid-bearing sequence at Buluk, northern

714 Kenya. Nature. 318, 175-178. <https://doi.org/10.1038/318175a0>.

715 Mendoza, M., Palmqvist, P., 2007. Hypsodonty in ungulates: an adaptation for grass  
716 consumption or for foraging in open habitat? J. Zool. 274, 134-142.  
717 <https://doi.org/10.1111/j.1469-7998.2007.00365.x>.

718 Menecart, B., Zoboli, D., Costeur, L., Pillola, G.L. 2015. On the systematic position of  
719 the oldest insular ruminant *Sardomeryx ochiriensis* (Mammalia, Ruminantia) and the early  
720 evolution of the Giraffomorpha. Journal of Systematic Palaeontology 17, 691-704.  
721 <https://doi.org/10.1080/14772019.2018.1472145>

722 Michel, L.A., Peppe, D.J., Lutz, J.A., Driese, S.G., Dunsworth, H.M., Harcourt-Smith,  
723 W.E.H., Horner, W.H., Lehmann, T., Nightingale, S., McNulty, K.P., 2014. Remnants of an  
724 ancient forest provide ecological context for Early Miocene fossil apes. Nat. Commun. 5, 1-9.  
725 <https://doi.org/10.1038/ncomms4236>.

726 Morgan, M.E., Kingston, J.D., Marino, B.D., 1994. Carbon isotopic evidence for the  
727 emergence of C4 plants in the Neogene from Pakistan and Kenya. Nature. 367, 162-165.  
728 <https://doi.org/10.1038/367162a0>.

729 Novello, A., Strömberg, C.A., Jacobs, B.F., McNulty, K.P., Michel, L.A., Uno, K.T., 2017.  
730 The role of grasses in east African vegetation during the past 30 million years: New results and  
731 perspectives from plant silica (phytolith) analyses. J. Vertebr. Paleontol. Abstract, S37, 170.

732 Peppe, D.J., Deino, A.L., Lehmann, T., Dunsworth, H.M., Harcourt-Smith, W.E.H.,  
733 McNulty, K.P., 2011. New age constraints on the early Miocene faunas of Rusinga and  
734 Mfangano Islands (Lake Victoria, Kenya). J. Vertebr. Paleontol. Abstract, 144, 237.

735 Peppe, D.J., McNulty, K.P., Deino, A.L., Michel, L.A., McCollum, M.S., Driese, S.G.,  
736 Dunsworth, H.M., Harcourt-Smith, W.E., Jenkins, K.E., Lehmann, T., 2016. Early Miocene

737 paleoenvironments of the Hiwegi Formation on Rusinga Island (equatorial Africa and Victoria,  
738 Africa, Lake Victoria, Kenya) and their implications for hominoid evolution. Geol. Soc. Am.  
739 Bull. Abstract, 48-7. <https://doi.org/10.1130/abs/2016AM-280981>.

740       Peppe, D., Deino, A., Driese, S., Fox, D., Kingston, J., Kinyanjui, R., Lukens, W., Lutz, J.,  
741 Michel, L., Oginga, K.O., Cote, S., Lehmann, T., MacLatchy, L., McNulty, K., Miler, E., Nengo,  
742 I., Rossie, J.B., 2017. Early Miocene paleoclimate and paleoenvironments across East Africa.  
743 Geol. Soc. Am. Bull. Abstract, 39-5.

744       Peppe, D., Cote, S., Deino, A., Driese, S.G., Fox, D.L., Kingston, J., Jenkins, K., 2018.  
745 Adaptable apes: reconstructing habitats through space and time in the early Miocene of East  
746 Africa. Am. J. Phys. Anthropol. Abstract, 165(S64), 203-204.

747       Peppe, D., Cote, S., Deino, A.L., Driese, S.G., Garrett, N., Hillis, K.R., Jacobs, B. F.,  
748 Jenkins, K.E., Kingston, J.D., Kinyanjui, R.N., Lehmann, T., Lukens, W.E., McNulty, K.P.,  
749 MacLatchy, L.M., Michel, L.A., Miller, E., Nengo, I., Novello, A., Oginga, K.O., Rossie, J.B.,  
750 Stromberg, C.A.E, Uno, K.T., 2020. Early Miocene evolution of open ecosystems and C4  
751 vegetation in equatorial East Africa. Geol. Soc. Am. Bull. Abstract, T167, 210.

