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1 **The case of the grass-eating suids in the Plio-Pleistocene Turkana Basin: 3D** 2 **dental topography in relation to diet in extant and fossil pigs**

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11 **Abstract**

12 Two separate subfamilies of Plio-Pleistocene African pigs (suids) consecutively evolved hypsodont
13 and horisodont molars with flat occlusal surfaces, commonly interpreted as an adaptive trait to a
14 grazing diet, similar to that of the present warthogs (*Phacochoerus* spp.). To investigate this
15 interesting case in detail, we studied the 3D dental topography of fossil specimens from the Turkana
16 Basin, using GIS-based methods. To establish baselines for interpretation of the Turkana Basin suids,
17 topography of third molars of extant suids with known diets were analysed: grazing warthog (*Ph.*
18 *africanus*), herbivorous mixed-feeder forest hog (*Hylochoerus meinertzhageni*), omnivorous
19 generalist wild boar (*Sus scrofa*), omnivorous fruit and tuber eater bush pig (*Potamochoerus* spp.)
20 and omnivorous fruit eater babirusa (*Babyrousa* spp.) In addition, we analysed supposedly browsing
21 Miocene suids, *Listriodon* spp. The same topographic measures were applied to Plio-Pleistocene
22 specimens from the Turkana Basin, Kenya: *Notochoerus euilus*, *Notochoerus scotti*, *Kolpochoerus*
23 *heseloni* and *Metridiochoerus andrewsi*. With some differences between techniques, 3D dental
24 topography analysis of extant suid molars mostly predicts the dietary differences between the species
25 correctly. The grazing *Ph. africanus* differs from both the omnivorous suids and the herbivorous
26 mixed-feeder *H. meinertzhageni* in all except one metrics. The omnivorous mostly tropical suids,
27 *Potamochoerus* and *Babyrousa*, primarily differ from the generalist, *S. scrofa*, in the orientation patch
28 count analysis, showing higher occlusal complexity in the latter. Although, there might be significant
29 caps between the morphological changes and the ecological changes, we conclude that based on
30 comparison of dental topography with the present-day suids, *N. scotti* and *M. andrewsi* were most
31 likely highly specialized grazers, while *N. euilus* and *K. heseloni* retained more of their ancestral,
32 omnivorous heritage, but consumed grasses more than the extant omnivorous suids.

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38 **Keywords:** 1) Dental topography, 2) GIS, 3) OPC, 4) Pigs, 5) Turkana Basin

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41 **Research highlights**

42 1. Dental topography can predict different diets in present-day wild pigs.

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44 2. The Plio-Pleistocene pigs in the Turkana Basin had dental topography mostly similar to
45 extant grazing warthog, although some species also had resemblances to omnivorous forest
46 pigs.

47

48 **1. Introduction**

49 Most of the present-day wild pigs (Suidae) are forest dwelling, omnivorous, medium-sized
50 artiodactyls, but greater diversity is known from the history of suids, since the Eocene (Harris and
51 White 1979, Pickford 1986, Ducrocq et al. 1998). One particularly interesting case in the evolution
52 of suids occurred in Africa, where hypsodont (high-crowned), multicusped and horisodont
53 (elongated) molars with folded enamel evolved during the Plio-Pleistocene (Cooke 1978, Harris and
54 White 1979, Bishop 2010). This trend appeared independently in two different subfamilies
55 (Tetraconodontinae and Suinae) in the same geographical area (Harris and White 1979). A third
56 independent example of the trend of hypsodonty and highly folded enamel in suids has been observed
57 by Pilgrim (1926) in less extreme form in the Miocene Asian genera *Hippohyus* and *Sivahyus*. The
58 appearance of hypsodont teeth with extra cusp pairs has been thought to indicate a dietary shift from
59 omnivory towards herbivory (plant eating) and especially to grazing (grass eating). In an analogous
60 transition in the more wooded habitats of the middle Miocene, listriodontine suids also shifted from
61 omnivory to herbivory, developing fully bilophodont teeth in the process (Pickford and Morales
62 2003).

