

1 **Relative abundances and palaeoecology of four suid genera in the Turkana Basin,** 2 **Kenya, during the late Miocene to Pleistocene**

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9

10 **Abstract**

11 Most suids (mammalia: Suidae, pigs) worldwide are omnivores in closed habitats, but the
12 African warthog (*Phacochoerus*) has special adaptations for grazing in open environments. Similar
13 specializations have been recorded from Plio-Pleistocene African suids. Four genera, *Nyanzachoerus*,
14 *Notochoerus*, *Kolpochoerus*, and *Metridiochoerus*, have been discovered in the late Miocene to
15 middle Pleistocene locations around the Turkana Basin.

16 We analyse the relative abundances of these four suid genera compared to other mammals,
17 from approximately 8 to 0.7 Ma. The data include most of the mammal specimens collected from
18 locations around the Kenyan side of the Turkana Basin. Species of genus *Nyanzachoerus* were
19 dominant before 4 Ma, but their relative abundance decreases through time thereafter. At the same
20 time, *Notochoerus* started to increase its relative abundance, then *Kolpochoerus*, and finally
21 *Metridiochoerus*. Their peak relative abundances do not overlap: *Notochoerus* peaks at 3.44-2.53 Ma,
22 *Kolpochoerus* at 2.53-1.87 Ma, and *Metridiochoerus* at 1.38-0.7 Ma.

23 We interpret the palaeoecology of these suids based on their relative abundance over time and
24 on published isotope and pollen data. We find that *Nyanzachoerus* was replaced by its abrasive-diet-
25 specialized successor *Notochoerus*, possibly in response to the rapid decrease in forest cover.
26 *Notochoerus* adapted at first to the expanding wood- and grasslands, and then to the more arid
27 shrublands. After a period of severe aridity around 2.7-2.5 Ma, more variable environments allowed
28 *Kolpochoerus* and *Metridiochoerus* to disperse, while *Notochoerus* disappeared, perhaps having lost
29 its competitive edge. Changes in the environment encouraged the expansion of grasslands over shrub
30 lands, favouring *Metridiochoerus*. *Kolpochoerus* persisted in the more closed areas near water
31 sources.

32

33 **Key words** (max 6): *Kolpochoerus*, *Metridiochoerus*, *Notochoerus*, *Nyanzachoerus*, *C4*, *ecological*
34 *niche*

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37 **Highlights**

- 38 · *Nyanzachoerus* was replaced by its abrasive-diet-specialized successor *Notochoerus*
39 following aridification of the environment.
- 40
- 41 · *Notochoerus* might have over-specialized for arid environments and lost its competitiveness
42 in more variable environments.
- 43
- 44 · *Kolpochoerus* and *Metridiochoerus* most likely had different ecological niches, despite their
45 similar C4-signal.

46

47 **1. Introduction**

48 Suids (mammalia: Suidae, pigs) are a widespread family of mainly omnivorous, non-
49 ruminant, forest dwelling, medium sized artiodactyls. However, in Africa, warthogs (*Phacochoerus*)
50 have special adaptations to grazing and to open environments: their legs are relatively longer than
51 those of other pigs, their orbits are placed high up on the back of the cranium (Ewer 1958), and their
52 third molars are hypsodont and have flat occlusal surfaces, commonly exposing over twenty tightly
53 packed columnar cusps (Owen 1850, Koeningswald 2011). The extinct Asian genera *Hippohyus* and
54 *Sivahyus* also had taller molars and more complicated enamel crenulation than most suids (Pilgrim
55 1926), but many extinct suids of Africa developed even more hypsodont teeth, and added more cusps
56 to their third molars during the Plio-Pleistocene (5.33-0.012 Ma) than did suids in Europe or Asia.
57 Here we examine the ecological context of their evolution. We want to know whether it is possible
58 to identify the competitive advantages of these suids in the setting of changing shared environments.

59 During the late Miocene to Pleistocene four suid genera, *Nyanzachoerus*, *Notochoerus*,
60 *Kolpochoerus* and *Metridiochoerus*, were abundant in the Turkana Basin of northern Kenya (Harris
61 and White 1979). *Nyanzachoerus* and *Notochoerus* belong to the extinct subfamily
62 Tetraconodontinae (Van der Made 1999). *Kolpochoerus* and *Metridiochoerus* belong to the subfamily
63 Suinae, which includes all living suids. All of these genera have in common morphological changes
64 in their third molars (Harris and White 1979), and an increase in $\delta^{13}\text{C}$ -values over time (Harris and
65 Cerling 2002, Cerling et al. 2015). Morphological changes to longer, flatter and more hypsodont
66 molars are typical adaptations for an abrasive diet (Janis and Fortelius 1988), which can mean that
67 the diet itself is abrasive or that abrasive particles are associated with the diet (Damuth and Janis
68 2011, Karme & Rannikko et al. 2016). Eating grass is well known to cause dental abrasion although
69 whether this is caused by siliceous phytoliths (Baker et al. 1959, McNaughton 1985, Epstein 1994,
70 Rabenold and Pearson 2014) or harder extrinsic mineral particles (Sanson et al. 2007, Lucas et al.
71 2013) is still debated; evidence for a significant abrasive effect of phytoliths relative to dust was
72 recently presented empirically by Merceron et al. (2016) and experimentally by Karme and Rannikko
73 et al. (2016). In addition, more positive $\delta^{13}\text{C}$ -values indicate diet containing C4-plants, e.g. mainly
74 tropical grasses (Cerling et al. 2015).

75 The expansion of C4-grasses, which started in the Miocene, continued in the Pliocene
76 (Retallack et al. 1990, Edwards et al. 2010), although the overall area of grasslands remained stagnant
77 or decreased during 12-1.4 Ma in northeast Africa (Feakins et al. 2013). Levin et al. (2011) concluded
78 from the isotopes of paleosol carbonates that there had been a steady increase in C4-plants in the
79 floodplain environments of the Omo-Turkana Basin since 4 Ma. However, the pollen record from

80 deep ocean cores show that shrubs were more common than grasses from 4.9 to 3 Ma in northeast
81 Africa (Bonnefille 2010, Liddy et al. 2016). The pollen data also suggest that an aridity shift occurred
82 around 4.3 Ma (Liddy et al. 2016) and peaked at 2.7-2.5 Ma (Bonnefille 2010). However, the ocean
83 core data might not adequately represent an area as distant from the Gulf of Aden as the Turkana
84 Basin. Open landscapes dominated by C4 biomass emerged only in the early Pleistocene (Ségalen et
85 al. 2007). Recently, Fortelius et al. (2016) used an ecometric analysis of the dental traits of large
86 mammals to estimate the precipitation levels of different Plio-Pleistocene localities of the Turkana
87 Basin, and concluded that the most arid time interval in the Turkana Basin was approximately
88 between 3 and 2 Ma.

89 The fossil data from the Turkana Basin and Omo Valley area have allowed researchers to
90 understand the past animal communities of eastern Africa, and the environment where our ancestors
91 were living (Leakey and Leakey et al. 1978, Harris et al. 1983, Harris et al. 1988, Harris et al. 2003,
92 Leakey and Harris 2003, Bobe et al. 2002, Bobe and Behrensmeyer 2004, Bobe and Leakey 2009,
93 Werdelin and Lewis 2013). The Turkana fossil record has also been a basis for research into the late
94 Oligocene, Miocene (Leakey et al. 2011) and Plio-Pleistocene (Behrensmeyer et al. 1997, Werdelin
95 and Lewis 2005) faunal turnover and climatic change (deMenocal 2004, Hernández Fernández and
96 Vrba 2006). Isotope analyses have been used to determine the dietary adaptations of mammals, which
97 are also used as an indicator of changing environments, especially from wooded closed habitats to
98 open grasslands (Harris and Cerling 2002, Bibi et al. 2013, Cerling et al. 2015). Suid and
99 proboscidean fossils are informative biostratigraphical indicators, because they underwent a rapid
100 species differentiation and radiation during the Plio-Pleistocene (Cooke and Maglio 1972). This,
101 combined with the easy identification of suid teeth, has undoubtedly led to extensive collection of
102 suid specimens, which has an effect to the relative abundance of suids among other mammals in the
103 collections. We are aware that the relative abundances of fossil taxa do not necessarily reflect the
104 abundances of species in the living communities; suids as a group are most likely over represented.
105 Within the suid family the relative abundances of suid taxa are nevertheless likely to reveal the
106 differences between the individual suid genera over time, however, and that is our focus here.

