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

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.

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

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Highlights

- *Nyanzachoerus* was replaced by its abrasive-diet-specialized successor *Notochoerus* following aridification of the environment.

- *Notochoerus* might have over-specialized for arid environments and lost its competitiveness in more variable environments.

- *Kolpochoerus* and *Metridiochoerus* most likely had different ecological niches, despite their similar C4-signal.

1. Introduction

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

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

The expansion of C4-grasses, which started in the Miocene, continued in the Pliocene (Retallack et al. 1990, Edwards et al. 2010), although the overall area of grasslands remained stagnant or decreased during 12-1.4 Ma in northeast Africa (Feakins et al. 2013). Levin et al. (2011) concluded 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 Leakeyand 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 Fernándes 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.

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2. Material and methods

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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 McDougal 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).

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

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

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

Table 1. Members and their ages and durations from west and east side of Lake Turkana (after Brown and 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 Formation[7]	4.2-4.11	0.09			
Upper Nawata Formation[8] (Lothagam)	6.54-5	1.54			
Lower Nawata Formation[9] (Lothagam)	7.91-6.54	1.37			

Superscripts show members that have been combined in the analysis.

3. Results

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

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

The abundance record of *Notochoerus* has a unimodal shape, e.g. it has a bell shaped, one-peaked curve (Fig. 1. red diamond-line). *Notochoerus* is first encountered during 4.35-3.97 Ma, while *Nyanzachoerus* is still the dominant suid genus. Approximately 5% of the mammal specimens are *Notochoerus* at that time. In the next time period, 3.97-3.44 Ma, *Notochoerus* becomes the dominant suid genus (7%). The peak abundance of *Notochoerus* is from 3.44 to 2.53 Ma, when 12% of the mammal specimens are identified as *Notochoerus*. During the next two time periods, 2.53-1.87 Ma and 1.87-1.53 Ma, the abundance of *Notochoerus* declines (approximately 7% and <1%, respectively).
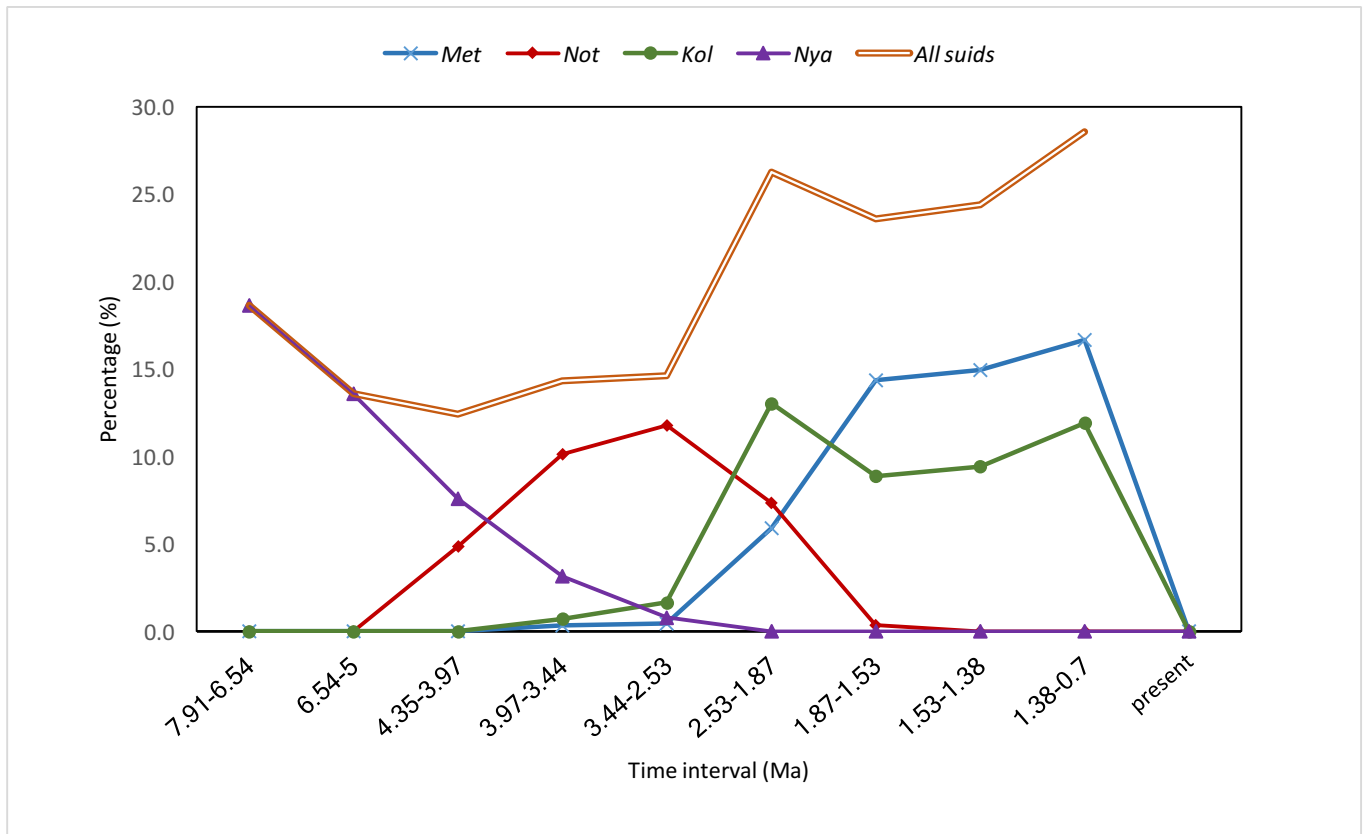
Figure 1. Relative abundances of the four suid genera *(Met = Metridiochoerus, Not = Notochoerus, Kol = Kolpochoerus, Nya = Nyanzachoerus)* specimens out of all mammal specimens in the Turkana Basin. Time intervals are dated from the tuff layers around Lake Turkana (Brown and McDougall 2011). Similar ages are combined between the east and west sides, and dates from the east side are used in the figure.