752       Pickford, M., 1984. Kenya Palaeontology Gazetteer, vol. 1: Western Kenya. Kenya  
753 National Museums. Spec. Publ. 1. National Museums of Kenya, Department of  
754 Sites and Monuments Documentation, Nairobi.

755       Pickford, M., 1985. A new look at *Kenyapithecus* based on recent discoveries in western  
756 Kenya. J. Hum. Evol. 14, 113–144. [https://doi.org/10.1016/S0047-2484\(85\)80002-6](https://doi.org/10.1016/S0047-2484(85)80002-6).

757       Pickford, M., 2002. Ruminants from the early Miocene of Napak, Uganda. Ann. Paleontol.  
758 88, 85-113. [https://doi.org/10.1016/S0753-3969\(02\)01041-8](https://doi.org/10.1016/S0753-3969(02)01041-8).

759       Pickford, M., Sawada, Y., Tayama, R., Matsuda, Y.-K., Itaya, T., Hyodo, H., Senut, B.,

760 2006. Refinement of the age of the middle Miocene Fort Ternan Beds, western Kenya, and its  
761 implications for Old World biochronology. *C. R. Geosci.* 338, 545-555.  
762 <https://doi.org/10.1016/j.crte.2006.02.010>.

763 Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as  
764 indicated by antelope remains. *J. Hum. Evol.* 27, 47-75. <https://doi.org/10.1006/jhev.1994.1035>.

765 Prothero, D.R., 2007. Family Moschidae, in: Prothero, D.R., Foss, S.E. (Eds.), *The*  
766 *Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore, Maryland, pp. 221-  
767 226.

768 Retallack, G. J., 1992. Comment on the paleoenvironment of *Kenyapithecus* at Fort  
769 Ternan. *J. Hum. Evol.* 23, 365–371. [https://doi.org/10.1016/0047-2484\(92\)90072-H](https://doi.org/10.1016/0047-2484(92)90072-H).

770 Rivals, F., Semprebon, G.M., 2006. A comparison of the dietary habits of a large sample of  
771 the Pleistocene pronghorn *Stockoceros onusrosagris* from the Papago Springs Cave in Arizona to  
772 the modern *Antilocapra americana*. *J. Vertebr. Paleontol.* 26, 495-500.  
773 [https://doi.org/10.1671/0272-4634\(2006\)26\[495:acotdh\]2.0.co;2](https://doi.org/10.1671/0272-4634(2006)26[495:acotdh]2.0.co;2).

774 Rivals, F., Solounias, N., Mithlacher, M.C., 2007. Evidence for geographic variation in  
775 the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from  
776 the diets of recent *Bison*. *Quat. Res.* 68, 338-346. <https://doi.org/10.1016/j.yqres.2007.07.012>.

777 Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary  
778 diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time  
779 and space. *Quat. Sci. Rev.* 28, 3388-3400. <https://doi.org/10.1016/j.quascirev.2009.09.004>.

780 Sánchez, I.M., Cantalapiedra, J.L., Ríos, M., Quirarte, V., Morales, J. 2015. Systematics  
781 and evolution of the Miocene three-horned Palaeomerycid ruminants (Mammalia,  
782 Cetartiodactyla). *PLoS ONE*. 10, e0143034. <https://doi.org/10.1371/journal.pone.0143034>.

783 Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus*  
784 *anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel  
785 stable isotopes. *J. Anthropol. Archaeol.* 22, 200-207. [https://doi.org/10.1016/S0278-](https://doi.org/10.1016/S0278-4165(03)00034-5)  
786 [4165\(03\)00034-5](https://doi.org/10.1016/S0278-4165(03)00034-5).

787 Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for  
788 Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. *Palaeogeogr.*  
789 *Palaeoclimatol. Palaeoecol.* 241, 301-319. <https://doi.org/10.1016/j.palaeo.2006.04.004>.

