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1 **Stable isotope analyses of tooth enamel carbonate of large herbivores from the Tugen**
2 **Hills deposits: palaeoenvironmental context of the earliest Kenyan hominids**

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11
12 **Running head:** Stable isotope analyses of herbivore tooth enamel from the Tugen Hills

13
14 **Keywords:** stable isotopes, tooth enamel, Tugen Hills, Neogene, large herbivores, *Orrorin tugenensis*

15
16

17 **Abstract**

18

19 Understanding shifts in past climatic and environmental conditions are crucial for throwing light
20 on human evolution. Available reconstructions of the palaeoecology of faunal and floral assemblages
21 indicate that the earliest Kenyan hominids, including *Orrorin tugenensis*, are associated with forest
22 landscapes. In this study, we present stable isotope data of tooth enamel carbonate of large
23 herbivores associated with these hominids in order further to evaluate their environmental context.
24 Fossil teeth were sampled in the Lukeino Formation (6.1-5.7 Ma, Late Miocene) and the Mabaget
25 Formation (5.3-4.5 Ma, Early Pliocene) at the foot of the Tugen Hills (Great Rift Valley). Despite
26 chemical changes in fossil enamel, preservation of the palaeoenvironmental signals is supported by
27 the difference in $\delta^{18}\text{O}$ between hippos and terrestrial fauna. Moreover, the giraffid specimen from the
28 Mabaget Formation exhibits one of the highest $\delta^{18}\text{O}$ values, as expected for a drought-tolerant animal.
29 The $\delta^{13}\text{C}$ of large herbivores indicates that the earliest Kenyan hominids inhabited a mixed $\text{C}_3\text{-C}_4$
30 environment as did *Ardipithecus* (Ethiopia) and *Sahelanthropus* (Chad), two early putative hominids.
31 The Tugen Hills might have been a wooded grassland with patches of woodland. There is no record of
32 closed-canopy forest at the time of deposition. We emphasize differences in food habits among
33 herbivore groups. Deinotheres, nearly all elephantids and the giraffid individual had a C_3 diet which
34 reflected browsing behaviour. The intake of C_4 plants prevailed for equids and gomphotheres and was
35 consistent with grazing habits. Most hippos and suids were mixed $\text{C}_3\text{-C}_4$ feeders and consequently
36 were generalist herbivores. Bovids and rhinos had a diet ranging from C_3 to C_4 plants. Variations in
37 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among faunal assemblages suggest changes in local climate and vegetation. Moister
38 conditions likely occurred in the Early Pliocene and the latest Miocene (ca. 5.7 Ma) than before. The
39 C_3 plant biomass would have increased in the latest Miocene. There were probably denser stands of
40 trees within the depositional environment during the Early Pliocene than in the Late Miocene, which is
41 consistent with palaeontological studies.

42

43

44 **1. Introduction**

45

46 The study of climate and environmental change is crucial for understanding human evolution.
47 It has traditionally been based on the ecological features of faunal and floral assemblages and the
48 depositional context of fossil remains, but recently stable isotope analyses of tooth enamel and
49 pedogenic carbonate have proved useful for exploring African Neogene ecosystems (Cerling et al.,
50 1997, 2011; Kingston and Harrison, 2007; Ségalen et al., 2007; Uno et al., 2011).

51

52 Throughout the Neogene, faunas and floras in Africa were influenced by major climatic
53 changes. The asynchronous growth of polar ice caps caused latitudinal shifts of climatic belts and
54 therefore modified continental environments. In the Early Miocene, tropical forest in Africa was
55 widespread on either side of the equator, but with the growth of the Antarctic ice sheet, the tropical
56 belt was displaced northwards and reached the southern part of Europe during the Middle Miocene
57 (Pickford and Morales, 1994; Pickford and Senut, 2003). Later, it shifted southwards to the current
58 position when the Arctic ice cap expanded during the Pliocene (Kennett, 1995; Zachos et al., 2001).
59 The aridification of Africa began in the southwest with the formation of the Namib Desert (17-16 Ma),
60 much earlier than the region of the present-day Sahara (8-7 Ma) (review in Senut et al., 2009).
61 Development of the Great Rift Valley modified atmospheric circulation patterns in East Africa and led
62 to unstable environmental conditions (Coppens, 1983; review in Senut, 2006a). The earliest
63 documented grassland ecosystem is in Uganda some 17.5 Ma ago (Pickford, 2002). Plants which use
64 C₄ pathway emerged around 10 Ma in Kenya (Uno et al., 2011) and expanded in the Plio-Pleistocene
65 when East African environments began going dry (review in Ségalen et al., 2007). Several animal
66 lineages in eastern and northern Africa were replaced by arid-adapted groups immigrating from
67 southern Africa and Eurasia. Other East African lineages withdrew westwards as the tropical forest
68 cover shrank (review in Senut et al., 2009).

69

70 Furthermore, hominids appeared in the Late Miocene in Kenya and possibly in Chad and
71 Ethiopia (review in Senut, 2006b, 2011). The origin of bipedalism is a major issue in the study of
72 human evolution as it is one of the markers of our lineage. For decades it was said to have emerged in
73 an open environment, and that the transition from quadrupedalism to bipedality took place in savanna

74 (savanna hypothesis). However, Pliocene hominids were partly arboreal, but were bipedal when on
75 the ground (review in Senut, 2006b, 2011). Trees were present in the environment (Bonnefille, 2010).
76 The discovery of *Orrorin tugenensis*, a Late Miocene biped, challenged the commonly accepted
77 savanna hypothesis because its postcranial bones indicated that it was a part time tree-dweller (Senut
78 et al., 2001; Pickford et al., 2002; Galik et al., 2004; Gommery and Senut, 2006). Palaeontological
79 studies of the faunal and floral assemblage suggest a well vegetated environment (Pickford and
80 Senut, 2001; Senut, 2006b; Pickford, 2011; Bamford et al., 2013). It was thus important to test these
81 ideas using an alternative approach.

82
83 Our study provides a perspective of the environmental context of the earliest Kenyan hominids
84 (including *Orrorin tugenensis*) through stable isotope analyses of teeth of large herbivores associated
85 with the hominid fossils. Tooth remains were collected in deposits in the eastern foot of the Tugen Hills
86 in the Baringo Basin of the Great Rift Valley (**figure 1**). The sampling localities fall within the Lukeino
87 and Mabaget Formations, dated from the Late Miocene to Early Pliocene (**figure 2**). Fossil teeth of
88 large herbivores were selected according to their abundance in the deposits and their potential for
89 yielding useful isotopic data. We investigated the stable isotope ratios of the biogenic carbonate in
90 enamel. Carbonate (CO_3^{2-}) is incorporated in the phosphate (PO_4^{3-}) and hydroxyl (OH^-) structural sites
91 of biological apatite which is the main constituent of teeth and bones. Bioapatite is a calcium
92 phosphate mineral, the chemical formula of which can be simplified to $\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{OH}, \text{CO}_3)$
93 (review in LeGeros and LeGeros, 1984). It is known to record the stable carbon isotope composition of
94 the diet (Krueger and Sullivan, 1984; Cerling and Harris, 1999; Passey et al., 2005) and the stable
95 oxygen isotope composition of the body water which depends on climatic and ecophysiological factors
96 (Longinelli, 1984; Luz and Kolodny, 1985; Kohn et al., 1996). Thus tooth enamel carbonate of wild
97 herbivores can be used to determine aspects of vegetation and climate of their ecosystems.

98
99 We analysed tooth enamel rather than bone or dentine because it is more resistant to
100 diagenesis (Lee-Thorp and van der Merwe, 1991; Quade et al., 1992; Ayliffe et al., 1994; Wang and
101 Cerling, 1994; Koch et al., 1997). Compared with bone and dentine, enamel is more mineralized and
102 exhibits a higher crystallinity and a lower porosity (LeGeros and LeGeros, 1984; Asscher et al., 2011).
103 As a result, the recrystallization of bioapatite and the pore-space infilling of secondary minerals are

104 more limited in enamel than in bone and dentine in the same taphonomic context (Michel et al., 1996;
105 Kohn et al., 1999).

106

107 In this paper, we assessed the state of preservation of fossil enamel from the Lukeino and
108 Mabaget Formations before using isotopic data to make palaeoenvironmental interpretations. Fluorine
109 (F), iron (Fe) and manganese (Mn) concentrations were measured in fossil specimens. They are trace
110 elements in modern teeth and bones (LeGeros and LeGeros, 1984; Elliott, 2002; Skinner, 2005).
111 Diagenetic F, Fe and Mn enrichment was observed in herbivore enamel from other Mio-Pliocene
112 deposits in the Kenyan Rift Valley (Kohn et al., 1999; Schoeninger et al., 2003a; Passey et al., 2007).
113 It is reported to result from pore-space infilling by Fe-Mn oxyhydroxides and
114 dissolution/recrystallization processes of bioapatite in which F⁻ replaces OH⁻. We verified that chemical
115 alteration of fossil specimens had no significant effect on palaeoenvironmental signals of biogenic
116 carbonate.

117

118 Based on the ¹³C/¹²C ratio ($\delta^{13}\text{C}$), we propose a dietary reconstruction of large herbivores
119 associated with the earliest Kenyan hominids from which we build a picture of the local vegetation.
120 Study of variation in ¹⁸O/¹⁶O ratio ($\delta^{18}\text{O}$) was aimed at exploring climate change in the Tugen Hills from
121 the Late Miocene to the Early Pliocene. Lastly we compared our stable carbon isotope data with those
122 obtained from herbivore faunas associated with early putative hominids in Chad and Ethiopia.