63 A common approach for interpreting paleodiets and paleoenvironments is to extract information from
64 hard tissues of present-day species for which diets and behavior are known, and apply the same
65 reasoning about diets to patterns extracted from preserved tissues of fossil species (Teaford and
66 Walker 1984, Cerling et al. 1997, Merceron et al. 2004, Hoppe et al. 2004, Ungar et al. 2007, Saarinen
67 et al. 2015, Fortelius et al. 2016). Isotope (Harris and Cerling 2002, Cerling et al. 2015) and
68 microwear (Bishop et al. 2006, Ungar et al. 2017, Lazagabaster et al. 2019) analyses from suid teeth
69 and morphological analyses from limb bones (Bishop 1999, Bishop et al. 2006) have used this way
70 to study the paleoecology of Plio-Pleistocene African suids. Most of these existing dietary studies of
71 African fossil suids are based on the methodologies developed for analyzing the grazing-browsing
72 spectrum of herbivory. To investigate the peculiar case of transition from omnivory towards grazing

73 of African fossil suid lineages, we need a methodology that would capture the omnivory-grazing
74 spectrum from the morphology of the teeth. Dental topography analysis offers such means to quantify
75 aspects of relief and occlusal complexity in relation to diets. Geographic Information Systems (GIS)
76 tools, originally developed for analysis of landscape topography, can be used to perform dental
77 topography analyses.

78 GIS tools consider tooth surfaces analogous to three dimensional landscapes (Reed 1997, Hunter and
79 Jernvall 1998, Zucotti et al. 1998, Ungar and Williamson 2000). GIS approaches allow measurements
80 from the whole occlusal surface, making it independent of landmarks, unlike geometric
81 morphometrics (Ungar and Williamson 2000, Evans 2013). Most GIS-based dental topography
82 studies to date have been focused on primates (M'Kirera and Ungar 2003, Ungar and M'Kirera 2003,
83 Dennis et al. 2004, Boyer 2008, Bunn et al. 2009, Winchester et al. 2014, Pampush et al. 2016,
84 Yamashita et al. 2016, Ungar et al. 2016). However, Orientation Patch Count (OPC, and Orientation
85 Patch Count Rotated OPCR) analysis, which is based on geographical orientation of patches on the
86 tooth surface, has also been applied to other animal groups (Evans et al. 2007, Evans and Jernvall
87 2009, Santana et al. 2011, Smits and Evans 2012, Wilson et al. 2012, Evans and Janis 2014). Pig
88 molars are typically characterized by lack of linear structures, such as lophs, commonly found in the
89 folivores or insectivores for which dental GIS metrics were primarily developed, and by a high
90 number of cusps and cusplets. The molar cusps of suids also feature folds, which create a radial pattern
91 of grooves as the cusps wear down (Hünemann 1968). In addition, adult suid molars typically have
92 much more exposed dentine than those of primates, for which GIS-based approaches have been
93 primarily developed. Pig molars therefore represent challenges for existing methods.

94 In this study five extant suid species, whose ecology and diet preferences are known, are compared
95 to four different Plio-Pleistocene suids from the Turkana Basin. In order to include browsing suids,
96 lacking in the modern fauna, specimens from the browsing fossil genus *Listriodon* (Hunter and
97 Fortelius 1994, Pickford and Morales 2003) are included in the analyses. Overall, the genera selected

98 to form the baselines for this study thus capture the full spectrum of plant-based diets (grazing,
99 browsing, mixed-feeding and omnivorous), allowing us to map fossil species of interest to any diet
100 based on their dental topography measurements. Present-day suids in this study are the common
101 warthog (*Ph. africanus*), bushpigs (*Potamochoerus* spp.), the forest hog (*Hylochoerus*
102 *meinertzhageni*), babirusas (*Babirusa* spp.) and the Eurasian wild boar (*Sus scrofa*).