790 Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An  
791 assessment of the dietary adaptations of Miocene to Recent Antilocapridae (Mammalia:  
792 Artiodactyla). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 332-347.  
793 <https://doi.org/10.1016/j.palaeo.2007.06.006>.

794 Semprebon, G.M., Rivals, F., 2010. Trends in the paleodietary habits of fossil camels from  
795 the Tertiary and Quaternary of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295,  
796 131-145. <https://doi.org/10.1016/j.palaeo.2010.05.033>.

797 Semprebon, G.M., Rivals, F., Solounias, N., Hulbert, R.C., 2016. Paleodietary  
798 reconstruction of fossil horses from the Eocene through Pleistocene of North America.  
799 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 442, 110-127.  
800 <https://doi.org/10.1016/j.palaeo.2015.11.004>.

801 Semprebon, G.M., Rivals, F., Janis, C.M., 2019. The role of grass vs. exogenous abrasives  
802 in the paleodietary patterns of North American ungulates. *Front. Ecol. Evol.* 7, 1-23.  
803 <https://doi.org/10.3389/fevo.2019.00065>.

804 Shipman, P., Walker, A., Van Couvering, J. A., Hooker, P. J., Miller, J. A., 1981. The Fort  
805 Ternan hominoid site, Kenya: geology, age, taphonomy, and paleoecology. *J. Hum. Evol.* 10,

806 49–72. [https://doi.org/10.1016/S0047-2484\(81\)80025-5](https://doi.org/10.1016/S0047-2484(81)80025-5).

807 Solounias, N., Moelleken, S.M.C., 1993. Tooth microwear and premaxillary shape of an  
808 archaic antelope. *Lethaia*. 26, 261-268. <https://doi.org/10.1111/j.1502-3931.1993.tb01529.x>.

809 Sponheimer, M., Reed, K.E., Lee-Thorp, J.A., 1999. Combining isotopic and  
810 ecomorphological data to refine bovid paleodietary reconstructions: a case study from the  
811 Makapansgat Limeworks hominin locality. *J. Hum. Evol.* 36, 705-718.  
812 <https://doi.org/10.1006/jhev.1999.0300>.

813 Strani, F., DeMiguel, D., Bellucci, L., Sardella, R., 2018. Dietary response of early  
814 Pleistocene ungulate communities to the climate oscillations of the Gelasian/Calabrian transition  
815 in Central Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 499, 102-111.  
816 <https://doi.org/10.1016/j.palaeo.2018.03.021>.

817 Tütken, T., Kaiser, T.M., Vennemann, T., Merceron, G., 2013. Opportunistic feeding  
818 strategy for the earliest Old World hypsodont equids: evidence from stable isotope and dental  
819 wear proxies, *PLoS ONE*. 8, e74463. <https://doi.org/10.1371/journal.pone.0074463>.

820 Ungar, P.S., Merceron, G., Scott, R.S., 2007. Dental microwear texture analysis of  
821 Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, Western Cape  
822 Province, South Africa. *J. Mammal. Evol.* 14, 163-181. [https://doi.org/10.1007/s10914-007-](https://doi.org/10.1007/s10914-007-9050-x)  
823 [9050-x](https://doi.org/10.1007/s10914-007-9050-x).

824 Ungar, P.S., Scott, J.R., Curran, S.C., Dunsworth, H.M., Harcourt-Smith, W.E.H,  
825 Lehmann, T., Manthi, F.K., McNulty, K.P., 2012. Early Neogene environments in East Africa:  
826 Evidence from dental microwear of tragulids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 342-343,  
827 84-96. <https://doi.org/10.1016/j.palaeo.2012.05.005>.

828 Ungar, P.S., Abella, E.F., Burgman, J.H.E., Lazagabaster, I.A., Scott, J.R., Delezene, L.K.,

829 Manthi, F.K., Plavcan, J.M., Ward, C.V., 2020. Dental microwear and Pliocene paleocommunity  
830 ecology of bovids, primates, rodents, and suids at Kanapoi. *J. Hum. Evol.* 140, 102315.  
831 <https://doi.org/10.1016/j.jhevol.2017.03.005>.