123

124 **2. Background**

125

126 **2.1 Geological context**

127

128 The Lukeino Formation is of Late Miocene age (Bishop et al., 1971; Pickford, 1975, Pickford
129 and Senut, 2001). Magnetostratigraphy and radiometric dating yielded ages from 6.1 to 5.7 Ma (Hill et
130 al., 1985; Deino et al., 2002; Sawada et al., 2002). This formation is about 100 m thick. It overlies the
131 Kabarnet Trachyte Formation and is covered by the Kaparaina Basalt Formation (**figure 2**). The
132 sediments are fluvio-lacustrine and consist mostly of sandstones, siltstones, tuffs and diatomites. The
133 Kapsomin Basalt and the Rormuch Sills (trachyte intrusions) are points of reference within the Lukeino

134 Formation, and enable us to distinguish three units: the Kapgoywa Member (ca. 6.1-5.8 Ma), the
135 Kapsomin Member (ca. 5.8 Ma) and the Kapcheberek Member (ca. 5.7 Ma). Remains of the hominid
136 *Orrorin tugenensis* were found in all three members (Pickford, 1975; Senut et al., 2001; Sawada et al.,
137 2002).

138

139 The Mabaget Formation is of Early Pliocene age (Pickford et al., 1983, 2004; Hill, 1985) and
140 overlies the Kaparaina Basalt Formation (**figure 2**). Its thickness varies throughout the basin. For
141 instance, there are about 150 m of sediments exposed at Pelion (type section) and 40 m at Mosionin.
142 Deposits are mainly sandstones, siltstones and tuffs, deposited in a fluvio-lacustrine system.
143 Radiometric dating provided ages from 5.3 to 3.8 Ma within the Mabaget Formation at Tabarin (Deino
144 et al., 2002). However, a minimum age of ca. 4.5 Ma would fit with the faunal evidence (Pickford et al.,
145 1983, 2004). This formation yielded remains of an indeterminate hominid, possibly *Australopithecus*
146 *praegens* or *Ardipithecus ramidus* (Ferguson, 1989; Pickford et al., 2004). A hominid mandible
147 discovered at Tabarin (Hill, 1985) was dated at 4.5-4.4 Ma by Deino et al. (2002).

148

149 2.2 Stable carbon isotopes

150

151 For wild large herbivores, bioapatite increases in $\delta^{13}\text{C}$ by 12-14‰ relative to plants that they
152 usually eat (Lee-Thorp et al., 1989; Cerling and Harris, 1999). Terrestrial plants have differences in
153 $\delta^{13}\text{C}$ which are related to the photosynthetic pathways, known as C_3 , C_4 and Crassulacean Acid
154 Metabolism (CAM) (Bender, 1971; Deines, 1980). In East African environments, $\delta^{13}\text{C}$ values range
155 from -35 to -23‰ for C_3 plants, and vary between -15 and -11‰ for C_4 plants. CAM plants have
156 intermediate values between C_3 and C_4 plants (Koch et al., 1991; Cerling and Harris, 1999; Cerling et
157 al., 2003c). Trees and most shrubs and forbs use C_3 pathway. The majority of East African grasses
158 are C_4 plants, except for those growing at high altitude, above 2500-3000 m (Tieszen et al., 1979;
159 Livingstone and Clayton, 1980). C_4 plants are better adapted than C_3 plants to low atmospheric CO_2
160 concentrations (<500 ppmv), high temperatures (>30°C), high irradiance levels and prolonged water
161 stress (Ehleringer, 1979; Ehleringer et al., 1991, 1997). Plants which use CAM pathway are mainly
162 succulents and favour arid environments due to their high water-use efficiency (Ehleringer, 1979).

163

164 The $\delta^{13}\text{C}$ of terrestrial plants is controlled by that of CO_2 from which they form (Farquhar et al.,
165 1989). The isotopic composition of atmospheric CO_2 ($\delta^{13}\text{C}_{\text{atm}}$) has been decreasing since the industrial
166 revolution (1800-1850 AD), due to the combustion of ^{13}C depleted fossil fuels. The pre-industrial
167 $\delta^{13}\text{C}_{\text{atm}}$ values (from 1000 to 1800 AD), determined from air trapped in ice cores, are around -6.5‰
168 (Friedli et al., 1986; Francey et al., 1999). The reconstruction of herbivore palaeodiet and
169 palaeovegetation based on the $\delta^{13}\text{C}$ of fossil teeth needs to take account of $\delta^{13}\text{C}_{\text{atm}}$ values over
170 geological time. Estimates of $\delta^{13}\text{C}_{\text{atm}}$ based on benthic foraminifera $\delta^{13}\text{C}$ records range between -6.7
171 and -6.1‰ from the Late Miocene to the Early Pliocene (7-4 Ma) (Levin et al., 2008; Tipple et al.,
172 2010), which is comparable to pre-industrial values.

173

174 Besides the isotopic composition of source air, the $\delta^{13}\text{C}$ of C_3 and C_4 plants can be influenced
175 by light levels and water availability (Ehleringer et al., 1986; Ehleringer and Cooper, 1988; Farquhar et
176 al., 1989; Stewart et al., 1995; Buchmann et al., 1996). Variations in $\delta^{13}\text{C}$ are also observed within C_4
177 plants due to different photosynthetic subpathways: the nicotinamide adenine dinucleotide-malic
178 enzyme (NAD), the nicotinamide adenine dinucleotide phosphate-malic enzyme (NADP) and the
179 phosphoenolpyruvate carboxykinase (PCK). For instance, isotopic values average -13‰ for NAD and
180 PCK grasses and -12‰ for nearly all NADP grasses in East Africa (Cerling et al., 2003c).
181 Furthermore, C_3 plants growing in dense tropical forest exhibit lower $\delta^{13}\text{C}$ values than those growing in
182 savanna and bushland. They are subjected to the “canopy effect” which combines the fixation of ^{13}C
183 depleted CO_2 from soil respiration (-25 to -28‰) with the low light levels beneath the canopy (Medina
184 and Minchin, 1980; van der Merwe and Medina, 1991; Jackson et al., 1993). In tropical Africa, the $\delta^{13}\text{C}$
185 mean value of C_3 plants is around -27‰ in savanna and bushland whereas it varies from -31 to -34‰
186 in understory of closed-canopy forest (Cerling et al., 2003c, 2004).

187

188 To reconstruct palaeodiets of large herbivores, we used the mixing C_3 - C_4 model established
189 by Cerling et al. (2005). The $\delta^{13}\text{C}$ values of herbivore enamel are divided into three dietary categories.
190 The predominantly C_3 diet is characterized by values lower than -8‰. The predominantly C_4 diet
191 exhibits values higher than -2‰. The mixed C_3 - C_4 diet includes values between -8 and -2‰. CAM
192 plants are not considered in the interpretation of $\delta^{13}\text{C}$ values because they are much less common
193 than C_3 and C_4 plants. They do not make a significant contribution to diets of extant large herbivores in

194 East Africa, except perhaps for black rhinos (*Diceros bicornis*) in arid and semi-arid environments
195 (Cerling and Harris, 1999).

196

197 2.3 Stable oxygen isotopes

198

199 The $\delta^{18}\text{O}$ of bioapatite depends on the temperature and the $\delta^{18}\text{O}$ of the fluid from which it
200 precipitates (Longinelli and Nuti, 1973; Kolodny et al., 1983; Amiot et al., 2007). As mammals are
201 homeothermic animals, they show a constant $\delta^{18}\text{O}$ offset between body water and PO_4 component in
202 bioapatite (Luz and Kolodny, 1985), and between PO_4 and CO_3 components in bioapatite ($\Delta \approx 9\%$)
203 (review in Martin et al., 2008). The $\delta^{18}\text{O}$ of body water of herbivores is chiefly controlled by the $\delta^{18}\text{O}$ of
204 ingested water (*i.e.* drinking water, water contained in food) and the physiological mechanisms of
205 water conservation (review in Kohn and Cerling, 2002).

206

207 The stable oxygen isotope composition of meteoric water ($\delta^{18}\text{O}_{\text{mw}}$) depends on temperature,
208 quantity of precipitation and the $\delta^{18}\text{O}$ of atmospheric water vapour. Precipitation is depleted in ^{18}O
209 from the equator to the poles (“latitude effect”), and with increasing altitude and distance from
210 coastlines (Dansgaard, 1964; Rozanski et al., 1993; Fricke and O’Neil, 1999; Gonfiantini et al., 2001;
211 Poage and Chamberlain, 2001). In the tropics, seasonal variations in $\delta^{18}\text{O}_{\text{mw}}$ are ascribed to the
212 “amount effect”. A negative correlation is observed between isotopic values and rainfall amounts
213 (Dansgaard, 1964; Rozanski et al., 1993, 1996). Moisture in the air is derived primarily from
214 evaporation of the ocean surface but, in some regions, water vapour supplied by evapotranspiration of
215 the land surface and terrestrial plants is a substantial source of precipitation (Brubaker et al., 1993)
216 and can affect the $\delta^{18}\text{O}_{\text{mw}}$. For instance, transpired moisture from the Sudd and the Congo Basin is
217 likely responsible for the high isotopic values of rainfall in Ethiopia (Levin et al., 2009).

218

219 A rise in temperature and a fall in relative humidity increase the rate of evaporation and plant
220 transpiration, and lead to the ^{16}O depletion of surface water, soil water and leaf water (Craig and
221 Gordon, 1965; Dongman et al., 1974). Leaf water is depleted in ^{16}O relative to soil water from which it
222 is derived (Yakir, 1992; Yakir and Sternberg, 2000). Body water of mammals is also affected by ^{16}O
223 depletion due to the loss of water vapour through sweating and panting (Kohn and Cerling, 2002). As

224 a result, the PO₄ and CO₃ components in herbivore bioapatite are expected to decrease in δ¹⁸O when
225 the environment evolves to more humid or colder conditions (« cooler » is a more appropriate word for
226 tropical regions). Variations in moisture source may also impact the isotopic values of bioapatite.