107 Patterson et al. (2017) analysed bovid and suid abundances from archaeological and
108 palaeontological sites across the upper Burgi, KBS, and Okote Members (1.95-1.38 Ma) of the Koobi
109 Fora Formation east of Lake Turkana, and Hakala (2012) measured suid abundances from the same
110 members. Both studies reported an increase in *Metridiochoerus* and decrease in both *Kolpochoerus*
111 and *Notochoerus* from the upper Burgi to the KBS Member. These studies are based on the same data
112 source as our analysis, however, they do not deal with the changes before the turnover between the

113 upper Burgi and the KBS, nor with the west side of Lake Turkana. In addition, abundance analyses
114 for bovids over the Plio-Pleistocene have been done to identify changes in the genus-level dominance
115 to reveal environmental changes (Bobe and Eck 2001, Bobe et al. 2007). Here, we extend the
116 comparison of the abundances of four suid genera from the late Miocene to Plio-Pleistocene,
117 including the fossil material from both sides of Lake Turkana.

118 While the morphological changes and isotope records suggest that all the suid genera adapted
119 to expanding grasslands, we want to know if their ecological niches were similar during the changing
120 climatic and environmental conditions of the Plio-Pleistocene. Site occupancy and locality coverage
121 have been used to understand dynamics in ecological and palaeoecological communities (Jernvall
122 and Fortelius 2004, Fortelius et al. 2014). In such a small geographical area as Turkana Basin, with
123 as abundant group as suids, presence/absence data shows no spatial differences as the suids are
124 present in almost every collection site. However, temporal separation can be seen. To obtain better
125 temporal separation between the genera, we investigate the pattern of relative abundances over time.
126 In the fossil record unimodality (the "hat" pattern, Liow et al. 2010) is well established for species,
127 genera, and higher taxa of terrestrial mammals (Jernvall and Fortelius 2004, Quental and Marshall
128 2013, Carotenuto et al. 2010), marine invertebrates (Foote et al. 2007, Tietje and Kiessling 2013, Raia
129 et al. 2016), and marine micro-organisms (Liow and Stenseth 2007), highlighting a lack of recovery
130 from decline. The pattern has been documented for occupancy, range, and diversity of species, as
131 proxies for abundances. The prevailing interpretation for the "hat" pattern in the fossil record is that
132 widespread and abundant species might, for multiple reasons, suffer an evolutionary slowdown, and
133 therefore be overtaken by fast- evolving, newly arisen species with properties more closely attuned
134 to current conditions (Fortelius et al. 2014).

135 The purpose of this study is to understand how a C4-diet specialist group reacted to
136 environmental changes during the Plio-Pleistocene in the Turkana Basin, in environments that also
137 saw the evolution of early hominins. We compare the relative abundances of four African suid genera
138 from the late Miocene to middle Pleistocene, and connect the changes in their abundances to
139 published isotope and pollen records (Harris and Cerling 2002, Braun et al. 2010, Cerling et al. 2015,
140 Liddy et al. 2016, Bonnefille 2010) to interpret their palaeoecology and interactions.

141

142 2. Material and methods

143 The data for this analysis come from the Turkana Basin Paleontology Database
144 (http://naturalhistory.si.edu/ete/ETE_Datasets_Turkana.html), which has been complemented by
145 other datasets for Lothagam, Kanapoi, and sites on the western side of Lake Turkana (curated by
146 Meave Leakey), and datasets from both sides of Lake Turkana after 2005. A summary of the updated
147 dataset has been published as supplementary material in Fortelius et al. 2016. Unfortunately, the
148 dataset contains locations only in Kenya, and excludes Ethiopia, which restricts the analysis of the
149 basin artificially by national borders.

150 The stratigraphic sequence can be divided into artificial bins of equal duration (for example
151 in Bibi and Kiessling 2015), or into primary members, which have exact dates but the durations are
152 not equal (Brown and MacDougal 2011). For consistency between east and west localities and to
153 preserve as fine as possible time resolution we have used the primary members as our time points,
154 which are dated by the interbedded tuff layers.

155 The Pliocene strata of the Turkana Basin in Kenya include the Kanapoi, Nachukui, and Koobi
156 Fora Formations. The Pleistocene strata include the Nachukui and Koobi Fora Formations. The
157 earliest data points (late Miocene) for this study are from the Lower and Upper Nawata Formations
158 (Brown and MacDougal 2011). Volcanic ash (tuff) layers can be found throughout the strata of the
159 Turkana Basin. Sediment units between the tuff layers have been formally defined as members (Table
160 1) (Brown and Feibel 1991, Brown and McDougall 2011). Tuff layers can be dated by radiometric
161 methods, which provide the age ranges for the members (McDougall and Feibel 1999). The durations
162 of the members range from 0.08 to 0.91 million years. Tuff layers also have unique chemical
163 compositions, which enables the correlation of the layers between localities (Cerling et al. 1979,
164 WoldeGabriel et al. 2005, Brown and McDougall 2011). In this analysis, members with similar ages
165 from both sides of the lake are treated as one unit, and the age ranges used are (see superscripts in
166 Table 1): 9 = 7.91-6.54 Ma, 8 = 6.54-5 Ma, 7 = 4.35-3.97 Ma, 6 = 3.97-3.44 Ma, 5 = 3.44-2.53 Ma,
167 4 = 2.53-1.87 Ma, 3 = 1.87-1.53 Ma, 2 = 1.53-1.38 Ma, and 1 = 1.38-0.7 Ma (after Brown and
168 McDougall 2011). Kanapoi, and two members of Lothagam (Kaiyumung and Apak) from the west
169 side, are combined with the Lonyumun Member from the east side. There are no specimens from the
170 west side Lonyumun Member. The localities of the South Turkwel (3.5 Ma), Eshoa Kakurongori (3
171 Ma), and Nakoret (2 Ma) are also added to the west side. These do not have defined members, but
172 their ages are estimated (Ward et al. 1999, Werdelin and Sanders 2010).

173 The dataset consists only of mammals, containing 14778 individual specimens. In order to be
 174 accepted into the analysis, the specimen had to have a member and a genus assigned. Altogether 8489
 175 specimens have both genus and member information. There are 2821 suid specimens in the dataset,
 176 of which 1784 have information about both genus and member.

177 The relative abundances of the suid genera among all mammal genera were calculated by
 178 dividing the number of specimens from one genus with the amount of all specimens found from
 179 specific members. The results are presented as percentages, visualized by using Excel 2013
 180 (Microsoft) and JMP Pro 11. We use relative abundances instead of absolute numbers because some
 181 localities, and thus members, are more intensively sampled or yield more specimens than others. We
 182 do not go beyond the genus level in the relative abundances (except with *N. euilus* and *N. scotti*),
 183 because misidentifications become more likely past that point, and due to the gradual changes in the
 184 morphology there are still some disagreements about the number of species.

185 It is agreed that *Nyanzachoerus/Notochoerus jaegeri* is the ancestor of genus *Notochoerus*
 186 (Harris and White 1979, Van der Made 1999, Bishop 2010), but the debate between its placement in
 187 *Nyanzachoerus* (Harris and White 1979, Van der Made 1999, Reda et al. 2017) or *Notochoerus*
 188 (Kullmer 1999, Bishop 2010,) continues. The 18 specimens identified as
 189 *Nyanzachoerus/Notochoerus jaegeri* are treated here as *Notochoerus jaegeri*.

190 Table 1. Members and their ages and durations from west and east side of Lake Turkana (after Brown and
 191 McDougall 2011).