Kolpochoerus appears in the record during 3.97-3.44 Ma (1%), while *Notochoerus* is the dominant suid, but all other genera are also present (Fig. 1. green large-dot-line). During 3.44-2.53 Ma the relative abundance of *Kolpochoerus* only increases by a small amount, from 1% to 2%. A huge increase occurs during the next time period of the upper Burgi, Lokalalei, and Kalochoro Members, 2.53-1.87 Ma. *Kolpochoerus* becomes the dominant suid genus in the records with approximately 13% of the total mammal specimens. During the next two time periods, 1.87-1.53 Ma and 1.53-1.30 Ma, the relative abundance of *Kolpochoerus* decreases slightly (being approximately 9% in both). During the last time period of this analysis, 1.38-0.7 Ma (Chari and Nariokotome Members), *Kolpochoerus* has a small increase in its abundance to approximately 12%.

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

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

Figure 2 shows the relative abundance of two separate *Notochoerus* species, *N. euilus* and *N. scotti*, which have different dental characteristics, along with the relative abundance of *Kolpochoerus*. The relative abundance of *N. euilus* decreases to zero when *Kolpochoerus* becomes the dominant suid between 3.44-2.53 Ma and 2.53-1.87 Ma. During the same interval, *N. scotti* has its peak relative abundance.