227

228 Two isotopic patterns are commonly observed in bioapatite of large herbivores from East
229 Africa. The δ¹⁸O is lower for hippos than for terrestrial fauna including bovids, elephants, equids,
230 giraffids, rhinos and suids (Bocherens et al., 1996; Cerling et al., 2003b, 2008). Hippos wallow in the
231 water during the day and forage for grass and other fodder at night (Estes, 1991; Kingdon, 1997). It is
232 argued that their amphibious lifestyle restricts the ¹⁸O enrichment of body water by reducing the loss of
233 water vapour from body cooling. Night-time intake of plants by hippos could also limit this isotopic
234 enrichment because plant transpiration is reduced during this period (Bocherens et al., 1996;
235 Clementz et al., 2008). Furthermore, δ¹⁸O values of herbivores with different behaviours record
236 different aspects of the same environment. The obligate-drinking species (e.g. black rhino, elephant,
237 hippo) track the δ¹⁸O_{mw} more faithfully than the drought-tolerant species (e.g. dikdik, giraffe, oryx). The
238 latter obtain most of their water from leaves and their isotopic values are impacted by changes in
239 relative humidity. The highest δ¹⁸O values are commonly observed in drought-tolerant herbivores at
240 the ecosystem level (Kohn et al., 1996; Cerling et al., 2003b, Levin et al., 2006).

241

242 **3. Materials and methods**

243

244 We studied 181 molars and premolars of large herbivorous mammals from sixteen localities of
245 the Lukeino and Mabaget Formations (**figure 2**). Teeth from the three members of the Lukeino
246 Formation were collected. Fossil specimens are distributed among nine families within three orders:
247 artiodactyls (bovids, giraffids, hippos and suids), perissodactyls (equids and rhinos) and
248 proboscideans (deinotheres, elephantids and gomphotheres). Deinotheres and gomphotheres are
249 extinct groups. Some teeth were identified at the species or genus level: *Nyanzachoerus jaegeri* (suid)
250 in the Mabaget Formation, *Nyanzachoerus tulotos* (suid) in the Lukeino Formation, *Anancus*
251 *kenyensis* (gomphothere), *Deinotherium bozasi* (deinothere), *Eurygnathohippus* (formerly *Hipparion*,
252 equid) and *Hippopotamus "sensu lato"* (hippo) in both formations. Updated faunal lists of these
253 formations were reported by Pickford et al. (2009).

254

255 An enamel powder was obtained from each tooth with a drill and a diamond burr. After
256 cleaning the tooth surface, samples were taken along a vertical groove on the crown. Bulk samples
257 cover several months to a few years of biomineralization, depending on the rate of enamel growth in
258 the species (see table 1 in Kohn, 2004) and the size of the tooth remains.

259

260 Measurements of F, Fe and Mn concentrations were performed on nineteen specimens from
261 the Lukeino Formation and twenty from the Mabaget Formation. These individuals are bovids (n=7),
262 deinotheres (n=2), elephantids (n=1), equids (n=2), giraffids (n=1), hippos (n=20), rhinos (n=2) and
263 indeterminate proboscideans (n=4). To provide comparative chemical data, we analysed four molars
264 and premolars of extant bovids (goats/sheep) from the Tugen Hills. These teeth were collected in the
265 field or in the vicinity of dwellings. Before performing the analyses, bulk samples were treated with 0.1
266 M acetic acid for 10 min to remove diagenetic carbonate. They were rinsed with deionized water and
267 then dried at 60-70°C. After that step, samples were dissolved in 30% nitric acid at 100°C for 1h.
268 Some 30 mg of sample were commonly used for these analyses. The fluorine content was analysed
269 with a fluoride ion selective electrode (*Mettler Toledo* electrode). The iron and manganese
270 concentrations were tested by ICP-AES (*Jobin Yvon 2000* spectrometer). Relative uncertainty of
271 measurements was about 5%. Results are presented in **Appendix 1**, Supplementary Material.

272

273 Stable isotope measurements were made on the CO₃ component of all fossil teeth (n=181).
274 Bulk samples were pretreated with 2% bleach for 15 min and 0.1 M acetic acid for 10 min. These two
275 reactions were aimed at removing organic contaminants and diagenetic carbonate, respectively.
276 Enamel powders were rinsed after each treatment and then dried at 60-70°C. Samples weighing 0.8-
277 1.2 mg were reacted with 100% phosphoric acid in single vessels under vacuum at 70°C for 12 min.
278 The resultant CO₂ was analysed by dual-inlet isotope-ratio mass spectrometry (GV Instruments
279 Isoprime spectrometer). The stable oxygen isotope ratio of carbonate in bioapatite was calculated
280 using the temperature-dependent fractionation factor between calcite and CO₂ produced as a result of
281 phosphoric acid digestion (Swart et al., 1991). The ¹³C/¹²C and ¹⁸O/¹⁶O ratios were reported in the δ
282 notation relative to the international standard PDB, in parts per mil, as: $\delta^{13}\text{C} (\text{‰}) = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}} /$
283 $({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} - 1] * 1000$ and $\delta^{18}\text{O} (\text{‰}) = [({}^{18}\text{O}/{}^{16}\text{O})_{\text{sample}} / ({}^{18}\text{O}/{}^{16}\text{O})_{\text{standard}} - 1] * 1000$. Corrections were

284 based on working carbonate standards calibrated to the reference material NBS-19. Analytical
285 precision of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was 0.1‰ for repeated measurements of the standards. Results are listed
286 in **Appendix 2**, Supplementary Material.

287

288 Statistics were performed using the *R* software. We used the Mann-Whitney test (1947) for
289 comparisons between two independent groups. The latter are significantly different if the p-value is
290 lower than the significance level α , fixed at 0.05 (5%).

291

292 **4. Results and discussion**

293

294 **4.1. State of preservation of fossil enamel**

295

296 All fossil specimens show higher F, Fe and Mn concentrations than extant individuals (**table**
297 **1**). On average, fossil enamel contains about 40 times more fluorine, 35 times more iron and 120
298 times more manganese than modern enamel. Comparable F, Fe and Mn concentrations were
299 measured in herbivore enamel from other Mio-Pliocene deposits in the Kenyan Rift Valley (Kohn et al.,
300 1999; Schoeninger et al., 2003a; Passey et al., 2007). No significant difference was observed between
301 individuals from the Lukeino Formation (n=19) and those from the Mabaget Formation (n=20) (p-
302 value=0.59 for [F], 0.43 for [Fe] and 0.73 for [Mn]). Moreover, the chemical composition of fossil
303 enamel is not significantly different between bovids (n=7) and hippos (n=20) (p-value=0.13 for [F],
304 0.20 for [Fe] and 0.69 for [Mn]). The other families were excluded from statistical comparisons due to
305 the low number of analysed specimens (see section 3). Trace element enrichment in fossil enamel
306 reflects the climatic conditions and tectono-volcanic activity of the East African Rift. Tropical
307 weathering of basaltic lava flows (*i.e.* mafic rocks) could be responsible for large amounts of Fe and
308 Mn in diagenetic fluids. High F concentrations in these fluids probably result from hydrothermal
309 alteration in the Baringo Basin (Renaut et al., 2002; Tarits et al., 2006). At Cheboit and Kapsomin in
310 the Lukeino Formation, there are extensive tufa deposits which accumulated around hot springs
311 (Pickford et al., 2009).

312

313 Previous studies emphasized chemical alterations of herbivore enamel from the Lukeino and
314 Mabaget Formations. Cathodoluminescence observations of fossil specimens other than those
315 analysed indicated an incorporation of rare earth elements and manganese into the apatite lattice
316 (Ségalen et al., 2008). Infrared spectroscopy highlighted a loss of structural carbonate and a gain in
317 crystallinity (Roche et al., 2010). In addition, fossil enamel exhibits a higher calcium/phosphorus mass
318 ratio than modern enamel (Roche et al., 2010).

319
320 Despite chemical alterations of fossil enamel, no correlation was observed between isotopic
321 ratios of biogenic carbonate and F, Fe and Mn concentrations. The stable carbon and oxygen isotope
322 ratios of fossil specimens fall within the statistical range of extant large herbivores from East Africa
323 (Bocherens et al., 1996; Cerling et al., 2003b; Levin et al., 2008). We measured values from -14.0 to
324 1.2‰ for $\delta^{13}\text{C}$, and between -5.8 and 4.9‰ for $\delta^{18}\text{O}$. Preservation of the palaeoenvironmental signals
325 in tooth enamel carbonate of large herbivores from the Lukeino and Mabaget Formations is supported
326 by the fact that the $\delta^{18}\text{O}$ values are consistent with the amphibious lifestyle of hippos and the drought
327 tolerance in giraffids. In each formation, hippos are significantly depleted in ^{18}O compared with
328 terrestrial fauna including bovids, equids, giraffids, proboscideans, rhinos and suids (p -value<0.001)
329 (**figure 3**). This isotopic difference was expected (see section 2.3). However, all $\delta^{18}\text{O}$ values of fossil
330 hippos, except one, are included in the statistical range of terrestrial herbivores, which is not observed
331 in modern counterparts (Bocherens et al., 1996; Cerling et al., 2003b, 2008). A possible explanation
332 for this is that hippos had a lower affinity for water habitat in Mio-Pliocene time than today. In the
333 Lukeino Formation, the $\delta^{18}\text{O}$ values average $-2.6 \pm 1.2\text{‰}$ for hippos ($n=16$) and $-0.3 \pm 2.5\text{‰}$ for
334 terrestrial herbivores ($n=55$). The mean values are $-2.0 \pm 1.3\text{‰}$ for hippos ($n=32$) and $-0.5 \pm 2.2\text{‰}$ for
335 terrestrial herbivores ($n=78$) sampled from the Mabaget Formation. The giraffid specimen from this
336 formation exhibits one of the highest $\delta^{18}\text{O}$ values (4.4‰), as expected for a drought-tolerant animal.
337 Extant giraffes are non-obligate drinkers (see section 2.3) and commonly have high $\delta^{18}\text{O}$ values, up to
338 11‰ (Cerling et al., 2003b, 2008; Kingston and Harrison, 2007).