Nachukui Formation (west)	Age (Ma)	Duration (Ma)	Koobi Fora Formation (east)	Age (Ma)	Duration (Ma)
Nariokotome ¹	1.30-0.70	0.6	Chari ¹	1.38-0.70	0.68
Natoo ²	1.48-1.30	0.18	Okote ²	1.53-1.38	0.15
Kaitio ³	1.87-1.48	0.39	KBS ³	1.87-1.53	0.34
Kalochoro (Nakoret) ⁴	2.33-1.87	0.46	Upper Burgi ⁴	1.95-1.87	0.08
Lokalalei ⁴	2.53-2.33	0.2	Lower Burgi ⁵	2.63-2.53	0.1
Lomekwi (Eshoa Kakurongori) ⁵	3.44-2.53	0.91	Tulu Bor ⁵	3.44-2.63	0.81
Kataboi (South Turkwel) ⁶	3.99-3.44	0.55	Lokochot ⁶	3.60-3.44	0.16
Lonyumun ⁷	4.35-3.99	0.36	Moiti ⁶	3.97-3.60	0.37
Kaiyumung ⁷ (Lothagam)	4.2-3.99	0.21	Lonyumun ⁷	4.35-3.97	0.38
Apak ⁷ (Lothagam)	4.24				
Kanapoi Formation⁷	4.2-4.11	0.09			
Upper Nawata Formation⁸ (Lothagam)	6.54-5	1.54			
Lower Nawata Formation⁹ (Lothagam)	7.91-6.54	1.37			

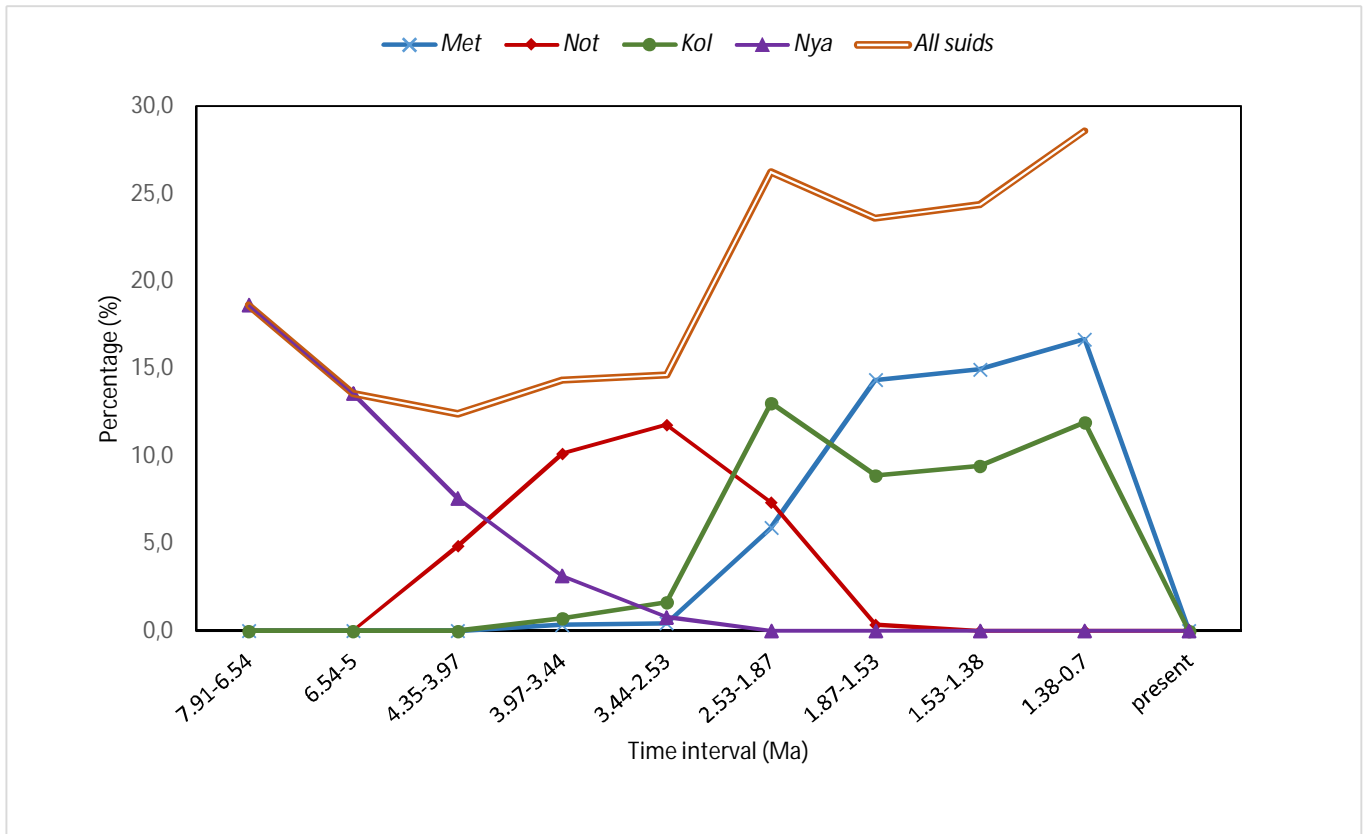
192 Superscripts show members that have been combined in the analysis.

194 **3. Results**

195 Relative abundances over time show all four suid genera peaking at different time intervals.
196 The relative abundance of all suids among all mammal specimens is approximately 12-15% before 2
197 Ma, and doubles to 24-29% afterwards (Fig. 1. orange double-line). Most likely these percentages are
198 due to intensive collection of suid specimens, and are biased compared to the living assemblage.

199 *Nyanzachoerus* is present in the first five time periods of our analysis (Fig. 1. violet triangle-
200 line). Its proportion relative to all mammal specimens declines over time in our time frame, so the
201 peak abundance of *Nyanzachoerus* is right at the start of our dataset (if not before). Of our four genera,
202 only *Nyanzachoerus* is present in the records from the Lower and the Upper Nawata. In the Lower
203 Nawata Formation, which spans one and a half million years (7.91-6.54 Ma), approximately 19% of
204 the mammal specimens found have been assigned to the genus *Nyanzachoerus*. Collections from the
205 Upper Nawata (6.54-5 Ma) present approximately 14% *Nyanzachoerus* specimens. *Nyanzachoerus*
206 is still the dominant suid present in the collections from the Kanapoi Formation and the Apak and
207 Kaiyumung Members from the west side of Lake Turkana, and the Lonyumun Member from the east
208 side of the lake, 4.35-3.97 Ma (7%), but during 3.97-3.44 Ma (Kataboi, Moiti, and Lokochot
209 Members) it declines to approximately 4%, then during 3.44-2.33 Ma (Tulu Bor, Lomekwi, and lower
210 Burgi Members) to <1%, and then disappears from the records.

211 The abundance record of *Notochoerus* has a unimodal shape, e.g. it has a bell shaped, one-
212 peaked curve (Fig. 1. red diamond-line). *Notochoerus* is first encountered during 4.35-3.97 Ma, while
213 *Nyanzachoerus* is still the dominant suid genus. Approximately 5% of the mammal specimens are
214 *Notochoerus* at that time. In the next time period, 3.97-3.44 Ma, *Notochoerus* becomes the dominant
215 suid genus (7%). The peak abundance of *Notochoerus* is from 3.44 to 2.53 Ma, when 12% of the
216 mammal specimens are identified as *Notochoerus*. During the next two time periods, 2.53-1.87 Ma
217 and 1.87-1.53 Ma, the abundance of *Notochoerus* declines (approximately 7% and <1%,
218 respectively).



219

Figure 1. Relative abundances of the four suid genera (*Met* = *Metridiochoerus*, *Not* = *Notochoerus*, *Kol* = *Kolpochoerus*, *Nya* = *Nyanzachoerus*) specimens out of all mammal specimens in the Turkana Basin. Time intervals are dated from the tuff layers around Lake Turkana (Brown and McDougall 2011). Similar ages are combined between the east and west sides, and dates from the east side are used in the figure.