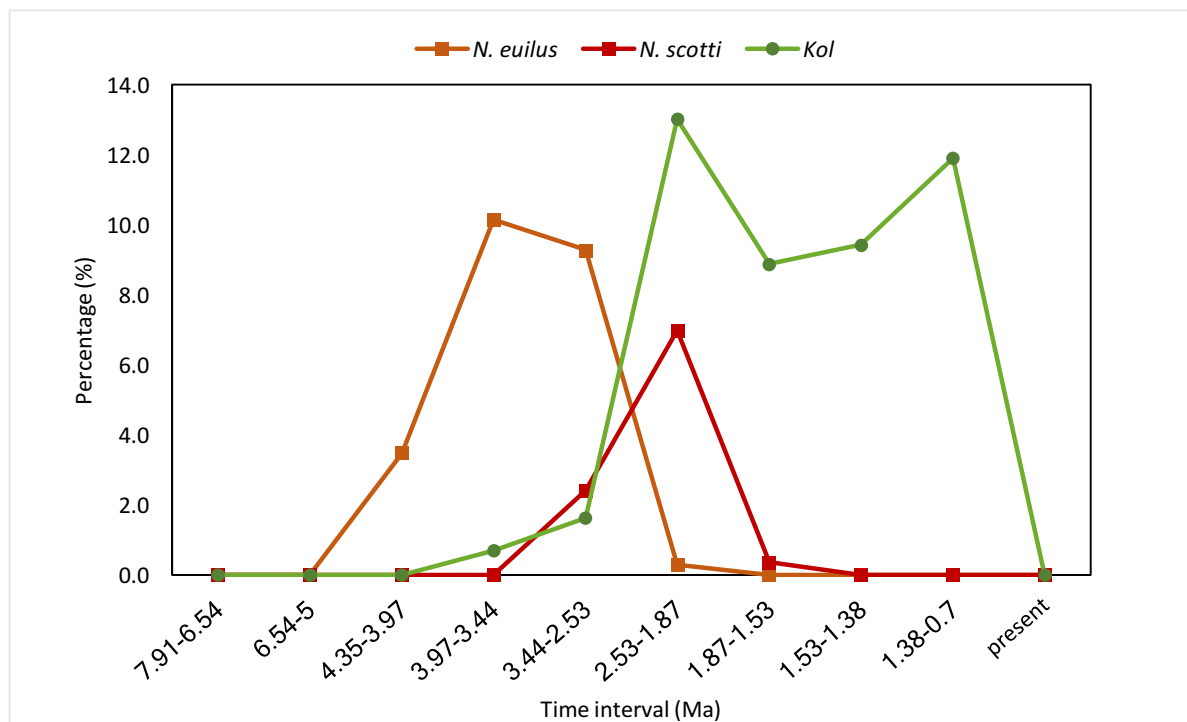
Figure 2. Relative abundances of *Notochoerus scotti* and *Notochoerus euilus* in relation to the relative abundance of *Kolpochoerus*. Time intervals are dated with tuff layers around Lake Turkana (Brown and McDougall 2011). Similar ages are combined between the east and west sides, and dates from the east side are used in the figure.

4. Discussion

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

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

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

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

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

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

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

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

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

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

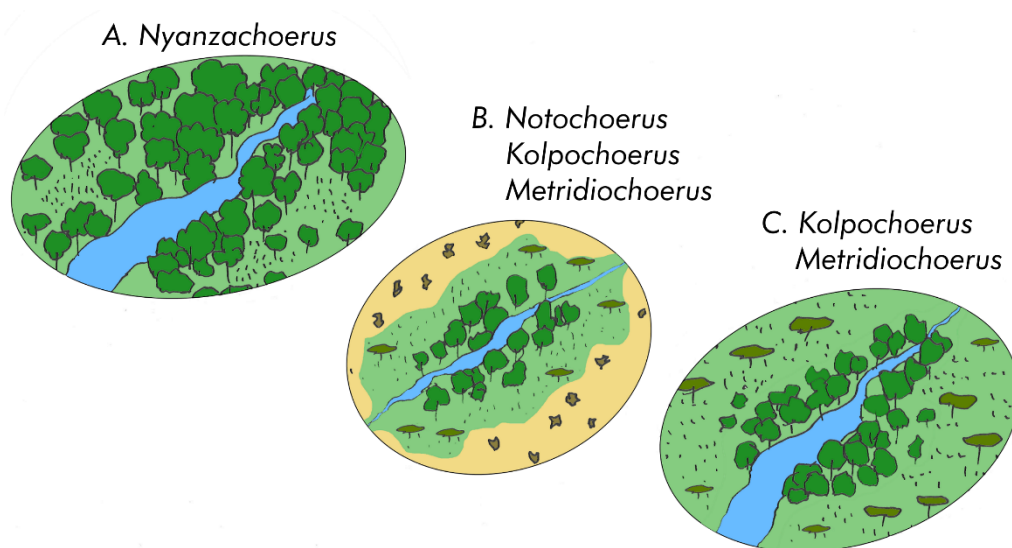354   which might help them survive the harsher seasons.

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.

5. Conclusions

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

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

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Acknowledgments

There are no conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.08.033.