339
340 Furthermore, the $\delta^{18}\text{O}$ values average $0.0 \pm 2.5\text{‰}$ for bovids ($n=32$), $-1.9 \pm 1.0\text{‰}$ for
341 deinotheres ($n=8$), $-3.1 \pm 1.9\text{‰}$ for elephantids ($n=8$), $2.1 \pm 1.9\text{‰}$ for equids ($n=13$), $0.2 \pm 1.1\text{‰}$ for
342 gomphotheres ($n=8$), $0.4 \pm 1.5\text{‰}$ for rhinos ($n=25$) and $-1.4 \pm 1.6\text{‰}$ for suids ($n=21$) in the Lukeino and

343 Mabaget Formations. Difference in $\delta^{18}\text{O}$ is significant between elephantids and equids which represent
344 the extremes ($p\text{-value}<0.001$). This is consistent with isotopic data of modern counterparts (Bocherens
345 et al., 1996; Cerling et al., 2008). We also calculated a mean $\delta^{18}\text{O}$ value of $-1.5 \pm 2.1\text{‰}$ for unidentified
346 fossil specimens ($n=17$) which are either elephantids or gomphotheres.

347

348 4.2. Palaeodiets of large herbivores

349

350 The $\delta^{13}\text{C}$ values of herbivore enamel indicate the presence of C_3 plant eaters, C_4 plant
351 consumers and mixed feeders in the Lukeino and Mabaget Formations (**figure 4**). These dietary
352 categories were previously observed in other Late Miocene and Early Pliocene faunas in East Africa
353 (Cerling et al., 2003a; Levin et al., 2008; White et al., 2009; Uno et al., 2011).

354

355 Bovids from the Lukeino and Mabaget Formations exhibit $\delta^{13}\text{C}$ values from -14.0 to 0.7‰ .
356 There are ten specimens with a C_3 diet, nine with a C_4 diet and thirteen with a mixed diet. The
357 distribution of isotopic values displays a gap of $5\text{-}6\text{‰}$ between two groups in each formation. One guild
358 comprises C_3 plant eaters whereas the second consists of C_4 plant consumers and mixed feeders,
359 except for one individual in the Lukeino Formation close to C_3 plant eaters ($\delta^{13}\text{C} = -7.7\text{‰}$). A
360 discontinuous range of $\delta^{13}\text{C}$ values for extant bovids is observed in East African environments and
361 results from browsing and grazing behaviours among species (Cerling et al., 2003c).

362

363 The giraffid specimen from the Mabaget Formation has a $\delta^{13}\text{C}$ value of -13.1‰ which
364 indicates a C_3 diet. The latter is observed in extant giraffes (*Giraffa camelopardalis*) and reflects the
365 intake of tree leaves (Cerling and Harris, 1999).

366

367 Fossil specimens of *Hippopotamus "sensu lato"* have $\delta^{13}\text{C}$ values between -13.1 and 0.2‰ .
368 Most individuals (30 out of 48) are mixed feeders. There are nine specimens with a C_3 diet and
369 another nine with a C_4 diet. Difference in $\delta^{13}\text{C}$ is not significant between individuals from the Lukeino
370 Formation ($n=16$) and those from the Mabaget Formation ($n=32$) ($p\text{-value}=0.23$). The mean value is $-$
371 $5.3 \pm 3.4\text{‰}$ for all specimens. Two individuals from the Mabaget Formation are clearly separated from
372 the others and exhibit the lowest $\delta^{13}\text{C}$ and highest $\delta^{18}\text{O}$ values (**figure 4a**). These ratios would not be

373 ecologically discrepant because such an isotopic variation among fossil hippos was previously
374 observed in Pliocene deposits in the Turkana Basin, a tectonically controlled lake system in northern
375 Kenya and southern Ethiopia (Schoeninger et al., 2003b). The heterogeneity of stable isotope values
376 for fossil hippos may reflect differences in their habitat (grassland vs. woodland, river vs. lake), as
377 observed in their modern counterparts (Boisserie et al., 2005; Cerling et al., 2008). These isotopic
378 studies also indicate that most extant hippos (*Hippopotamus amphibius*) are mixed feeders with a
379 predominant intake of C₄ plants.

380

381 The $\delta^{13}\text{C}$ values of suids from the Lukeino and Mabaget Formations vary between -11.5 and -
382 1.4‰. Most individuals (17 out of 21) are mixed feeders. Three specimens have C₃ diet and one a C₄
383 diet. Values average $-6.6 \pm 2.3\text{‰}$ for *Nyanzachoerus tulotos* (n=8) in the Lukeino Formation, and -4.8
384 $\pm 1.9\text{‰}$ for *Nyanzachoerus jaegeri* (n=13) in the Mabaget Formation. Although the interspecific
385 difference is not significant (p-value=0.10), the highest values (above -4‰) were only observed in
386 *Nyanzachoerus jaegeri* (4 out of 13 individuals). *Nyanzachoerus jaegeri* could have a higher intake of
387 grasses (C₄ plants) than *Nyanzachoerus tulotos*. This interpretation is in agreement with their dental
388 morphology. *Nyanzachoerus tulotos* has brachyodont cheek teeth (*i.e.* low-crowned teeth) whereas
389 *Nyanzachoerus jaegeri* is characterized by hypsodont cheek teeth (*i.e.* high-crowned teeth) (Harris
390 and Cerling, 2002). The latter species is better adapted to the intake of grasses which are very
391 abrasive plants due to their high phytolith content (Piperno, 2006). Published $\delta^{13}\text{C}$ data of
392 nyanzachoeres provide additional support for our palaeodietary reconstruction (Harris and Cerling,
393 2002; Levin et al., 2008).

394

395 Specimens of the equid *Eurygnathohippus* (formerly called *Hipparion*) show $\delta^{13}\text{C}$ values from -
396 4.8 to 0.2‰ for both formations. The majority of individuals (9 out of 13) has a C₄ diet and the
397 remaining specimens are mixed feeders. This result is consistent with the dentition of these fossil
398 equids which have hypsodont cheek teeth reflecting their grazing habits (Bernor et al., 2010). Other
399 isotopic studies also demonstrate the predominant intake of C₄ plants in *Eurygnathohippus* (Levin et
400 al., 2008; White et al., 2009; Uno et al., 2011). No significant difference in $\delta^{13}\text{C}$ was observed between
401 individuals from the Lukeino Formation (n=8) and those from the Mabaget Formation (n=5) (p-
402 value=0.88). The mean value is $-1.4 \pm 1.5\text{‰}$ for all specimens.

403

404 Rhinos from the Lukeino and Mabaget Formations have $\delta^{13}\text{C}$ values from -13.7 to -0.8‰.
405 Among the individuals analysed, there are ten with a C_3 diet, four with a C_4 diet and eleven with a
406 mixed diet. The range of $\delta^{13}\text{C}$ values is discontinuous in each formation. For specimens from the
407 Mabaget Formation, a gap was observed between -5.8 and -3.4‰, within the category of mixed
408 feeders. There are two guilds: one toward the C_3 diet (n=14), the other toward the C_4 diet (n=4). We
409 noticed three groups in the Lukeino Formation: C_3 plant eaters ($\delta^{13}\text{C}$ lower than -11‰, n=2), C_4 plant
410 consumers ($\delta^{13}\text{C}$ higher than -2‰, n=2) and mixed feeders ($\delta^{13}\text{C}$ between -8 and -5‰, n=3). The
411 heterogeneity of $\delta^{13}\text{C}$ values for fossil rhinos could reflect interspecific variation in diet.
412 *Brachytherium lewisi*, *Ceratotherium praecox*, *Diceros bicornis* and *Diceros cf. pachygnathus* were
413 reported in faunal lists of the Lukeino and Mabaget Formations (Pickford et al., 2009). In Africa today,
414 there are two rhino species with different dietary habits. The black rhino (*Diceros bicornis*) is a browser
415 and consequently a C_3 plant eater whereas the white rhino (*Ceratotherium simum*) is a grazer
416 characterized by a C_4 diet (Bocherens et al., 1996; Cerling et al., 2003b).

417

418 The $\delta^{13}\text{C}$ values of *Deinotherium bozasi* vary between -12.7 and -11.9‰ for both formations.
419 All specimens have a C_3 diet, which is consistent with their dentition. Deinotheres have brachyodont
420 and lophodont cheek teeth which are adapted to browsing (Shoshani and Tassy, 1996). They are
421 reported to have maintained a C_3 diet throughout the entire record in East Africa (Cerling et al., 1999;
422 Uno et al., 2011). One individual was analysed in the Lukeino Formation. Its $\delta^{13}\text{C}$ value is included in
423 the statistical range of the seven specimens from the Mabaget Formation. The mean value is $-12.2 \pm$
424 0.3‰ for all individuals.