220

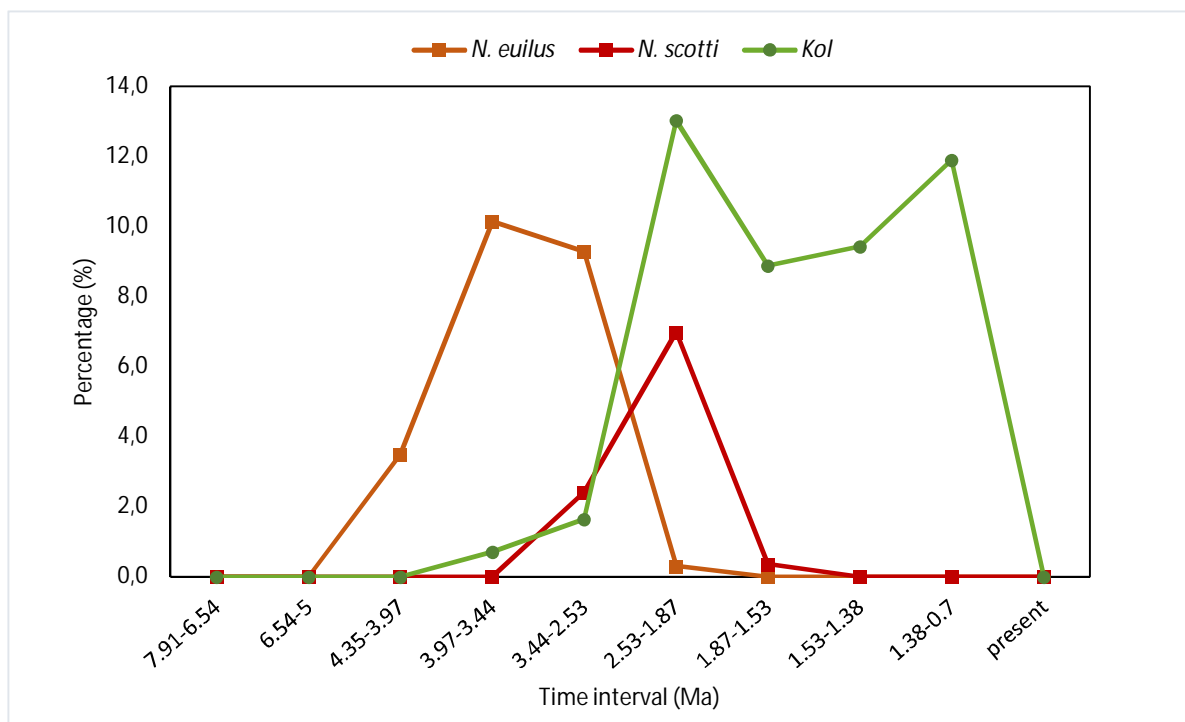
221 *Kolpochoerus* appears in the record during 3.97-3.44 Ma (1%), while *Notochoerus* is the
 222 dominant suid, but all other genera are also present (Fig. 1. green large-dot-line). During 3.44-2.53
 223 Ma the relative abundance of *Kolpochoerus* only increases by a small amount, from 1% to 2%. A
 224 huge increase occurs during the next time period of the upper Burgi, Lokalalei, and Kalochoro
 225 Members, 2.53-1.87 Ma. *Kolpochoerus* becomes the dominant suid genus in the records with
 226 approximately 13% of the total mammal specimens. During the next two time periods, 1.87-1.53 Ma
 227 and 1.53-1.38 Ma, the relative abundance of *Kolpochoerus* decreases slightly (being approximately
 228 9% in both). During the last time period of this analysis, 1.38-0.7 Ma (Chari and Nariokotome
 229 Members), *Kolpochoerus* has a small increase in its abundance to approximately 12%.

230 *Metridiochoerus* appears in the record at the same time as *Kolpochoerus*, during 3.97-3.44
 231 Ma (Fig. 1. blue x-line). However, less than 1% of the mammal specimens from this period are
 232 identified as the genus *Metridiochoerus*. The situation does not change during 3.44-2.53 Ma; again,

233 less than 1% of the specimens are *Metridiochoerus*. When *Kolpochoerus* becomes the dominant suid
 234 genus during 2.5-1.87 Ma, the relative abundance of *Metridiochoerus* also increases (6%). However,
 235 *Notochoerus* is still more abundant than *Metridiochoerus* at that time. The dominance of
 236 *Metridiochoerus* starts 1.87-1.53 Ma. While *Kolpochoerus* has a slight decrease, *Metridiochoerus*
 237 increases its proportion among mammal specimens during 1.87-1.53 Ma and 1.53-1.38 Ma, to
 238 approximately 14% and 15%, respectively. The peak abundance of *Metridiochoerus* is in the last time
 239 period of this analysis, 1.38-0.7 Ma. Out of all mammal specimens, approximately 17% are identified
 240 as *Metridiochoerus*.

241 Figure 2 shows the relative abundance of two separate *Notochoerus* species, *N. euilus* and *N.*
 242 *scotti*, which have different dental characteristics, along with the relative abundance of *Kolpochoerus*.
 243 The relative abundance of *N. euilus* decreases to zero when *Kolpochoerus* becomes the dominant suid
 244 between 3.44-2.53 Ma and 2.53-1.87 Ma. During the same interval, *N. scotti* has its peak relative
 245 abundance.

246



247

Figure 2. Relative abundances of *Notochoerus scotti* and *Notochoerus euilus* in relation to the relative abundance of *Kolpochoerus*. Time intervals are dated with tuff layers around Lake Turkana (Brown and McDougall 2011). Similar ages are combined between the east and west sides, and dates from the east side are used in the figure.

248 4. Discussion

249 The relative abundances of the extinct suids of the Turkana Basin as derived from the
250 palaeontological data are probably higher than their actual abundances in their living communities.
251 The sampling frequency of suids has been high, as they have been used as biostratigraphical indicators
252 because of their fast speciation and easy identification (Cooke and Maglio 1972), and their durable
253 teeth have a high preservation potential. However, while the percentages might not tell us their real
254 abundance among all mammals at a specific point in time, they probably do reveal the abundance
255 differences between the individual suid genera over time, which is our main interest in this study.

256 The four suid genera show unimodal patterns of rise and decline over time. To the best of our
257 knowledge, our study is the first one to document the unimodality pattern in the fossil record directly
258 for abundances. However, our dataset is limited to the localities of Turkana Basin in Kenya, and at
259 the moment represents only that specific area. We observe that *Nyanzachoerus* has a steady decrease
260 in relative abundance, with no recovery. The abundance curve of *Notochoerus* is unimodal. Similarly,
261 the abundance curves of the two species of *Notochoerus* are unimodal: *N. euilus* peaking at 3.97-3.44
262 Ma, and *N. scotti* peaking at 2.53-1.87 Ma. *Kolpochoerus* peaks at 2.53-1.87 Ma, and then declines,
263 but it has a second peak during the latest time interval 1.3-0.7 Ma. *Metridiochoerus* has a peak in its
264 relative abundance in the last time interval.

265 *Nyanzachoerus* is the only one of the four studied genera found in the two oldest time intervals
266 used here. The duration of both the Upper and the Lower Nawata are over a million year long; any
267 finer details on relative abundance during those intervals cannot be discerned. However, it is evident
268 that *Nyanzachoerus* declines towards the recent, and is not found in locations that are younger than 2
269 million years. Species of *Nyanzachoerus* thought to show a shift from a soft browse diet to a more
270 abrasive diet requiring grinding (Cooke and Ewer 1972). Their $\delta^{13}\text{C}$ -values furthermore rise from
271 7.91-6.54 Ma to 4.35-3.97 Ma (see appendix), indicating that more grasses were possibly introduced
272 into their diet.