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Appendix

Occurrence of suid genera at the east and west of Lake Turkana localities

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

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

δ^{13}C-values over time

The δ^{13}C isotope record contain 96 measurements from Cerling et al. (2015), 17 measurements from Braun et al. (2010, but corrected in Cerling et al. 2015), and 45 measurements from Harris and Cerling (2002, also used in Cerling et al. 2015). Measurements from specimens recovered from localities only in Kenya have been taken into this analysis. The original data, the methods used in obtaining them, and the visualisations can be found in the original publications and their supplementary materials. We re-visualized the data to match the time intervals used in this study 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.

Figure S1 shows δ^{13}C data from Cerling et al. (2015), Harris and Cerling (2002), and Braun et al. (2010). The data have been categorized according to the five time intervals used in this study (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 contain too few measurements. Full statistical tests can be found in Appendix.
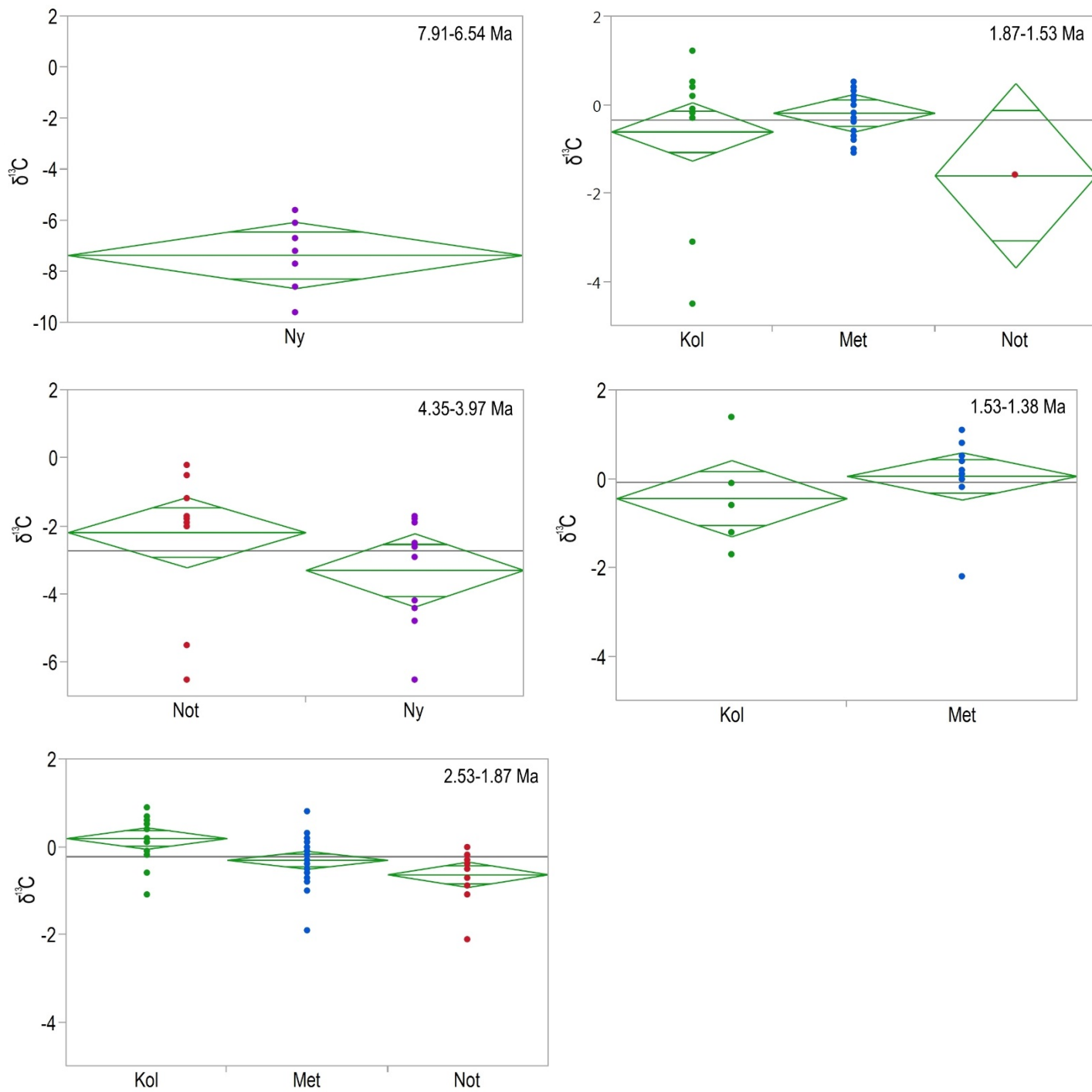
The time interval 7.91-6.54 Ma represents the time when *Nyanzachoerus* was the only genus represented from the four genera analysed. The δ^{13}C-values of *Nyanzachoerus* (mean –7.4, n = 7) indicate a mixed C3-C4 diet.