103

104 *Ecology of the present-day suids*

105 Two species of warthogs are described in the present fauna: *Ph. africanus*, the common warthog, and
106 *Ph. aethiopicus*, the desert warthog (Randi et al. 2002, Butynski and de Jong 2017). The biology of
107 the desert warthog is still mainly unknown. *Phacochoerus africanus* consumes mainly grasses, they
108 are powerful diggers and they prefer open grassland habitats with short grasses (Ewer 1958, Field
109 1970, Field and Laws 1970, Jarman 1972, Hirst 1973, Harris and Cerling 2002, Treydte 2006). The
110 results of stable carbon isotopic analysis of their enamel indicate that C₄ resources are their main food
111 source (Harris and Cerling 2002). In addition, warthogs can digest fiber more efficiently than other
112 wild suids (Clauss et al. 2008). Their third molars are hypsodont and horisodont, and frequently have
113 over ten columnar cusps (Owen 1850, Ewer 1957). The roots of their third molars have delayed
114 maturation, which enable the third molars to grow almost continuously while in use (Spinage and
115 Jolly 1974). Old individuals often have their first and second molars worn out and only have their
116 third molars remaining for mastication. The occlusal relief is mainly low, reflecting wear by abrasion
117 (Fortelius and Solounias 2000).

118 Bush pig species (*Potamochoerus larvatus* and *Po. porcus*, also called the red river hog) are
119 predominantly nocturnal and rooting species that are rarely seen in open environments (Skinner et al
120 1976, Breytenbach and Skinner 1982, Ghiglieri 1982, Vercaemmen et al. 1993). *Potamochoerus*
121 *larvatus* inhabits eastern and southern parts of Africa whereas *Po. porcus* is found in western and

122 central Africa, although they have overlapping ranges in some areas in central parts of Africa
123 (Vercammen 1993, Seydack 2017, Melletti et al. 2017). They have been observed to consume a
124 diversity of plants, tubers, fruits, fungi, insects, even crocodile eggs and mammals, although they
125 prefer fruits when available (Skinner et al 1976, Breytenbach and Skinner 1982, Ghiglieri 1982,
126 Vercammen et al. 1993). *Potamochoerus porcus* is reported to have powerful jaws capable of
127 crushing seeds (Herring 1985). The two species have been found to have different dental microwear
128 texture (Lazagabaster 2019). However, Souron et al. (2015b) did not find similar differences, which
129 can be result from differences in technical parameters or the sampling of different populations. The
130 difference found by Lazagabaster (2019) might occur due to the ecological differences in their
131 habitats, *Po. larvatus* in woodlands and *Po. porcus* in rainforests: seasonality, food availability,
132 vegetation structure and soil composition. The third molars of *Potamochoerus* are low-crowned and
133 bunodont.

134 The forest hog (*Hylochoerus meinertzhageni*) is reported to both graze and browse, but not having a
135 strong rooting behavior (d'Huart 1978, Ewer 1970). Stable carbon isotopes of their hair indicate them
136 to be C₃ consumers (Cerling and Viehl 2004). However, in high altitudes stable carbon isotopes are
137 not a good proxy for grass versus browse diet as many grasses use C₃ pathway in those environments.
138 Stable carbon isotopic analysis of their enamel indicate that they consume mainly C₃ plants in Kenya
139 (Aberdares and Nanyuki), Zaire (Ituri Forest) and Uganda (Queen Elizabeth Park) (Harris and Cerling
140 2002). Consumption of grasses has been reported to increase during the wet seasons (Cerling and
141 Viehl 2004). They inhabit thick vegetation areas from mountain bamboo forests to bushlands (Reyna-
142 Hurtado et al. 2017). Differences observed in dental microwear between forest hogs and other suids
143 have been interpreted to reflect the observed mixed-feeding habits of *Hylochoerus* (Souron et al.
144 2015b). Insects and their larvae might also be an important part of their diet (Ewer 1970). Cusp pairs
145 in their molars tend to form transverse crest like structures or lophs on the tooth surface and their

146 third molars are moderately high-crowned. The cusps are not tightly packed, which makes the relief
147 high. Extra cusplets are few and arranged into longitudinal valleys between the crests (Herring 1985).