273 The two most common species of *Notochoerus* in the Turkana Basin are *N. euilus* and *N.*
274 *scotti*. They both have specimens with isotope signals indicating C4-plant consumption (Cerling et
275 al. 2015). However, *N. euilus* has specimens with more negative $\delta^{13}\text{C}$ -values, indicating more mixed
276 feeding. The latter, combined with the dental characteristics (Harris and White 1979), post-cranial
277 parts (Bishop 1999), and estimates of precipitation (Fortelius et al. 2016), suggest that *N. euilus* lived
278 in an intermediate habitat with partial tree cover. However, grass possibly provided food during more
279 harsh time intervals, such as dry seasons. This could have been the reason for the disappearance of

280 the *Nyanzachoerus* species; they might have been inhabiting dense forests and riparian woodlands
281 much like modern *Potamochoerus porcus* (Kingdon 1979), but around 6.3 Ma tree cover was vastly
282 decreasing over eastern Africa (Bonnefille 2010). There are no post-cranials analysed from *N. scotti*,
283 but the hypsodonty and length of molars indicate an abrasive diet (Harris and White 1979). Together
284 with the extremely hypsodont molars, isotope data (Cerling et al. 2015), and precipitation estimates
285 (Fortelius et al. 2016), it seems that *N. scotti* was specialized to utilize dry grasses. The characteristics
286 of the molars of *N. scotti* could also have been affected by the dust and sand of arid open areas, as the
287 African climate became periodically cooler and drier in the late Pliocene (Liddy et al. 2016,
288 deMenocal 1995). This suggests the possibility that *N. scotti* was not adapting to expanding grasses,
289 as its predecessors did, but to even more arid shrublands with higher sand and dust loads than in
290 grasslands with higher precipitation.

291 Figure 2 shows how *N. euilus* disappears, and at the same time *Kolpochoerus* becomes the
292 most abundant suid in the collections, around 2.53-1.87 Ma. *Kolpochoerus* might have benefitted
293 from the disappearance of *N. euilus*. We propose that while *N. scotti* was expanding into the shrub
294 lands, *Kolpochoerus* inhabited the sparse woody areas such as gallery forests near rivers, which
295 possibly were also the habitat of *N. euilus*. Harris and Cerling (2002) mention a link between $\delta^{18}\text{O}$
296 values and external water dependency: the higher the $\delta^{18}\text{O}$ value is, the less external water an animal
297 drinks, i.e. it gets the needed water from its diet. However, the link is not straightforward, nor simple
298 (Harris and Cerling 2002). All measured oxygen isotopes show negative values, indicating that
299 *Kolpochoerus* was consuming water from rivers or the lake (Harris and Cerling 2002), and most
300 probably was living near these water sources.

301 Isotope studies show that *Kolpochoerus* had C4 components in its diet throughout its time
302 range (Harris and Cerling 2002, Bishop et al. 2006, Cerling et al. 2015). However, the morphology
303 of *Kolpochoerus* molars does not suggest a grazing diet. The C4-signal could also have been obtained
304 from other plants (Bishop et al. 2006): for example, papyrus (*Cyperus papyrus*), and some arid
305 environment shrubs of the *Amarantheceae* genus, are C4-plants (Peters and Vogel 2005, Feakins et
306 al. 2013). The mesodont crown height of the molars (Harris and White 1979) and post-cranial
307 morphology (Bishop 1994, Bishop et al. 1999) indicate that they were living in an intermediate or
308 woodland habitat. We suggest here that the molar morphology, which retains basic suine
309 characteristics, with some height and length increases over time, and the C4-signal, together indicate
310 that *Kolpochoerus* was a digger and an omnivore (Kullmer 1999), consuming mainly C4-grass roots,
311 fresh grass shoots and optionally fauna supported by C4 vegetation. However, the microwear of
312 *Kolpochoerus* lower molars was different from that of *Potamochoerus* (Bishop et al 2006), which

313 also has an omnivorous diet and digging habits. Towards the end of the Pleistocene, *Kolpochoerus*
314 possibly also consumed above ground grass parts, as its molars tend to get more hypsodont,
315 horizontally elongated, and worn flat in many specimens.

316 *Kolpochoerus* and *Metridiochoerus* are found in the collections with *Notochoerus* at 3.97-
317 3.44 Ma, 3.44-2.53 Ma and 2.53-1.87 Ma. The dispersal of *Kolpochoerus* and *Metridiochoerus*
318 species to the Turkana region might be linked to the more humid phases of the Pliocene (Bonnefille
319 2010, Feibel 2011), when wooded areas extended further, and linked landscapes allowing migration
320 of early members of *Kolpochoerus* and *Metridiochoerus* to the area. After 2.53-1.87 Ma *Notochoerus*
321 disappears, and *Metridiochoerus* becomes the most common suid genus in the collections. *N. scotti*
322 seems to have been well suited to an arid and open environment. Desert shrub vegetation started to
323 dominate northeast Africa approximately 5.5 Ma, and declined around 2.7-2.5 Ma when there was an
324 aridity peak, according to the deep-sea core pollen data (Bonnefille 2010). The 3rd molar evolution in
325 *N. scotti* could then be more related to arid shrublands, desertification, the consumption of dry grass
326 and desert shrubs and increased dust load, rather than grassland expansion itself, which would have
327 been the main driver in the 3rd molar evolution and expansion of *Metridiochoerus* after 1.8 Ma.
328 However, *N. scotti* may have become morphologically, physically, or behaviourally too specialized
329 for the almost desert-like environment (Raia et al. 2016), and then lost the competitive edge against
330 early *Kolpochoerus* and *Metridiochoerus* after grasslands started to expand 2.5 Ma (Ségalen et al
331 2007, Hernández Fernández and Vrba 2006, Bonnefille 2010, Levin et al. 2011).

332 *Kolpochoerus* and *Metridiochoerus* more or less maintain their relative abundance from 1.87
333 to 0.7 Ma. The dominant *Metridiochoerus* species was *M. compactus*, whose third molar height
334 exceeded that of *N. scotti*, with a similar third molar length (Harris and White 1979). A smaller sized
335 *M. modestus* also appeared (Harris and White 1979). Many localities yield both *Metridiochoerus* and
336 *Kolpochoerus* specimens (specimen counts are reported in the appendix). However, it is likely that
337 *Kolpochoerus* and *Metridiochoerus* did have different ecological niches. On the east side of the lake,
338 localities preserving only *Metridiochoerus* are more numerous than on the west side (see the appendix
339 for specimen counts). During 1.53-1.38 Ma, when *N. scotti* has disappeared from the collections,
340 *Metridiochoerus* has the highest $\delta^{13}\text{C}$ -values, and it thus seems that *Metridiochoerus* really did
341 become a grassland specialist. The oxygen isotope data of Harris and Cerling (2002) show that,
342 although *Metridiochoerus* has variable values, some individuals got their water from their diet, and
343 thus might have been able to live further away from water sources. *Metridiochoerus* became the
344 ultimate open grassland suid, while *Kolpochoerus* stayed near water sources and denser vegetation

345 despite the evolution of the third molar. Figure 4. shows a sketch of possible habitats available for
346 the genera.

347 All in all, the view that C4-signals should only be associated with grasses, and that grasses
348 should be associated with the most arid type of habitats, is a very simplified perspective. Distribution
349 of C4 grasses in past may have been patchier so animals could have $\delta^{13}\text{C}$ values suggesting grazing
350 diet whilst having locomotor morphology suggesting closed or intermediate habitat preference
351 (Bishop et al. 2006). In addition, an area like the Turkana Basin has most likely always contained a
352 variety of habitats that cannot be clumped into one type, and time intervals as long as those used here
353 cannot differentiate between annual or decadal seasonality, which force animals towards adaptations
354 which might help them survive the harsher seasons.