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

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

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

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

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Figure S1. δ¹³C-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.

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640 **Statistical tests** for the δ^{13}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.
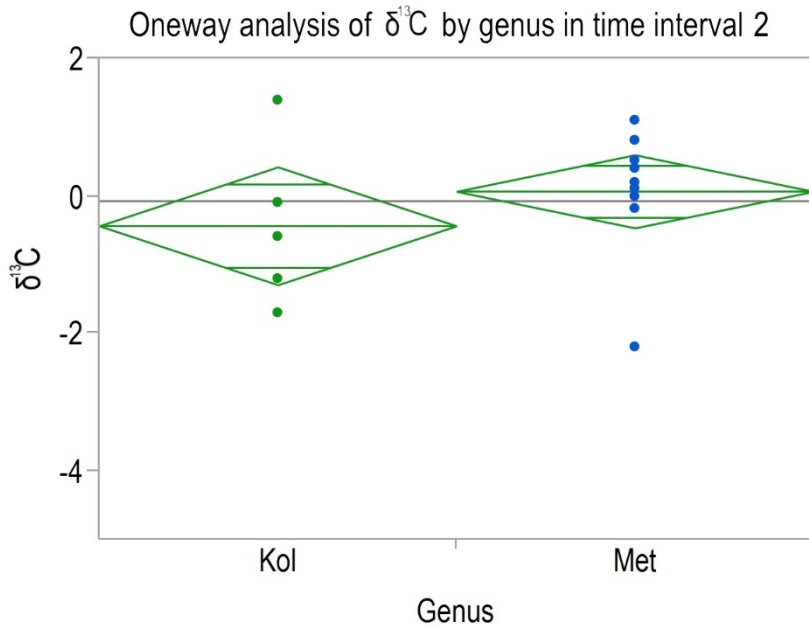
Oneway analysis of δ^{13}C by genus in time interval 2

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

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Figure	Levene´s	Shapiro-Wilk Kol	Shapiro-Wilk Met	Shapiro-Wilk Not	Shapiro-Wilk Nya	Anova	Welch´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 0.0002, Kol-Met 0.0084, Met-Not 0.156
d13C_int7	0.9195	-	-	0.0033	0.1639	-	-	0.0359	-
d13C_int9	-	-	-	-	-	-	-	-	-
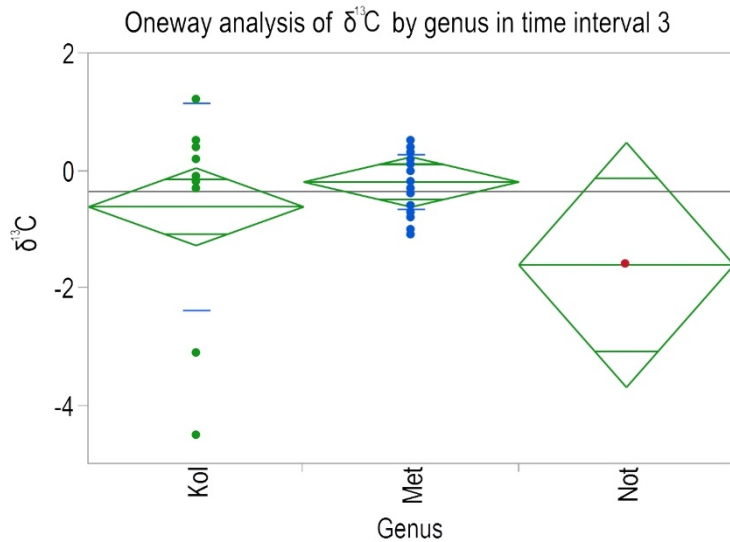
Oneway analysis of $\delta^{13}C$ by genus in time interval 3