425

426 For *Anancus kenyensis*, the $\delta^{13}\text{C}$ values range from -2.1 to 1.2‰. Almost all individuals have a
427 C_4 diet (7 out of 8). One specimen from the Lukeino Formation is a mixed feeder, very close to C_4
428 plant eaters. The cheek teeth of *Anancus kenyensis* are brachyodont and bunodont with thick enamel
429 and the crown is usually heavily invested by cementum. On the basis of the dental morphology, this
430 gomphothere species was reported to be adapted to the intake of nuts (tough fruits) and/or grasses
431 (abrasive plants) (Shoshani and Tassy, 1996). Isotopic data of *Anancus kenyensis* are in agreement
432 with grazing habits. They cannot be explained by a prevalent intake of nuts which leads to a C_3

433 signature of bioapatite. The predominantly C₄ diet of *Anancus* is also confirmed by other isotopic
434 studies (Levin et al., 2008; White et al., 2009; Uno et al., 2011). Three individuals were analysed in the
435 Mabaget Formation. Their δ¹³C values range within those of the five specimens from the Lukeino
436 Formation. The mean value is -0.1 ± 1.1‰ for all individuals.

437

438 Elephantids from the Lukeino and Mabaget Formations exhibit δ¹³C values between -12.4 and
439 -3.2‰. Nearly all specimens are C₃ plant consumers (7 out of 8). One individual from the Mabaget
440 Formation has a mixed diet, rich in C₄ plants. Stable isotope analyses of extant African elephants
441 (*Loxodonta*) indicate diets dominated by C₃ plants, even though some specimens show evidence for a
442 mixed C₃-C₄ diet (Cerling et al., 1999).

443

444 Another 17 specimens of proboscideans from the two formations were investigated but could
445 not be identified due to the small size of the tooth remains. They are either elephantids or
446 gomphotheres (*Anancus kenyensis*). Their δ¹³C values vary from -12.4 to 0.7‰. Values of C₃ plant
447 eaters (n=5) plot apart from those of mixed feeders (n=4) and C₄ plant consumers (n=8). The C₃ diet
448 group is likely composed of elephantids whereas the C₄/mixed diet guild may comprise gomphotheres
449 and elephantids.

450

451 4.3. Past vegetation and climate of the Tugen Hills

452

453 The Lukeino Formation mammalian fauna is dominated by impalas and colobus monkeys, and
454 suggests that the environment comprised thicket, woodland and forest (Pickford and Senut, 2001).
455 Remains of water chevrotains, tree civets, fruit bats and lorises attest to the presence of forest areas
456 (Pickford et al., 2009, Pickford, 2011). Some fossil leaves from this formation are associated with
457 woodland or dry evergreen forest, others suggest a more humid forest (Senut, 2006b; Senut et al.,
458 2010; Bamford et al., 2013). The faunal assemblage of the Mabaget Formation, including water
459 chevrotains and peafowls, suggests that the environment was heavily vegetated (Pickford et al., 2004,
460 2009).

461

462 The $\delta^{13}\text{C}$ values of fossil large herbivores indicate that the earliest Kenyan hominids inhabited
463 a mixed $\text{C}_3\text{-C}_4$ environment. They are comparable to those of extant large herbivores living in East
464 African savanna and bushland, taking into account the correction for the anthropogenic ^{13}C depletion
465 of atmospheric CO_2 (Bocherens et al., 1996; Cerling et al., 2003b; Levin et al., 2008). By contrast,
466 extant herbivores living in dense tropical forest - C_3 ecosystem marked by the “canopy effect” - exhibit
467 much lower isotopic values than those measured (Cerling et al., 2004). However, a minority of fossil
468 specimens (n=17) show $\delta^{13}\text{C}$ values lower than -12‰ which may reflect C_3 diets in wooded areas.
469 Such negative values were observed in bovids (n=5), giraffids (n=1), hippos (n=1), proboscideans
470 (n=8) and rhinos (n=2) from the Mabaget Formation (**figure 4a**) and the Kapcheberek and Kapsomin
471 Members of the Lukeino Formation (**figure 4b,c**). Trees did not form a continuous cover in the Tugen
472 Hills during the Late Miocene and Early Pliocene but they could have formed fairly dense stands
473 where water supply was optimal. Given the depositional context of the fossil remains, patches of
474 woodland were probably located around the Lukeino and Mabaget palaeolakes and along the rivers
475 which drained into the lakes (*i.e.* riparian vegetation).

476

477 C_3 diets of hippos, rhinos and suids from the Lukeino Formation were only observed in the
478 Kapcheberek Member, the uppermost unit (**figure 4b**). Nearly all bovid specimens from this member
479 were C_3 plant eaters unlike those from the lower stages of the formation (**figure 4c,d**). These results
480 suggest that there was more C_3 vegetation within the Tugen Hills in the latest Miocene (*ca.* 5.7 Ma)
481 than before (*ca.* 6.1-5.8 Ma). A greater C_3 plant biomass could reflect a higher woody cover (*i.e.* more
482 trees and shrubs). The lowest values of C_3 plant consumers were observed in ten individuals from the
483 Mabaget Formation (-12.5 to -14.0‰) (**figure 4a**). $\delta^{13}\text{C}$ values of C_3 plants decrease in shaded and
484 watered conditions (Ehleringer et al., 1986; Ehleringer and Cooper, 1988; Farquhar et al., 1989;
485 Stewart et al., 1995). A possible explanation is that the Tugen Hills were more wooded (leading to less
486 light on the ground) and/or more humid during the Early Pliocene (*ca.* 5.3-4.5 Ma) than in the Late
487 Miocene (*ca.* 6.1-5.7 Ma). This is consistent with palaeontological studies based on faunal
488 assemblages (Pickford et al., 2004, 2009). Pollen data from sediments in the Gulf of Aden and
489 offshore the Niger delta suggest a tree expansion in tropical Africa from roughly 5.5 to 3.5 Ma
490 (Bonnefille, 2010). A decline of C_4 grass biomass in northeastern Africa by 4.3 Ma is indicated by
491 decreased $\delta^{13}\text{C}$ values of plant leaf wax from marine deposits of the Gulf of Aden (Feakins et al.,

492 2013). Moreover, a shift to more negative $\delta^{13}\text{C}$ values in pedogenic carbonate from Awash and
493 Turkana Basins suggests that peaks of woody vegetation occurred between 3.9 and 3.2 Ma in
494 Northeast Africa (Cerling et al., 2011).

495

496 There are fifteen individuals from the Mabaget Formation and eleven from the Kapcheberek
497 Member which show lower $\delta^{18}\text{O}$ values than those from the lower members of the Lukeino Formation.
498 These values range from -3.3 to -5.8‰ (**figure 4a,b**) and they were observed in bovids (n=5), hippos
499 (n=7), proboscideans (n=10), rhinos (n=1) and suids (n=3). They could reflect a stronger “amount
500 effect” on $\delta^{18}\text{O}_{\text{mw}}$, implying that moister conditions occurred in the Tugen Hills during the latest
501 Miocene and the Early Pliocene than before. Rainfall patterns in East Africa today are controlled by
502 major air streams (*i.e.* northeast and southeast monsoons, westerlies), the position of convergence
503 zones (*i.e.* Intertropical Convergence Zone, Congo Air Boundary), topography and sea surface
504 temperature (SST) fluctuations in the Indian and Atlantic Oceans (Nicholson, 1996). Observational
505 studies emphasize that warmer Indian Ocean SST are currently associated with more rain in East
506 Africa (review in Cane and Molnar, 2001). Such conditions might have occurred in the latest Miocene
507 and the Early Pliocene. Increased moisture would have led to more C_3 vegetation in the latest
508 Miocene, as suggested by $\delta^{13}\text{C}$ values. Specimens from the Mabaget Formation do not exhibit more
509 negative $\delta^{18}\text{O}$ values than those from the Kapcheberek Member. Local moisture in the Early Pliocene
510 would have been comparable to that of the latest Miocene. This suggests that the shift to lower $\delta^{13}\text{C}$
511 values in C_3 plant eaters from the Mabaget Formation is a result of vegetation change. Denser stands
512 of trees - where understory grew in lower light conditions - likely appeared within the Tugen Hills in the
513 Early Pliocene. Statistical comparisons between fossil assemblages at the species level are necessary
514 to confirm or refute these hypotheses; a larger dataset of fossil enamel samples, particularly from the
515 Miocene deposits, is required for these comparisons. Furthermore, the aridity index established by
516 Levin et al. (2006) could not have been applied to fossil assemblages. It takes account of enamel $\delta^{18}\text{O}$
517 values of giraffid, dikdik and oryx (two bovid taxa) which are evaporation sensitive herbivores.
518 Unfortunately, we had only one giraffid individual (from the Mabaget Formation) and bovid specimens
519 in both formations were too fragmented to be identified at the genus or species level.

520

521 4.4. Large herbivores associated with early potential hominids in Chad and Ethiopia

522

523 The $\delta^{13}\text{C}$ values of fossil large herbivores from the Tugen Hills were compared with those for
524 counterparts associated with early putative hominids: *Ardipithecus kadabba*, *Ardipithecus ramidus* and
525 *Sahelanthropus tchadensis* (**figure 5**). In these species, the claimed bipedalism - a distinctive trait of
526 the family Hominidae in the study of hominoid evolution - needs to be reassessed because of
527 insufficient evidence (Senut, 2006b, 2011). Isotopic data of herbivore enamel were compiled from
528 Zazzo (2001), Boisserie et al. (2005), Levin et al. (2008) and White et al. (2009).

529

530 Remains of *S. tchadensis* were discovered in the Toros Menalla deposits in the Djurab Desert
531 (Chad) and they were dated at 7-6 Ma on the basis of the faunal assemblage (Brunet et al., 2002).
532 Radiometric dating yielded ages between 7.2 and 6.8 Ma for the sediments thought to contain the
533 hominid fossils (Lebatard et al., 2008), but their stratigraphic position is unclear (Beauvilain, 2008). A
534 detailed study of anthracothere remains from Toros Menalla indicated that the deposits probably span
535 the period 10 to 6 Ma (Pickford, 2008). Palaeontological and sedimentological studies suggest that *S.*
536 *tchadensis* inhabited a perilacustrine vegetation including gallery and islet forests, wooded savanna
537 and grassland close to a sandy desert (Vignaud et al., 2002; Brunet et al., 2004; Schuster et al.,
538 2006).