355

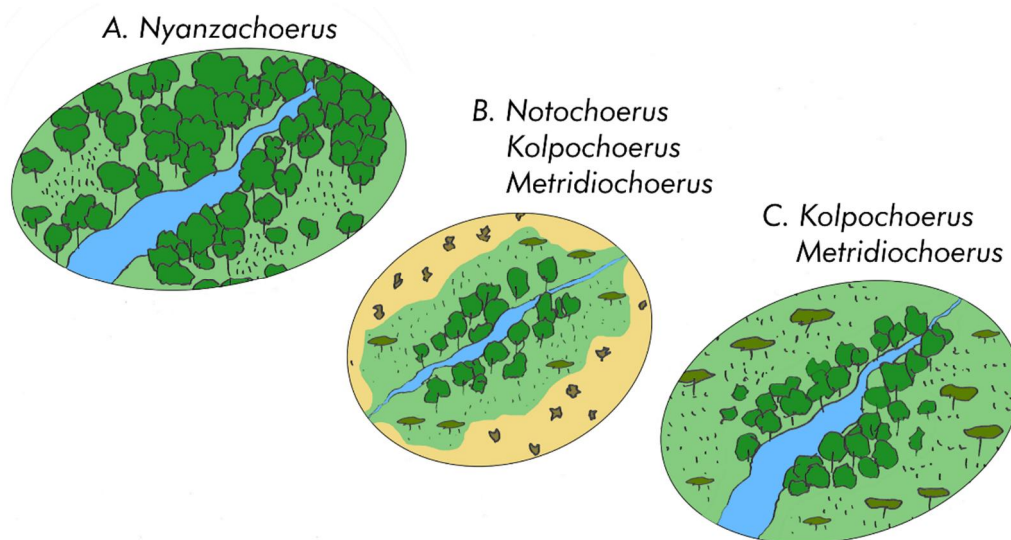


Figure 3. A sketch of the environments where the four suid genera might have been living. A) Woody landscape, forests, grass openings; B) riparian woodlands, woody grasslands, shrublands, deserts; C) riparian woodlands, woody grasslands, savanna.

357 **5. Conclusions**

358 The analysis of the dataset reveals the relationships between the relative proportions of the
359 suid genera in the stratigraphic members of the Turkana Basin. There are unimodal patterns seen in
360 the relative abundance curves, indicating that *Nyanzachoerus* was replaced by *Notochoerus*, and
361 *Notochoerus* was in turn replaced by *Kolpochoerus* and *Metridiochoerus*. Species of the genus
362 *Nyanzachoerus* were dominant before 4 Ma, although the dataset only has two long units from one
363 site to sample that time interval (the Lower and Upper Nawata from Lothagam). The relative
364 abundance of *Nyanzachoerus* decreases throughout the time intervals in the dataset. At the same time,
365 *Notochoerus* starts to increase its relative abundance, followed by *Kolpochoerus*, and finally
366 *Metridiochoerus*. Their peak relative abundances in Turkana Basin do not overlap in the dataset:
367 *Notochoerus* peaks at 3.44-2.53 Ma, *Kolpochoerus* at 2.53-1.87 Ma, and *Metridiochoerus* at 1.38-0.7
368 Ma.

369 The unimodal patterns of the relative abundances, and the fact that the peak times of the genera
370 are not overlapping, suggest that each genera had their time of success in the Turkana Basin area.
371 *Nyanzachoerus* was replaced by *Notochoerus*, which was more specialized for an abrasive diet. The
372 rapid decrease of forest habitats might have played a part in this process. *Notochoerus* adapted at first
373 to the expanding wood- and grasslands (*N. euilus*), and then possibly to even more arid shrublands
374 (*N. scotti*). After the period of most severe aridity, more variable environments gave *Kolpochoerus*
375 and *Metridiochoerus* a better chance to disperse, while *Notochoerus* disappeared, having lost the
376 competitive edge of open shrub land specialization. Changes in the climate encouraged the expansion
377 of grasslands over the shrublands, where *Metridiochoerus* dispersed to. *Kolpochoerus* likely stayed
378 in the more closed areas near the lake and rivers. The strong C4-signal suggests that *Kolpochoerus*
379 may have been an omnivorous digger with a diet dominated by storage organs and fresh growth of
380 C4 plants and optionally fauna supported by C4 vegetation.

381

382

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396

397 **Appendix A. Supplementary data**

398 Supplementary data to this article can be found online at
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593 **Occurrence of suid genera at the east and west of Lake Turkana localities**

594 Table S1 shows how many localities from each time interval contain which genera (M =
 595 *Metridiochoerus*, K = *Kolpochoerus*, N = *Notochorus*, and Ny = *Nyanzachoerus*, and their
 596 combinations). Time is presented by group numbers from the oldest (9) to the youngest (1) members
 597 (Table 1). The major differences between the east and west side are: 1) there are no locations on the
 598 east side where only *Metridiochoerus* and *Notochoerus* were present; 2) there are no locations on the
 599 east side where only *Notochoerus* was present; and 3) there are more locations on the east side where
 600 either only *Metridiochoerus* or only *Kolpochoerus* was present. In locality occurrence, the specimen
 601 had to have comloc (computational location = location bound to a member, Fortelius et al. 2016)
 602 information with genus and member information, and if there was at least one specimen from the
 603 comloc, it was occupied by that genus.

Table S1. Occurrence of the four suid genera in localities on the east and west side of Lake Turkana.

East	7.91- 6.54	6.54-5	4.35- 3.97	3.97- 3.44	3.44- 2.53	2.53- 1.87	1.87- 1.53	1.53- 1.38	1.38-0.7
NyMnk					1				
NyNk					1				
NyMn									
NyN				1	1				
Ny			1						
Nk					3	1			
Mn									
Mk						1	13	12	1
Mnk						12	5		
N									
M						2	4	2	1
K						1	1		1
West									
NyMnk									
NyNk					1				
NyMn					1				
NyN			3	3	1				
Ny	1	1		1					
Nk					2				
Mn					1	1			
Mk						2	5	2	2
Mnk					2	3	1		
N				1	2	2			
M								4	
K								1	

604

605 (Ny = *Nyanzachoerus*, N = *Notochoerus*, M = *Metridiochoerus* and K = *Kolpochoerus*) The number in each cell shows how
 606 many localities have yielded the genera shown in the first column, during the age group shown in the first row.

607 $\delta^{13}\text{C}$ -values over time

608 The $\delta^{13}\text{C}$ isotope record contain 96 measurements from Cerling et al. (2015), 17
609 measurements from Braun et al. (2010, but corrected in Cerling et al. 2015), and 45 measurements
610 from Harris and Cerling (2002, also used in Cerling et al. 2015). Measurements from specimens
611 recovered from localities only in Kenya have been taken into this analysis. The original data, the
612 methods used in obtaining them, and the visualisations can be found in the original publications and
613 their supplementary materials. We re-visualized the data to match the time intervals used in this study
614 specifically: 7.91-6.54 Ma, 4.35-3.97 Ma, 2.53-1.87 Ma, 1.87-1.53 Ma and 1.53-1.38 Ma.

615 Figure S1 shows $\delta^{13}\text{C}$ data from Cerling et al. (2015), Harris and Cerling (2002), and Braun
616 et al. (2010). The data have been categorized according to the five time intervals used in this study
617 (7.91-6.54 Ma, 4.35-3.97 Ma, 2.53-1.87 Ma, 1.87-1.53 Ma and 1.53-1.38 Ma). Other time intervals
618 contain too few measurements. Full statistical tests can be found in Appendix.