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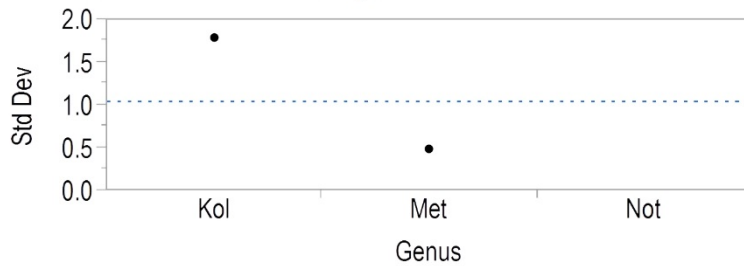
Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
Kol	10	1.770405	1.276000	1.050000
Met	24	0.479413	0.413542	0.412500
Not	1	.	0.000000	0.000000

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

644

Oneway analysis of $\delta^{13}C$ by genus in time interval 4
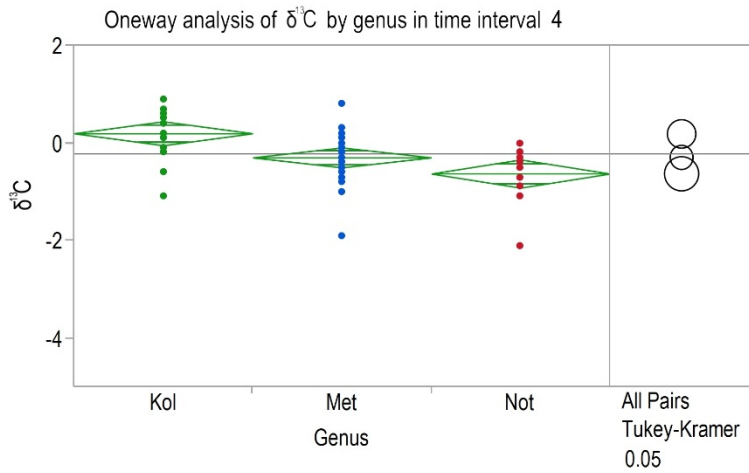
Oneway Anova

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	
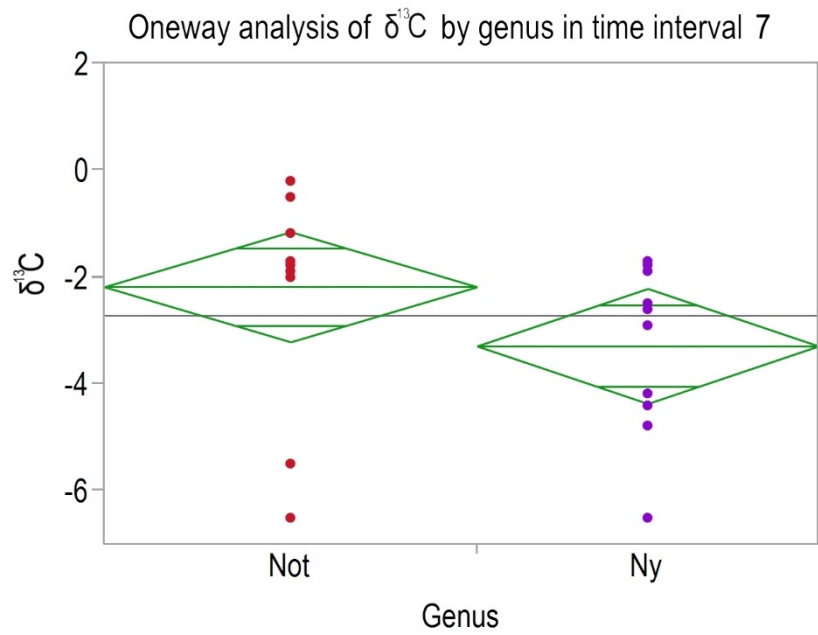
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Oneway analysis of $\delta^{13}C$ by genus in time interval 7

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*

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