539

540 In the Awash River Valley (Ethiopia), the remains of *A. kadabba* (5.8-5.2 Ma) and *A. ramidus*
541 (4.5-4.3 Ma) were found in the Late Miocene Adu-Asa Formation and the Early Pliocene Sagantole
542 Formation, respectively (White et al., 1994, 1995; Haile-Selassie, 2001; Semaw et al., 2005; Simpson
543 et al., 2007). Palaeontological studies indicate that *Ardipithecus* might have lived in a woodland with
544 forest patches (WoldeGabriel et al., 2001, 2009; Haile-Selassie et al., 2004; White et al., 2009)
545 whereas the $\delta^{13}\text{C}$ values for pedogenic carbonate suggest a more open ecosystem (Cerling et al.,
546 2010, 2011).

547

548 The $\delta^{13}\text{C}$ values for large herbivores range from -11.3 to 2.0‰ in the Toros Menalla sites
549 (n=46), and vary between -15.7 and 3.3‰ in the Adu-Asa and Sagantole Formations (n=286). They
550 indicate that *Sahelanthropus* and *Ardipithecus* lived in mixed $\text{C}_3\text{-C}_4$ environments as did the Mio-
551 Pliocene hominids from the Tugen Hills. Values lower than -12‰ were not observed in large

552 herbivores from Toros Menalla. One bovid from the Adu-Asa Formation and some deinotheres and
553 giraffids from the Sagantole Formation show such negative values. These observations suggest that
554 woodland represented a scarce or patchy cover within these depositional environments. There is no
555 record of closed-canopy vegetation.

556

557 Deinotheres from the Sagantole Formation had a C₃ diet. Their values are close to those of
558 coeval specimens from the Mabaget Formation. Nearly all giraffids from the Chadian and Ethiopian
559 deposits were C₃ plant eaters. One individual from the Sagantole Formation is reported to have had a
560 C₄ diet (Levin et al., 2008). The intake of C₄ plants prevailed for equids and gomphotheres from the
561 Toros Menalla sites and the Adu-Asa and Sagantole Formations. Fossil elephantids from the Awash
562 River Valley had a C₄ or mixed diet whereas those from the Tugen Hills were C₃ plant consumers or
563 mixed feeders. C₃, C₄ and mixed diets were observed in bovids, hippos, rhinos and suids from the
564 Chadian and Ethiopian deposits.

565

566 The highest $\delta^{13}\text{C}$ values of bovids, equids, rhinos and suids are recorded by specimens from
567 the Sagantole Formation and they emphasize the relevance of the C₄ grass biomass within the
568 depositional environment. Maximum values are about 1‰ for suids, 2‰ for equids and suids, and 3‰
569 for bovids. It is worth noting that variations in relative abundance of the NAD, NADP and PCK grasses
570 within ecosystems may cause slight differences in $\delta^{13}\text{C}$ among C₄ plant eaters. Herbivore enamel
571 associated with a diet of NADP grasses is ¹³C enriched by about 1‰ compared to that associated with
572 diet of NAD/PCK grasses (Cerling and Harris, 1999). The latter favour xeric habitat whereas NADP
573 grasses are more common in mesic habitat (Hattersley, 1992; Cerling et al., 2003c). Water stress and
574 light levels can also affect $\delta^{13}\text{C}$ values of C₄ grasses (Buchmann et al., 1996) and consequently the
575 isotopic composition of herbivore enamel. C₄ grasses generally exhibit the highest $\delta^{13}\text{C}$ values in
576 sunny-watered conditions (Buchmann et al., 1996).

577

578 A minority of hippos from the Lukeino and Mabaget Formations had a C₃ diet (9 out of 48
579 specimens). We observed no C₃ plant eating hippos from the Adu-Asa and Sagantole Formations and
580 only one individual from Toros Menalla is reported to have had a C₃ diet (Boisserie et al., 2005). These

581 observations suggest that there was a greater C₃ plant biomass (*i.e.* possibly a higher woody cover)
582 near rivers and lakes within the Tugen Hills than in the other depositional environments.

583

584 Lastly we notice that Early Pliocene suids (Mabaget and Sagantole Formations) had higher
585 $\delta^{13}\text{C}$ values than their Late Miocene counterparts (Adu-Asa and Lukeino Formations and Toros
586 Menalla sites). Increased intake of C₄ grasses among suids is correlated with the development of
587 hypsodonty during the Plio-Pleistocene (Harris and Cerling, 2002).

588

589 **5. Conclusion**

590

591 The aim of this study was to explore the environment of the earliest Kenyan hominids, using
592 the stable carbon and oxygen isotope composition of tooth enamel carbonate of large herbivores. The
593 $\delta^{13}\text{C}$ values show differences in diet among taxa between 6.1 and 4.5 Ma (**figure 6**). Deinotheres,
594 giraffids and nearly all elephantids had a C₃ diet that reflects a browsing behaviour. Equids and
595 gomphotheres were mainly C₄ plant eaters, which indicates grazing habits. Most hippos and suids
596 were mixed C₃-C₄ feeders and they were therefore generalist herbivores. Bovids and rhinos had a diet
597 which varied from C₃ to C₄ plants.

598

599 The presence of C₃ plants (trees, shrubs and forbs) and C₄ plants (tropical grasses) in the
600 Tugen Hills during this period indicates a complex of heterogeneous habitats for the fauna including
601 hominids. The palaeontological studies of the faunal assemblages from the Lukeino and Mabaget
602 Formations and the leaf remains from the Lukeino Formation suggested that there was forest at the
603 time of deposition (Pickford and Senut, 2001; Pickford et al., 2004; Senut, 2006b; Pickford, 2011;
604 Bamford et al., 2013). However, the $\delta^{13}\text{C}$ of herbivore enamel emphasizes the significance of C₄ grass
605 biomass in the Tugen Hills, indicating that trees did not form a continuous cover. Isotopic data would
606 fit with a savanna ecosystem (*i.e.* a wooded grassland as defined by White, 1986). But, fairly low
607 isotopic values (between -12‰ and -14‰) do not exclude the presence of patches of woodland
608 (**figure 6**). The latter were likely located in perilacustrine and riparian areas, given the depositional
609 context of the fossil remains.

610

611 We observed variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among faunal assemblages which may reflect
612 changes in local climate and vegetation. The $\delta^{18}\text{O}$ data suggest that the Tugen Hills experienced more
613 humid conditions in the Early Pliocene (ca. 5.3-4.5 Ma) and the latest Miocene (ca. 5.7 Ma) than
614 before (ca. 6.1-5.8 Ma). The $\delta^{13}\text{C}$ values indicate that the C_3 plant biomass might have increased
615 within the depositional environment during the Late Miocene. The Tugen Hills were probably more
616 wooded in the Early Pliocene than before, which is consistent with palaeontological studies (Pickford
617 et al., 2004, 2009). It is worth noting that our study focussed on large herbivores which represent a
618 part of the fauna discovered in the two formations. Integrating other groups (e.g. gastropods, rodents,
619 primates) in the isotopic approach is necessary to refine the environmental context of the earliest
620 Kenyan hominids.

621
622 Postcranial studies show that *Orrorin tugenensis* was a bipedal hominid which could also
623 climb trees (Senut et al., 2001; Pickford et al., 2002; Galik et al., 2004; Gommery and Senut, 2006).
624 This suggests that human bipedalism originated in a mixture of grassy and wooded areas. Patches of
625 woodland provide food such as fruits but also the possibility to escape from savanna predators.
626 Variations in altitude, latitude and tectonics played a role in the distribution of diverse ecosystems
627 (Bailey et al., 2011) and ultimately in the distribution of hominoids (including hominids) and locomotor
628 behaviours, which happen to be more diverse than previously expected. Reconstructing detailed
629 environments in which hominids emerged is still a challenge and further geochemical studies need to
630 be performed in late Middle Miocene deposits, a period in which the dichotomy between the great
631 apes and the hominids might have occurred (Arnason et al., 2000; Senut and Pickford, 2004;
632 Langergraber et al., 2012).

633

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635

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645 **References**

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- 1046
- 1047

1048 **Figure captions**

1049

1050 **Figure 1:** Location of the Tugen Hills deposits (red square).

1051

1052 **Figure 2:** Stratigraphic section of the Lukeino and Mabaget Formations. Radiometric dates and
1053 geomagnetic reversal ages are reported in Pickford et al. (1983), Hill et al. (1985), Deino et al. (2002)
1054 and Sawada et al. (2002).

1055

1056 **Figure 3:** Box and whisker plots of $\delta^{18}\text{O}$ values for hippos and terrestrial herbivores from the Lukeino
1057 and Mabaget Formations. The number of specimens is given in brackets for each group. Outliers are
1058 shown as filled circles. “MB” = Mabaget Formation (5.3-4.5 Ma), “LK” = Lukeino Formation (6.1-5.7
1059 Ma).

1060

1061 **Figure 4:** $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of large herbivores from the Mabaget Formation (a), the Kapcheberek
1062 Member of the Lukeino Formation (b), the Kapsomin Member of the Lukeino Formation (c) and the
1063 Kapgoywa Member of the Lukeino Formation (d). The number of specimens is given in brackets for
1064 each group. “indet. probos.” = indeterminate proboscideans.