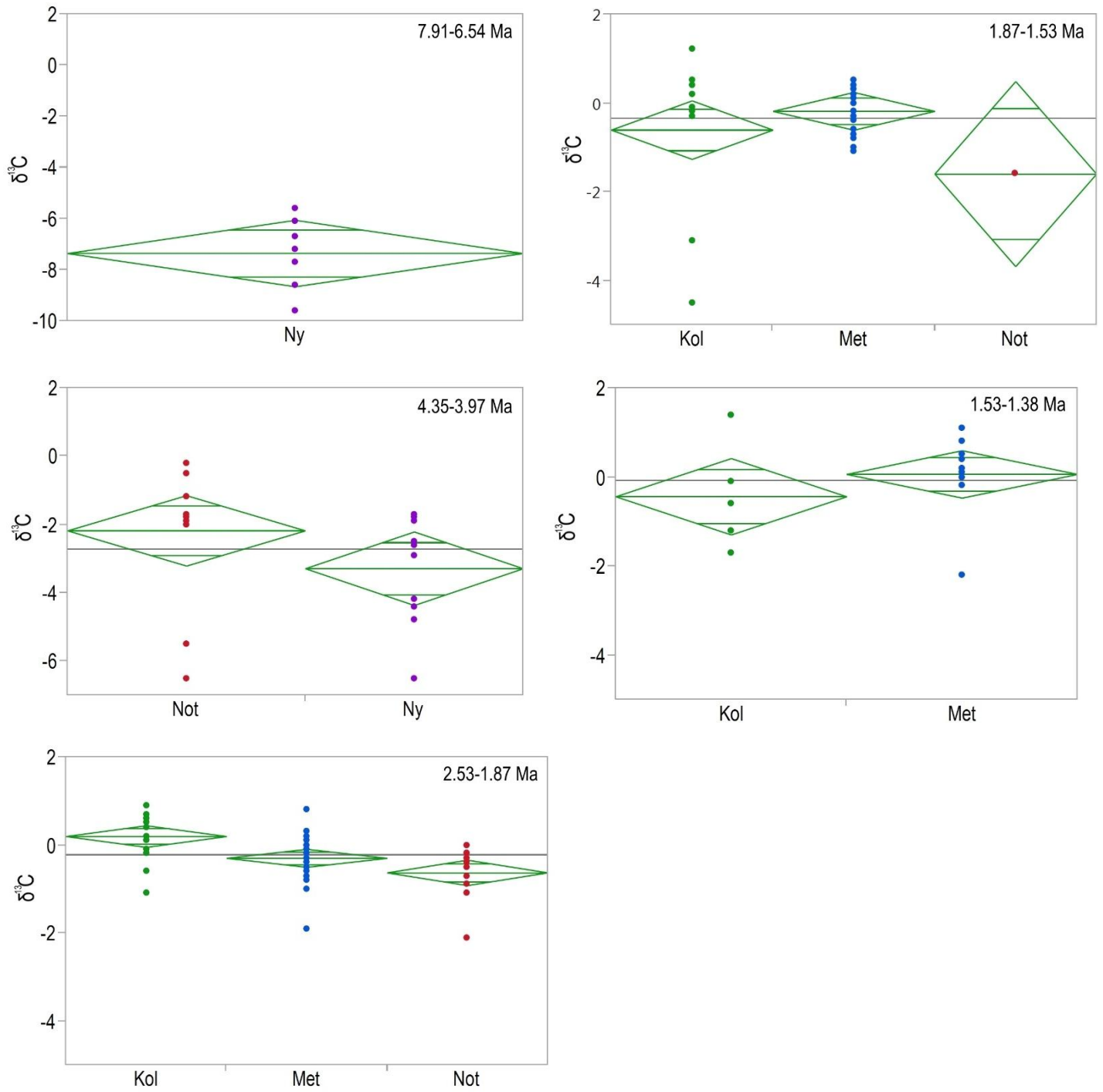
619 The time interval 7.91-6.54 Ma represents the time when *Nyanzachoerus* was the only genus
620 represented from the four genera analysed. The $\delta^{13}\text{C}$ -values of *Nyanzachoerus* (mean -7.4 , $n = 7$)
621 indicate a mixed C3-C4 diet.

622 During 4.35-3.97 Ma the mean $\delta^{13}\text{C}$ -value of *Nyanzachoerus* rises (mean -3.3 , $n = 11$), and
623 members of *Notochoerus* show a variety of $\delta^{13}\text{C}$ -values (mean -2.2 , $n = 12$). Kruskal-Wallis test
624 indicates that there is a statistically significant difference between the two genera ($p = 0.0359$).

625 During 2.53-1.87 Ma *Kolpochoerus* (mean 0.19 , $n = 18$), *Metridiochoerus* (mean -0.30 , $n =$
626 26) and *Notochoerus* (mean -0.63 , $n = 13$) all show high $\delta^{13}\text{C}$ -values, indicating a predominantly C4-
627 diet. Tukey HSD test shows significant difference between *Kolpochoerus* and *Notochoerus* ($p =$
628 0.0002), and *Kolpochoerus* and *Metridiochoerus* ($p = 0.0084$).

629 The mean $\delta^{13}\text{C}$ of *Metridiochoerus* (mean -0.19 , $n = 24$) increases during 1.87-1.53 Ma. Two
630 specimens of *Kolpochoerus* show much more negative $\delta^{13}\text{C}$ -values than others, lowering the mean
631 $\delta^{13}\text{C}$ of *Kolpochoerus* (mean -0.61 , $n = 10$). For *Notochoerus*, there is only one sampled specimen,
632 which shows lower $\delta^{13}\text{C}$ than the other genera (mean -1.6). There is no significant difference between
633 the groups.

634 The last interval, 1.53-1.38 Ma, includes only *Kolpochoerus* and *Metridiochoerus*. The mean
635 $\delta^{13}\text{C}$ of *Kolpochoerus* (mean -0.44 , $n = 5$) is lower than *Metridiochoerus* (mean 0.06 , $n = 13$), which
636 again has a higher mean than during the earlier time interval. However, there is no significant
637 difference between the two genera.

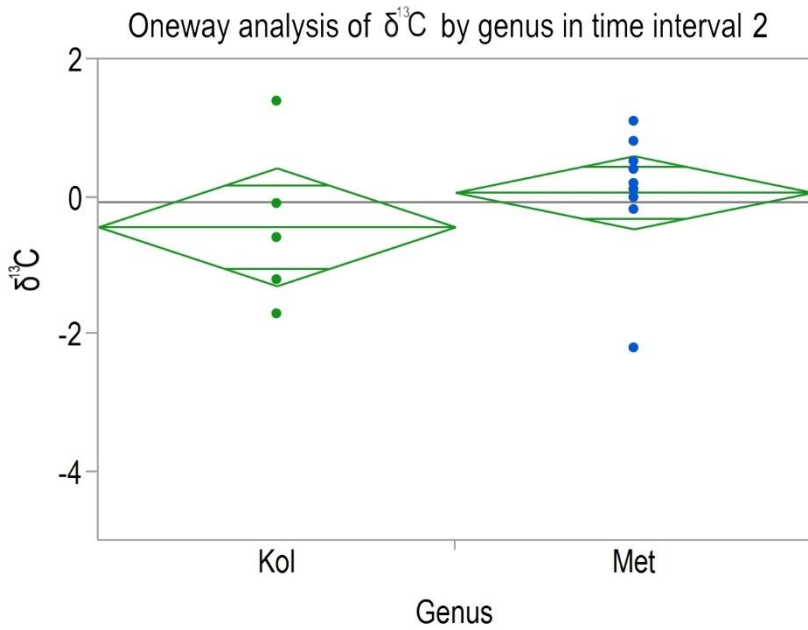


638

Figure S1. $\delta^{13}\text{C}$ -values from Cerling et al. (2015), Harris and Cerling (2002) and Braun et al. (2010) shown in the time intervals used in this analysis. The vertical span of each diamond represents the 95% confidence interval for the mean of each group. The black line shows the mean of all groups together.

639

640 **Statistical tests** for the $\delta^{13}\text{C}$ data from Cerling et al. (2015), Harris and Cerling (2002) and Braun et
 641 al. (2010). Time interval 2 = 1.53-1.38 Ma, time interval 3 = 1.87-1.53 Ma, time interval 4 = 2.53-
 642 1.87 Ma and time interval 7 = 4.35-3.97 M.