832 Uno, K.T., Cerling, T.E., Harris, J.M., Kunitatsu, Y., Leakey, M.G., Nakatsukasa, M.,  
833 Nakaya, H., 2011. Late Miocene to Pliocene carbon isotope record of differential diet change  
834 among East African herbivores. *PNAS.* 108, 6509-6514.  
835 <https://doi.org/10.1073/pnas.1018435108>.

836 Uno, K. T., Polissar, P.J., Jackson, K.E., deMenocal, P.B., 2016. Neogene biomarker  
837 record of vegetation change in eastern Africa. *PNAS.* 113, 6355-6363.  
838 <https://doi.org/10.1073/pnas.1521267113>.

839 van Asperen, E.N., Kahlke, R.D., 2017. Dietary traits of the late Early Pleistocene *Bison*  
840 *meneri* (Bovidae, Mammalia) from its type site Untermassfeld (Central Germany) and the  
841 problem of Pleistocene ‘wood bison.’ *Quat. Sci. Rev.* 177, 299-313.  
842 <https://doi.org/10.1016/j.quascirev.2017.10.002>.

843 Whitworth, T., 1958. Miocene ruminants of East Africa. *Fossil Mammals E. Afr.* 15, 1-50.  
844 <https://doi.org/10.5962/bhl.title.118753>.

845 Xafis, A., Saarinen, J., Bastl, K., Nagel, D., Grímsson, F., 2020. Palaeodietary traits of  
846 large mammals from the middle Miocene of Gračanica (Bugojno Basin, Bosnia-Herzegovina).  
847 *Palaeobio. Palaeoenv.* 100, 457-477. <https://doi.org/10.1007/s12549-020-00435-2>.

848 Yamada, E., Hasumi, E., Miyazato, N., Akahoshi, M., Watabe, M., Nakaya, H., 2016.  
849 Mesowear analyses of sympatric ungulates from the late Miocene Maragheh, Iran. *Palaeobio.*  
850 *Palaeoenv.* 96, 445-452. <https://doi.org/10.1007/s12549-016-0237-0>.

**Table 1.** Fossil localities used in this study, divided into three time bins for analysis.

<b>Time Bin</b>	<b>Localities</b>	<b>Locality Coordinates</b>	<b>Locality Age</b>	<b>Ruminant taxa included in this analysis</b>
<b>#1 20 – 19 Ma</b>	Napak	02° 06' N, 34° 12' E	~20 Ma (Bishop et al., 1969; MacLatchy et al., 2006)	<i>Walangania africanus</i> <i>Dorcatherium songhorensis</i>
	Tinderet (Songhor, Chamtwarra, Legetet, Koru, Mteitei Valley, and Kapurtay)	00° 01' S, 35° 18' E	~20-19.5 Ma (Bishop et al., 1969)	<i>Walangania africanus</i> <i>Dorcatherium songhorensis</i> <i>Dorcatherium parvum</i>
<b>#2 18.5 – 17 Ma</b>	Rusinga (Hiwegi Formation)	00° 24' S, 34° 12' E	18 – 18.3 Ma (Drake et al., 1988; Peppe et al., 2011, 2016)	<i>Canthumeryx sirtensis</i> <i>Walangania africanus</i> <i>Dorcatherium pigotti</i> <i>Dorcatherium parvum</i> <i>Dorcatherium chappuisi</i>



Mfangano	00° 28' S, 34° 3' E	~18 Ma (Drake et al., 1988)	<i>Canthumeryx sirtensis</i> <i>Walangania africanus</i> <i>Dorcatherium</i> cf. <i>pigotti</i> <i>Dorcatherium parvum</i> <i>Dorcatherium chappuisi</i>
Karungu	00° 52' S, 34° 12' E	17.7 – 17.2 Ma (Drake et al., 1988; Lukens et al., 2017)	<i>Walangania africanus</i> <i>Dorcatherium pigotti</i> <i>Dorcatherium parvum</i>
Kalodirr	3° 20' N, 35° 45' E	16.8 – 17.5 Ma (Boschetto et al., 1992)	<i>Canthumeryx sirtensis</i> <i>Walangania africanus</i> <i>Dorcatherium</i> cf. <i>pigotti</i> <i>Dorcatherium moruorotensis</i> <i>Dorcatherium chappuisi</i>
Moruorot	3° 17' N, 35° 50' E	16.8 – 17.5 Ma (Boschetto et al., 1992)	<i>Canthumeryx sirtensis</i> <i>Walangania africanus</i> <i>Dorcatherium</i> cf. <i>pigotti</i>