1065

1066 **Figure 5:** $\delta^{13}\text{C}$ values of fossil large herbivores from the Tugen Hills (Kenya), the Awash River Valley
1067 (Ethiopia) and the Djurab Desert (Chad). The number of specimens is given in brackets for each
1068 group. Box and whisker plots are used for groups including at least five individuals, and outliers are
1069 shown as filled circles. “MB” = Mabaget Formation (5.3-4.5 Ma), “LK” = Lukeino Formation (6.1-5.7
1070 Ma), “SG” = Sagantole Formation (5.2-3.9 Ma), “AA” = Adu-Asa Formation (6.4-5.2 Ma) and “TM” =
1071 Toros Menalla deposits (7-6 Ma). Stable isotope data of Chadian palaeofauna are taken from Zazzo
1072 (2001) and Boisserie et al. (2005). Ages of Toros Menalla sites are indicated in Vignaud et al. (2002)
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1075 al. (1994, 2001), Renne et al. (1999), Kleinsasser et al. (2008) and Quade et al. (2008).

1076

1077 **Figure 6:** Dietary reconstruction of large herbivores from the Lukeino and Mabaget Formations, based
1078 on $\delta^{13}\text{C}$ values of tooth enamel. Individuals are classified according to age and families. The
1079 unidentified proboscidean specimens are not represented in the figure.

1080

1081 **Table captions**

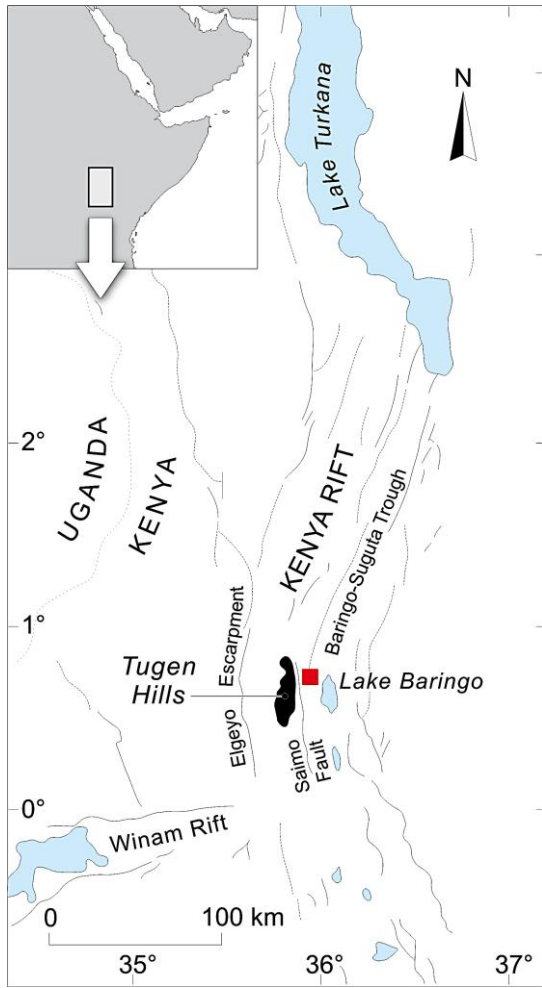
1082

1083 **Table 1:** Summary of fluorine, iron and manganese concentrations in tooth enamel of extant and fossil
1084 large herbivores from the Tugen Hills. "Fm." = formation, "SD" = standard deviation.

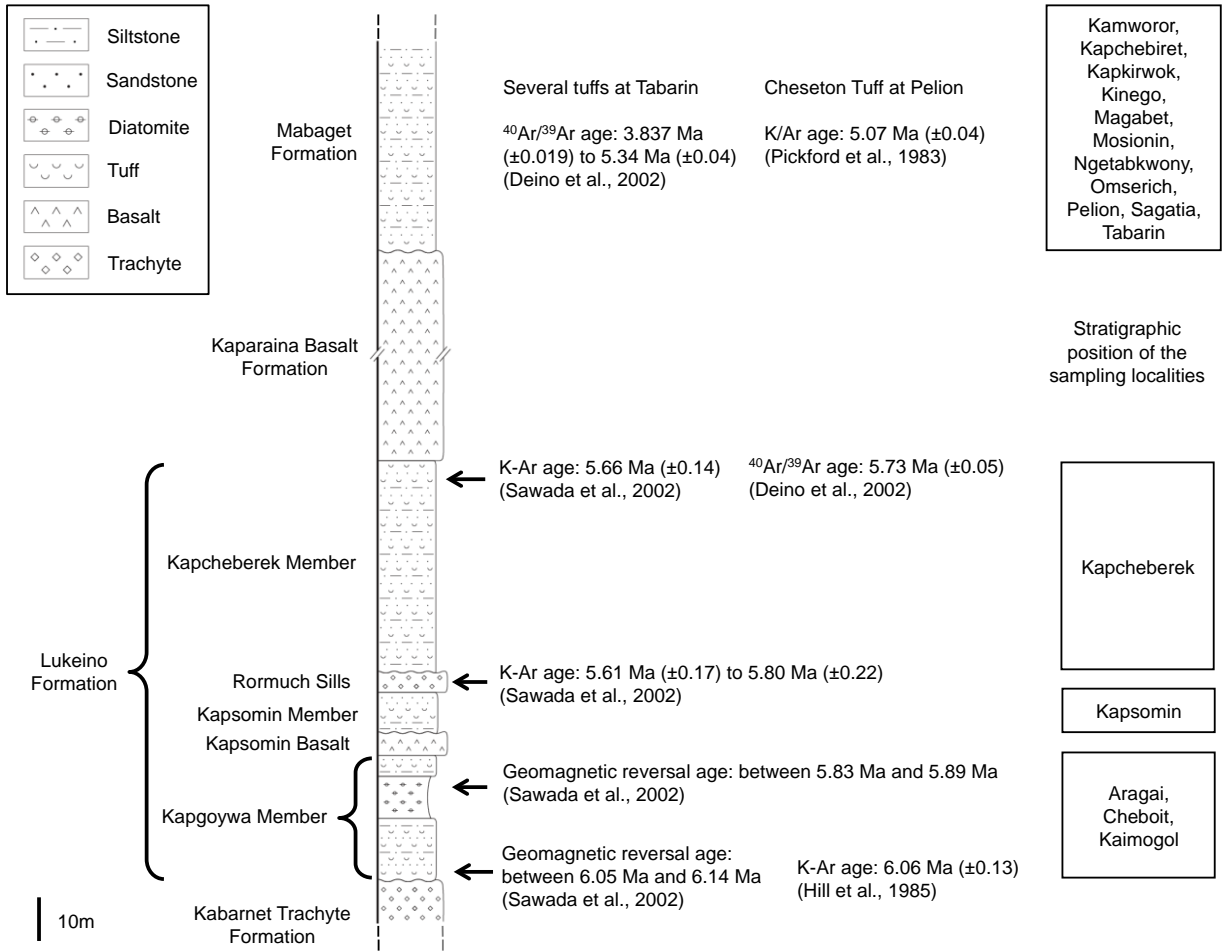
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1086 **Figure 1**

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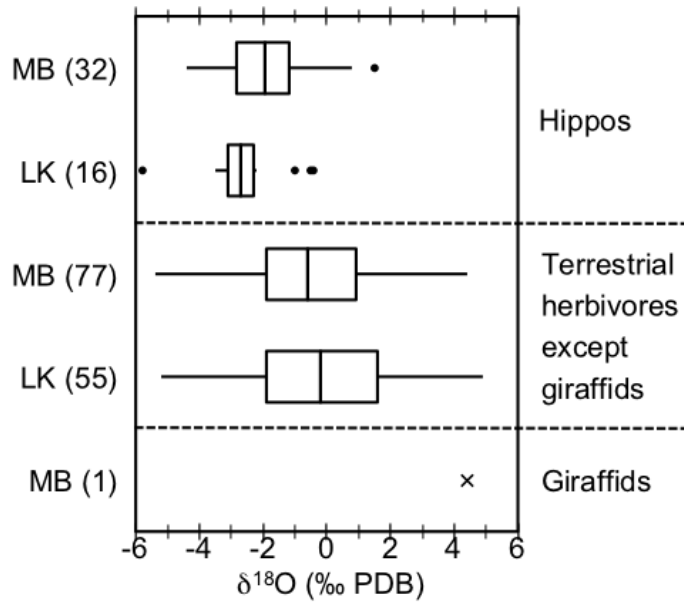