148 *Sus scrofa* has an omnivorous and broad generalist diet and it inhabits a wide range of tropical and
149 temperate environments (Long 2003, Ballari and Barrios-Garcia 2014). The wild boar is also the
150 ancestor of domestic pigs. It has bunodont third molars with highly folded enamel and increased
151 number of cusps compared to *Potamochoerus*.

152 *Babryrousa* species live in the tropical islands of Indonesia (Long 2003). Most of them are almost
153 hairless, and the males have peculiar upper canines protruding through their skin (Macdonald 2017,
154 Sheherazade et al. 2017). Babirusas prefer closed rainforest environment and they have been reported
155 to consume mainly fruits, but also leaves, insects and other animal material (Leus et al. 1992, Leus
156 1994, Long 2003, Tulung et al 2013). They are capable of cracking nuts and do not show strong
157 rooting behavior because their nose lacks a large rostral bone that makes efficient rooting possible
158 (Leus et al. 1992, Tulung et al. 2013). Their molars are low crowned, bunodont and does not show
159 tendency towards increased horizodonty.

160 Images of the occlusal surface of one specimen from each group are shown in supplementary material
161 S1.

162

163 *Overview of the fossil suid species*

164 The Turkana Basin is rich in Plio-Pleistocene fossil bearing sediments and known for numerous
165 hominin finds (Leakey and Leakey 1978, Wood and Leakey 2011). At least three groups of suids are
166 known from the Plio-Pleistocene Turkana Basin (White and Harris 1977, Cooke 1978, Bishop 1999).
167 According to White and Harris (1977), group 1 consists of *Nyanzachoerus*, which leads to
168 *Notochoerus*, group 2 consists of *Kolpochoerus* species, which very likely includes *Hylochoerus*, and
169 group 3 consists of *Metridiochoerus* species, which have been considered to be the ancestors of

170 *Phacochoerus* (Cooke 1978, Harris and White 1979, Kullmer 1999). *Potamochoerus* has been put to
171 its own group (Harris and White 1979, Cooke 1978), although other studies consider it as a part of
172 the *Kolpochoerus* group (Bishop 1999).

173 *Notochoerus euilus* and *N. scotti* were tetraconodontines, a now extinct suid subfamily famous for
174 their large premolars (Van der Made 1998). Although, the later species *N. euilus* and *N. scotti* had
175 greatly reduced premolars compared to the earlier species. *Kolpochoerus* and *Metridiochoerus* are
176 part of the Suinae subfamily, like all present-day suids. The ancestry of *Kolpochoerus* and
177 *Metridiochoerus* has been suggested to be in the Eurasian *Propotamochoerus* (via *Dasychoerus* and
178 *Potamochoeroides*, respectively), which dispersed into Africa in the late Miocene or early Pliocene
179 (Pickford 2012, Pickford and Obada 2016).

180 Tetraconodontine suids were the most abundant suids in the latest Miocene and early Pliocene in
181 eastern Africa. *Notochoerus* species were large-sized and their third molars had more cusp pairs than
182 nyanzachoeres (Harris and White 1979). Post-cranial analysis from the earliest one, *Notochoerus*
183 *euilus*, suggested that the species was inhabiting an intermediate environment between a savanna and
184 a forest (Bishop 1999). According to the stable carbon isotope analyses, *Notochoerus* species in the
185 Turkana Basin were C₃-C₄ mixed feeders between 4.3 and 4.0 Ma and predominantly C₄-grazers by
186 2.0 Ma (Cerling et al. 2015). *Notochoerus scotti* and *N. clarki* were the last *Notochoerus* species
187 (White and Suwa 2004). In Turkana Basin, *N. scotti* was more abundant. Its third molars were the
188 largest among Plio-Pleistocene suids, although the later *Metridiochoerus compactus* had the most
189 hypsodont molars (Harris and White 1979).