	Buluk	4° 20' N, 36° 34' E	~17 Ma (McDougall and Watkins, 1985)	<i>Canthumeryx sirtensis</i> <i>Dorcatherium chappuisi</i> <i>Dorcatherium cf. pigotti</i>
<b>#3 15 – 13.7 Ma</b>	Maboko	00° 9' S, 34° 36' E	~15 Ma (1984; Feibel and Brown, 1991)	<i>Dorcatherium chappuisi</i> <i>Dorcatherium pigotti</i> <i>Dorcatherium parvum</i> <i>Climacoceras africanus</i> Bovidae (at least two species- <i>Homoiodorcas</i> sp. and <i>Hypsodontus pickfordi</i> )
	Fort Ternan	00° 13' S, 35° 20' E	13.7 Ma (Pickford, 1984; Pickford et al., 2006)	<i>Dorcatherium chappuisi</i> <i>Climacoceras gentryi</i> <i>Paleotragus primaevus</i> <i>Kipsigicerus labidotus</i> <i>Hypsodontus tanycerus</i> Bovidae (at least two additional taxa – <i>Gentrytragus thomasi</i> and <i>Gazella</i> sp.)

**Table 2.** Hypsodonty and mesowear data divided by Time Bin, taxonomic group, and mandibular vs. maxillary dentition.

Taxon	Group	Age	Dentition	Mesowear			Hypsodonty			
				n	Mean	SD	n	Mean	Min	Max
<i>Dorcatherium</i>	Tragulidae	20-19 Ma	maxillary	47	1.19	0.40	29	0.67	0.53	0.79
<i>Dorcatherium</i>	Tragulidae	20-19 Ma	mandibular	60	1.4	0.56	25	0.63	0.53	0.79
<i>Walangania</i>	Pecora	20-19 Ma	maxillary	52	1.56	0.54	29	0.68	0.56	0.76
<i>Walangania</i>	Pecora	20-19 Ma	mandibular	58	1.64	0.61	21	0.64	0.53	0.77
<i>Canthumeryx</i>	Pecora	18.5-17 Ma	maxillary	3	1.67	0.58	0	-	-	-
<i>Canthumeryx</i>	Pecora	18.5-17 Ma	mandibular	8	1.88	0.46	1	0.72	-	-
<i>Dorcatherium</i>	Tragulidae	18.5-17 Ma	maxillary	61	1.26	0.48	29	0.67	0.55	0.83
<i>Dorcatherium</i>	Tragulidae	18.5-17 Ma	mandibular	59	1.22	0.42	25	0.6	0.5	0.67
<i>Walangania</i>	Pecora	18.5-17 Ma	maxillary	6	1.33	0.84	6	0.68	0.65	0.73
<i>Walangania</i>	Pecora	18.5-17 Ma	mandibular	5	1	-	4	0.66	0.6	0.71
Bovidae	Pecora	15.5-14 Ma	maxillary	40	1.33	0.62	20	0.88	0.71	1.21
Bovidae	Pecora	15.5-14 Ma	mandibular	52	1.63	0.49	23	0.84	0.69	1.04
<i>Climacoceras</i>	Pecora	15.5-14 Ma	maxillary	14	1.43	0.51	5	0.86	0.78	0.98
<i>Climacoceras</i>	Pecora	15.5-14 Ma	mandibular	23	1.57	0.51	11	0.78	0.7	0.88
<i>Dorcatherium</i>	Tragulidae	15.5-14 Ma	maxillary	31	1.26	0.44	19	0.68	0.56	0.81
<i>Dorcatherium</i>	Tragulidae	15.5-14 Ma	mandibular	40	1.15	0.36	17	0.63	0.52	0.7
<i>Paleotragus</i>	Pecora	15.5-14 Ma	maxillary	10	1.2	0.42	12	0.7	0.63	0.76
<i>Paleotragus</i>	Pecora	15.5-14 Ma	mandibular	10	1.5	0.53	6	0.64	0.61	0.7