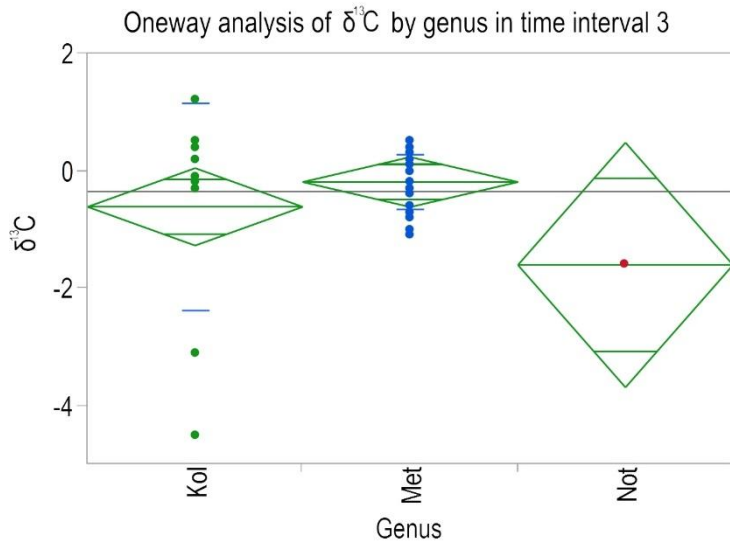


Wilcoxon / Kruskal-Wallis Tests (Rank Sums)					
Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
Kol	5	35.000	47.500	7.0000	-1.187
Met	13	136.000	123.500	10.4615	1.187

2-Sample Test, Normal Approximation		
S	Z	Prob> Z
35	-1.18655	0.2354

1-way Test, ChiSquare Approximation		
ChiSquare	DF	Prob>ChiSq
1.5277	1	0.2165

Figure	Levene's	Shapiro-Wilk Kol	Shapiro-Wilk Met	Shapiro-Wilk Not	Shapiro-Wilk Nya	Anova	Weich's	Kruskal-Wallis	Tukey HSD
d13C_int2	0.2506	0.7401	0.0057	-	-	-	-	0.2354	-
d13C_int3	0.0011	0.0061	0.1438	-	-	-	0.4751	0.2881	-
d13C_int4	0.9481	0.1487	0.0999	0.5868	-	0.0002	-	-	Kol-Not
d13C_int7	0.9195	-	-	0.0033	0.1639	-	-	0.0359	0.0002, Kol-
d13C_int9	-	-	-	-	-	-	-	-	Met 0.0084, Met-Not 0.156



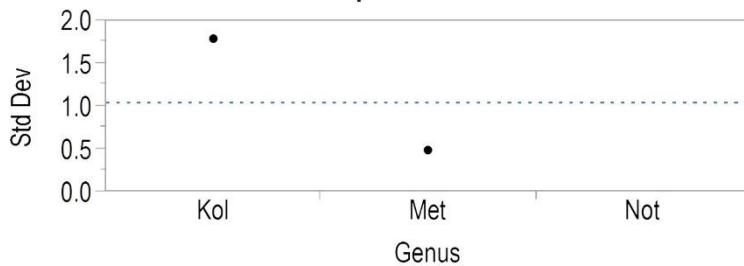
Wilcoxon / Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected Score	Score Mean	(Mean-Mean0)/Std0
Kol	10	198.500	180.000	19.8500	0.659
Met	24	428.500	432.000	17.8542	-0.107
Not	1	3.000	18.000	3.0000	-1.440

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
2.4887	2	0.2881

Tests that the Variances are Equal



Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
Kol	10	1.770405	1.276000	1.050000
Met	24	0.479413	0.413542	0.412500
Not	1	.	0.000000	0.000000

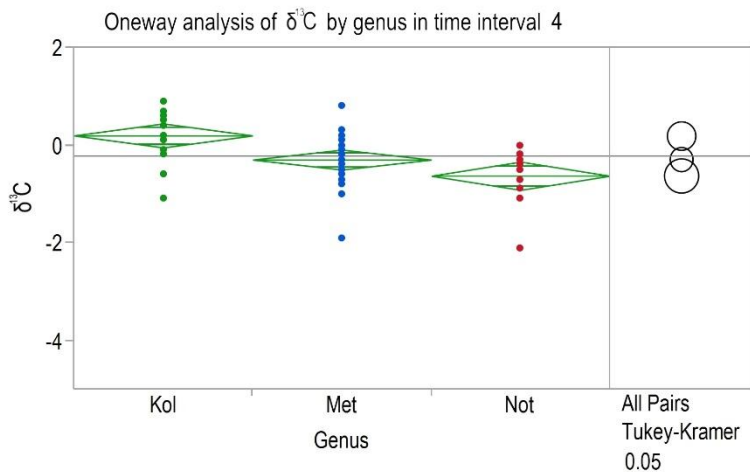
Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	6.7503	1	32	0.0141*
Brown-Forsythe	4.4571	1	32	0.0427*
Levene	12.8170	1	32	0.0011*
Bartlett	24.0113	1	.	<.0001*

Warning: Small sample sizes. Use Caution.

Welch's Test

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
0.5526	1	9.5549	0.4751



Oneway Anova

Summary of Fit

Rsquare	0.27219
Adj Rsquare	0.245234
Root Mean Square Error	0.519564
Mean of Response	-0.2193
Observations (or Sum Wgts)	57

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Genus	2	5.451635	2.72582	10.0976	0.0002*
Error	54	14.577137	0.26995		
C. Total	56	20.028772			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
Kol	18	0.19444	0.12246	-0.0511	0.4400
Met	26	-0.30000	0.10189	-0.5043	-0.0957
Not	13	-0.63077	0.14410	-0.9197	-0.3419

Std Error uses a pooled estimate of error variance

Means Comparisons

Comparisons for all pairs using Tukey-Kramer HSD

Confidence Quantile

q*	Alpha
2.40999	0.05

LSD Threshold Matrix

Abs(Dif)-HSD

	Kol	Met	Not
Kol	-0.41738	0.11051	0.36946
Met	0.11051	-0.34728	-0.09456
Not	0.36946	-0.09456	-0.49113

Positive values show pairs of means that are significantly different.

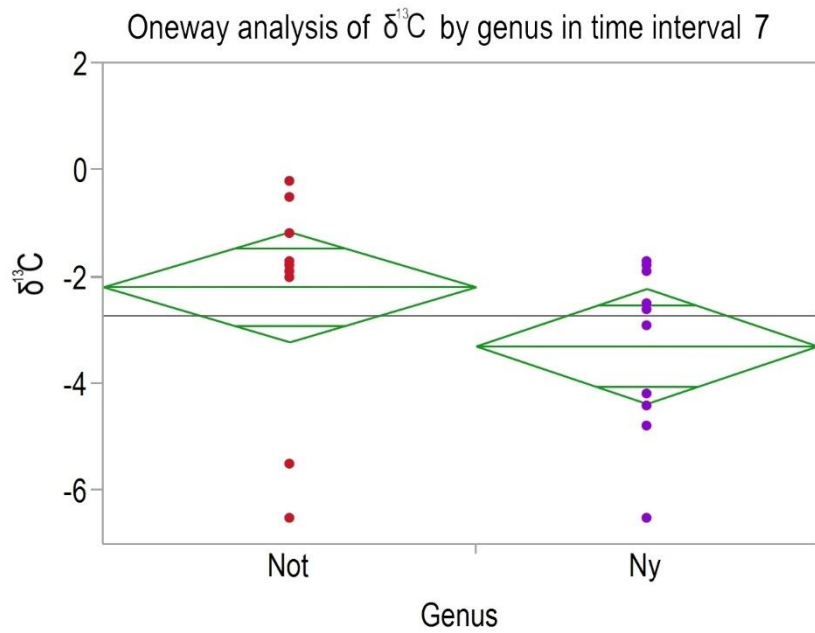
Connecting Letters Report

Level	Mean
Kol	A 0.1944444
Met	B -0.3000000
Not	B -0.6307692

Levels not connected by same letter are significantly different.

Ordered Differences Report

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
Kol	Not	0.8252137	0.1891090	0.369463	1.280964	0.0002*
Kol	Met	0.4944444	0.1593099	0.110510	0.878379	0.0084*
Met	Not	0.3307692	0.1764872	-0.094563	0.756101	0.1560



Wilcoxon / Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Expected		
			Score	Score Mean	(Mean-Mean0)/Std0
Not	12	178.500	144.000	14.8750	2.098
Ny	11	97.500	132.000	8.8636	-2.098

2-Sample Test, Normal Approximation

S	Z	Prob> Z
97.5	-2.09774	0.0359*

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
4.5309	1	0.0333*