190 Many species of kolpochoeres have been recognised throughout Africa (Brunet and White 2001,
191 Haile-Selassie and Simpson 2013, Souron et al. 2015a). Most of the kolpochoeres found from the
192 Turkana Basin have been referred to as *Kolpochoerus heseloni*. Some specimens from the Turkana
193 Basin localities from Pleistocene could be assigned to *K. olduvaiensis*, which is a derived
194 chronospecies of *K. heseloni*, and possess longer and higher third molars than *K. heseloni* (Gilbert

195 2008). *Kolpochoerus olduvaiensis* is sometimes included within the latter species (Harris and White
196 1979). The Turkana Basin kolpochoeres had third molars that increased in height and length during
197 their evolutionary lineage (Cooke and Maglio 1972). However, they never became as hypsodont as
198 *N. scotti* or *M. compactus* (Cooke 2007). Nonetheless, isotope studies have demonstrated that
199 *Kolpochoerus* was a dominant C₄ consumer (Harris and Cerling 2002, Cerling et al. 2015). Post-
200 cranial studies have indicated habitats of intermediate openness for *Kolpochoerus heseloni* (Bishop
201 1999).

202 *Metridiochoerus* appeared in the Turkana Basin in the Pliocene. Most of the *Metridiochoerus* species
203 had hypsodont cheek teeth, although the earliest specimens had a rather low crown height (White et
204 al. 2006). The crown height of *M. andrewsi* increased throughout the Pliocene and the Pleistocene,
205 culminating in the appearance of the early Pleistocene *Metridiochoerus compactus*, which possessed
206 extremely high-crowned molars (Harris and White 1979, Cooke 2007). Isotope studies have
207 demonstrated that *Metridiochoerus* species consumed mostly C₄ plants throughout their history
208 (Cerling et al. 2015).

209 The shift to a higher crown and more cusp pairs in the third molars evolved independently in
210 *Nyanzachoerus-Notochoerus*, *Kolpochoerus*, and *Metridiochoerus* lineages in the Plio-Pleistocene
211 Africa. In the Turkana Basin, *Notochoerus scotti* and *Metridiochoerus compactus* demonstrated
212 extreme hypsodonty in their molars, while the changes in *Kolpochoerus heseloni* were less extreme.
213 The Miocene listriodontine suids are known for their bilophodont molar morphology. Based on the
214 molar morphology and dental microwear, they have been classified as browsers (Hunter and Fortelius
215 1994, Pickford and Morales 2003).

216 Since the warthog is the only living suid displaying dominant grazing behavior as has been generally
217 attributed to the African fossil suids, our hypothesis is that the dental surface topography of the third
218 molars of the Plio-Pleistocene suids is most similar to that of the warthog and differs from all other
219 extant suids and *Listriodon*.

221 **2. Material and methods**

222 *Specimens*

223 Third molars were chosen to be used in the study as isolated third molars of many fossil suids can be
224 identified to genus or even species level (Kullmer 1999). Third molars in wear also indicate mature
225 individuals, which are expected to consume foods characteristics of the species (Spinage and Jolly
226 1974).

227 Extant suid specimens were scanned in the collections of the Museum für Naturkunde, Berlin,
228 Germany (see S3). One upper and one lower third molar were scanned from each extant suid skull.
229 The skulls were selected based on age/wear stage: third molar in complete wear, but second molar
230 not fully worn down, and a good condition of the third molars, i.e., no cracked teeth. Fifteen skulls
231 per taxon (*Ph. africanus* Gmelin 1788, *Potamochoerus* spp. Gray 1854 and *S. scrofa* Linnaeus 1758)
232 were selected for scanning. All warthog skulls in the collection have been labelled as *Ph. aethiopicus*
233 Pallas 1767 because earlier only one species of warthogs was acknowledged, the common warthog,
234 and it was referred to as *Ph. aethiopicus*, which is the older name (Lydekker 1915, Randi et al. 2002).
235 Today, the common warthog is referred as *Ph. africanus*, and the desert warthog as *Ph. aethiopicus*.
236 The majority of the specimens in the collections are common warthogs (*Ph. africanus*) rather than
237 desert warthogs (*Ph. aethiopicus*). Thus, the specimens used in this analysis are all *Ph. africanus*
238 according to the cranio-mandibular morphology.