**Table 3.** Results of univariate statistical analyses performed on the mesowear dataset.

	Tooth position	Comparison	Univariate significance test	Tukey HSD test
Time Bin #1	maxillary	tragulid – pecoran	Welch Two Sample t-test, $t = -3.8695$ , $df = 93.37$ , $p\text{-value} = 0.0020$	n/a
	mandibular	tragulid – pecoran	Welch Two Sample t-test, $t = -2.117$ , $df = 115.60$ , $p\text{-value} = 0.037$	n/a
Time Bin #2	maxillary	tragulid – <i>Walangania</i>	ANOVA, $F = 1.02$ $df = 2, 67$ , $p\text{-value} = 0.37$	$p\text{-value} = 0.94$
		tragulid – <i>Canthumeryx</i>		$p\text{-value} = 0.34$
	mandibular	<i>Walangania</i> – <i>Canthumeryx</i>		$p\text{-value} = 0.60$
		tragulid – <i>Walangania</i>	ANOVA, $F = 10.76$ $df = 2, 69$ , $p\text{-value} = 0.00009$	$p\text{-value} = 0.47$

		tragulid –		p-value = 0.0001
		<i>Canthumeryx</i>		
		<i>Walangania</i> –		p-value = 0.0008
		<i>Canthumeryx</i>		
Time Bin #3	maxillary	tragulid –	ANOVA, F = 0.481, df = 3, 91, p-value =	p-value = 0.75
		<i>Climacoceras</i>	0.70	
		tragulid –		p-value = 0.99
		<i>Paleotragus</i>		
		tragulid – Bovidae		p-value = 0.95
		<i>Climacoceras</i> –		p-value = 0.73
		<i>Paleotragus</i>		
		<i>Climacoceras</i> –		p-value = 0.92
		Bovidae		
		<i>Paleotragus</i> –		p-value = 0.91
		Bovidae		

	mandibular	tragulid – <i>Climacoceras</i>	ANOVA, F = 9.08, df = 3, 121, p-value = 0.00002	p-value = 0.004
		tragulid – <i>Paleotragus</i>		p-value = 0.14
		tragulid – Bovidae		p-value = 0.00001
		<i>Climacoceras</i> – <i>Paleotragus</i>		p-value = 0.98
		<i>Climacoceras</i> – Bovidae		p-value = 0.93
		<i>Paleotragus</i> – Bovidae		p-value = 0.83
Tragulids	maxillary	Time Bin #1 – Time Bin #2	ANOVA, F = 0.378, df = 2, 136, p-value = 0.69	p-value = 0.70
		Time Bin #1 – Time Bin #3		p-value = 0.80

		Time Bin #2 – Time		p-value = 0.99
		Bin #3		
	mandibular	Time Bin #1 – Time	ANOVA, F = 4.03, df = 2, 156, p-value =	p-value = 0.09
		Bin #2	0.02	
		Time Bin #1 – Time		p-value = 0.02
		Bin #3		
		Time Bin #2 – Time		p-value = 0.74
		Bin #3		
Pecorans	maxillary	Time Bin #1 – Time	ANOVA, F = 2.49, df = 2, 122, p-value =	p-value = 0.84
		Bin #2	0.09	
		Time Bin #1 – Time		p-value = 0.07
		Bin #3		
		Time Bin #2 – Time		p-value = 0.82
		Bin #3		
	mandibular	Time Bin #1 – Time	ANOVA, F = 0.15, df = 2, 154, p-value =	p-value = 0.86
		Bin #2	0.86	