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1093 **Figure 3**

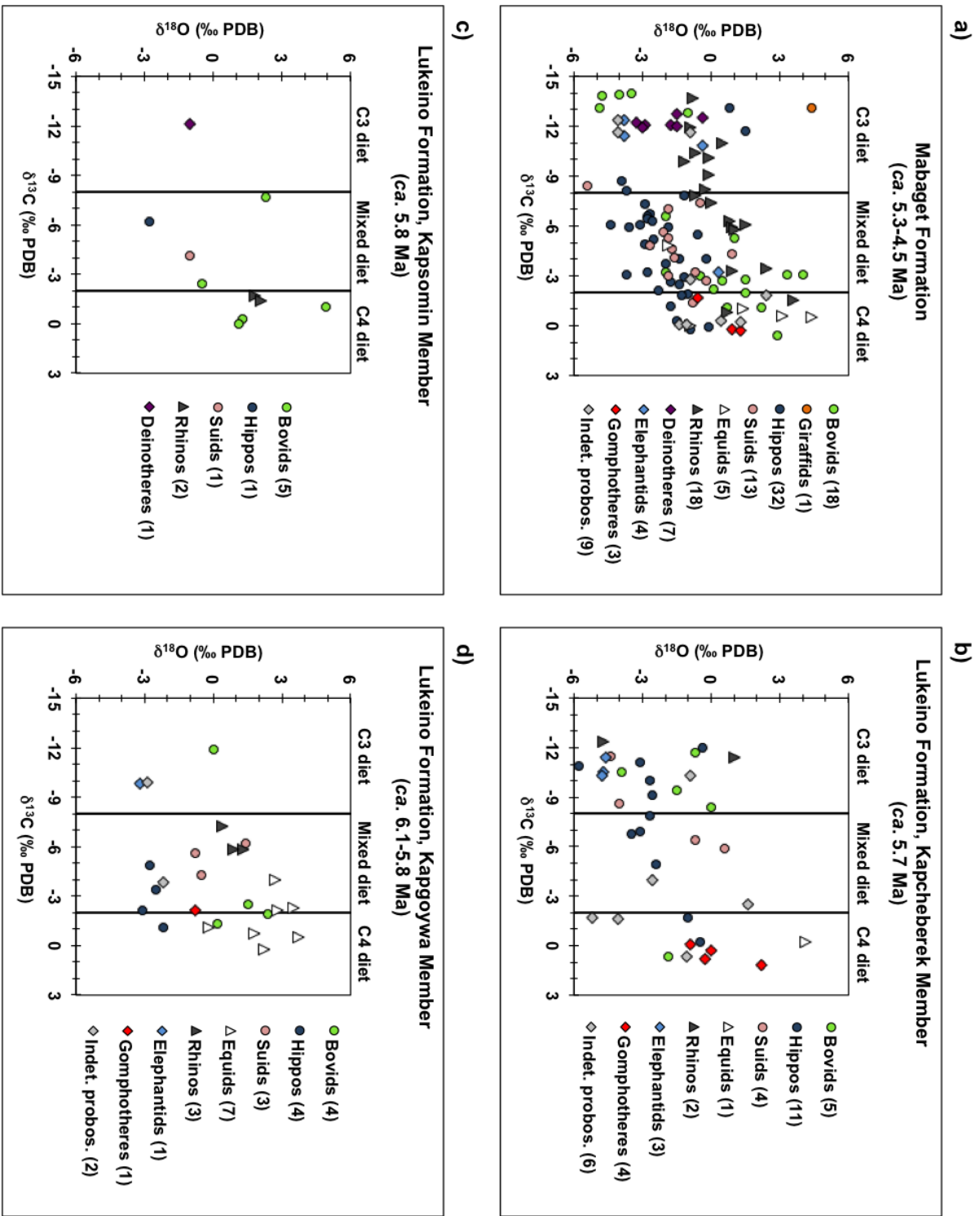
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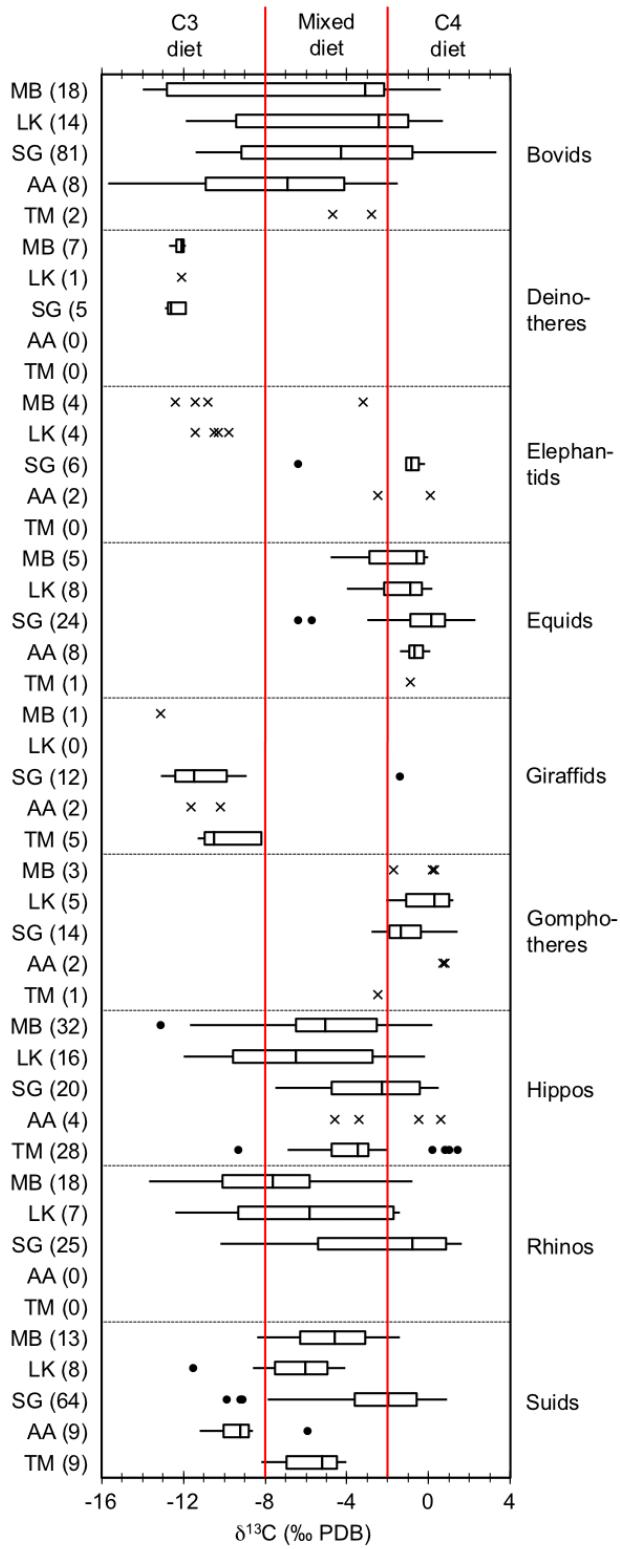
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Figure 4

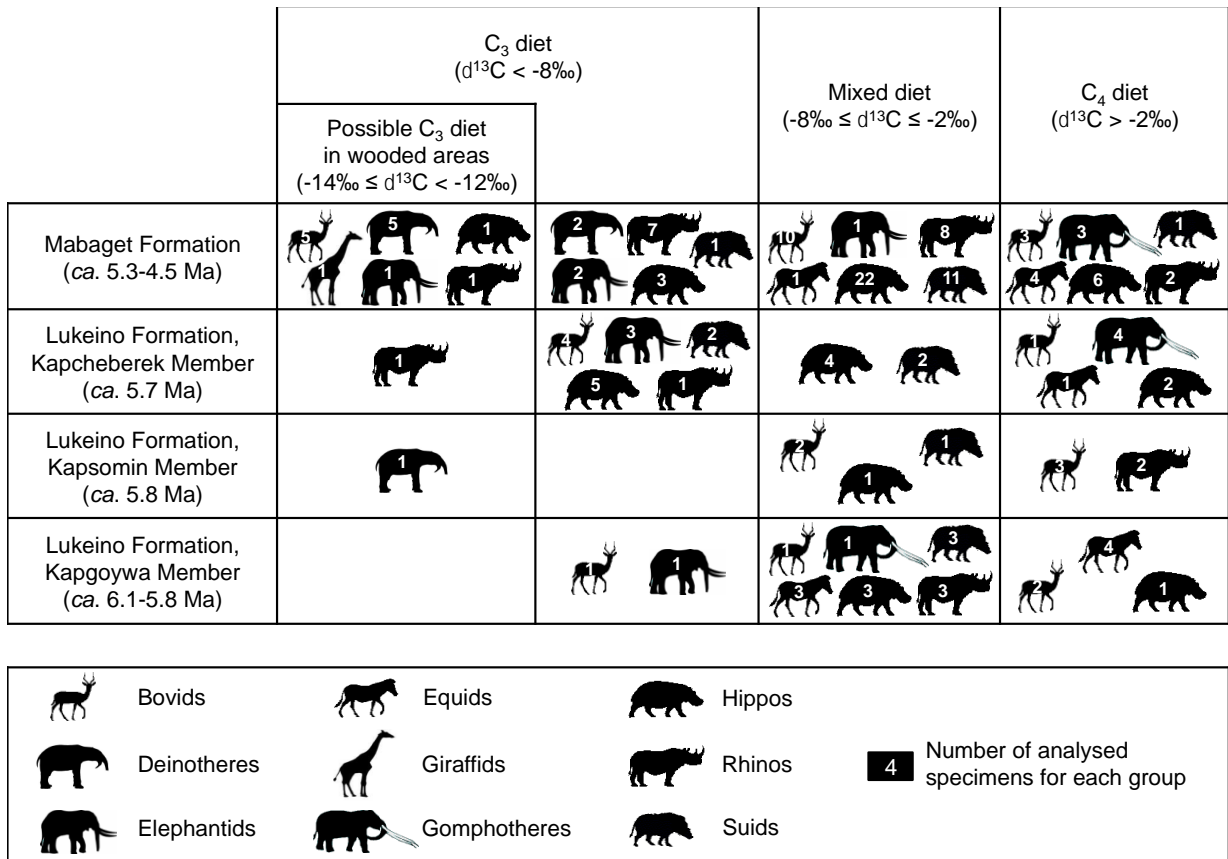


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1102 **Figure 6**

1103



1104

1105

1106 **Table 1**

1107

		Modern specimens (n=4)	Specimens from the Mabaget Fm. (n=20)	Specimens from the Lukeino Fm. (n=19)
[F] ppm	Range	149 to 334	4 845 to 19 946	4 072 to 18 862
	Mean (\pm SD)	241 (\pm 67)	9 879 (\pm 4 274)	9 405 (\pm 4 512)
[Fe] ppm	Range	98 to 180	1 069 to 12 909	600 to 19 648
	Mean (\pm SD)	125 (\pm 33)	4 441 (\pm 3 188)	4 163 (\pm 4 500)
[Mn] ppm	Range	10 to 15	226 to 3 008	453 to 2 132
	Mean (\pm SD)	11 (\pm 2)	1 322 (\pm 820)	1 409 (\pm 557)

1108