		Time Bin #1 – Time Bin #3		p-value = 0.95
		Time Bin #2 – Time Bin #3		p-value = 0.92
<i>Walangania</i>	maxillary	Time Bin #1- Time Bin #2	Welch Two Sample t-test, t = -1.003, df = 6.33, p-value = 0.35	n/a
	mandibular	Time Bin #1 – Time Bin #2	Welch Two Sample t-test, t = -7.86, df = 58, p-value < 0.00001	n/a
Fort Ternan	maxillary	<i>Kipsigicerus</i> –	Welch Two Sample t-test, t= 0.34, df =	n/a
Bovidae		<i>Hypsodontus</i>	20.91, p-value = 0.74	
	mandibular	<i>Kipsigicerus</i> –	Welch Two Sample t-test, t= -0.35, df =	n/a
		<i>Hypsodontus</i>	24.54, p-value = 0.73	
Rusinga	maxillary	<i>D. chappuisi</i> – <i>D.</i>	ANOVA, F = 1.24, df = 2, 36, p-value =	p-value = 0.53
<i>Dorcatherium</i>		<i>pigotti</i>	0.30	
		<i>D. chappuisi</i> – <i>D.</i>		p-value = 0.99
		<i>parvum</i>		



	<i>D. pigotti</i> – <i>D.</i>		p-value = 0.29
	<i>parvum</i>		
mandibular	<i>D. chappuisi</i> – <i>D.</i>	ANOVA, F = 2.87, df = 2, 36, p-value =	p-value = 0.15
	<i>pigotti</i>	0.070	
	<i>D. chappuisi</i> – <i>D.</i>		p-value = 0.068
	<i>parvum</i>		
	<i>D. pigotti</i> – <i>D.</i>		p-value = 0.99
	<i>parvum</i>		

---

## Figure Captions

**Figure 1.** Map of eastern Africa showing all of the early and middle Miocene fossil sites included in this study. Time bins are indicated as follows: time bin #1 = blue; time bin #2 = turquoise; time bin #3 = green.

**Figure 2.** Representative ruminant specimens that were included in this study and scored for mesowear (on the sharpest cusp). A) KNM-FT 1047, maxilla of the bovid *Gentrytragus thomasi*. Mesowear score on M2 paracone = 2. B) KNM-RU 46441, mandible of the tragulid *Dorcatherium pigotti*. Mesowear score on m2 metaconid = 1. C) KNM-FT 675, maxilla of the bovid *Hypsodontus tanycerus*. Mesowear score on M2 metacone = 4. D) NAP I PEG 2'64, mandible of the tragulid *Dorcatherium songhorensis*. Mesowear score on m1 entoconid = 3. E) KNM-RU 5163, lower molar of the giraffoid *Canthumeryx sirtensis*. Mesowear score on metaconid = 2. F) KNM-FT 3007, upper molar of the giraffoid *Paleotragus primaevus*. Mesowear score on paracone = 1. G) KNM-SO 174, upper molar of *Walangania africanus*. Mesowear score on paracone = 2. All scale bars are 10 mm.

**Figure 3.** Hypsodonty results for A) maxillary and B) mandibular molars. Box plots show the median, and upper and lower quartiles for tragulids and pecorans, separated by time bin. Whiskers represent the range of the data (minimums and maximums). Points represent the hypsodonty index for each individual.

**Figure 4.** Mesowear results for A) maxillary and B) mandibular molars showing the percentage of specimens that were assigned to each mesowear category. Raw data can be found in Table S1.

**Figure 5.** Modern mesowear scores separated by A) maxillary and B) mandibular molars. Box plots show the median and upper and lower quartiles for modern browsers, mixed feeders, and grazers. Whiskers represent the range of the data (minimums and maximums). Modern data is compiled from the species average scores in Fraser et al. (2014: Table 1). We have followed the dietary classifications given by Fraser et al. (2014) but note that other studies use slightly different dietary classifications for some taxa (e.g., Gagnon and Chew (2000)). Note that the highly variable scores for mixed feeders in the maxillary molars (a) is being driven largely by the muntjac, which has unusually low mesowear scores for a mixed feeder. If this data point were removed, none of our fossil taxa would overlap with the mixed feeder range in the maxillary molars. Fossil data points represent the mean mesowear score for each fossil taxon in this study, divided by time bin (Table 2).