239 *Potamochoerus* skulls have all been labelled as *Po. porcus* Linnaeus 1758, but there was a note among
240 the specimens indicating that many of the skulls are actually *Po. larvatus* F. Cuvier 1822. According
241 to the country the specimens have been collected from, the specimens from South Africa, Tanzania
242 and Angola are likely *Po. larvatus* and the specimens from Cameroon and Togo are likely *Po. porcus*.
243 The specimens of bushpigs in this study are referred to as *Potamochoerus* spp.

244 *Hylochoerus meinertzhageni* Thomas 1904 skulls were rare, and only four were in sufficiently good
245 condition to be included in the study.

246 Finally, five skulls labelled as *Babyrousa babyrussa* Linnaeus 1758 (as all babirusas are labelled in
247 the collection) were included in the materials to represent tropical rainforest suids. Most of the
248 babirusas with locality information are from the island of Sulawesi, therefore the specimens used here
249 are most likely *Babyrousa celebensis* Deninger 1909 (Macdonald 2017). The specimens of babirusa
250 in this study are referred to as *Babyrousa* spp.

251 Included fossil species from the Turkana Basin, Kenya, are *Notochoerus euilus* Hopwood 1926,
252 *Notochoerus scotti* Leakey 1943, *Kolpochoerus heseloni* Leakey 1943 and *Metridiochoerus andrewsi*
253 Hopwood 1926. Images of the occlusal surface of the specimens are shown in supplementary material
254 S2. The Turkana Basin specimens were scanned at the collections of the National Museums of Kenya
255 (see S4). All specimens were isolated third molars from the Koobi Fora Formation, on the east side
256 of the Lake Turkana. The specimens of *N. euilus* have been found in strata dated between 4 and 1.9
257 Ma (Lonyumun member, Tulu Bor member, and Upper Burgi member), while all the other specimens
258 have been found in strata dated between 2 and 1.5 Ma (Upper Burgi member, KBS member, and
259 Okote member). However, one of the *K. heseloni* specimens have been found in the Area 1, which
260 have strata from Okote to Chari members. This specimen might represent the chronospecies *K.*
261 *olduvaiensis*. Due to the low number of the specimens we include the specimen into the analyses as
262 part of the *K. heseloni* set. The chosen specimens were mostly in middle wear, though there were
263 clear differences in the wear between specimens. In most cases all the cusps were in wear, but in
264 some specimens the last cusp pair was still unworn. Four lower and five upper third molars of *M.*
265 *andrewsi*, one lower and six upper third molars from *K. heseloni*, one lower and two upper third
266 molars from *N. scotti* and six upper third molars from *N. euilus* were included in the analyses.
267 Comparison between the upper and lower molars of extant suids revealed that their means were
268 statistically different in some species and some analyses (see S5.1) and especially in the case of OPC

269 they should be analysed separately. There were unfortunately too few fossil specimens to analyze
270 only one category, and we therefore analysed both upper and lower molars of the extant species.
271 Despite the statistical difference, the difference of the mean values of upper and lower teeth from the
272 mean value of all teeth of the same species was small compared to the mean values between species
273 and thus do not change the pattern (see S5.2).

274 Miocene specimens were scanned from casts made from specimens of different collections (see S6).
275 The casts are housed in the collection of M. Fortelius in the Department of Geosciences and
276 Geography, University of Helsinki, Finland. Miocene specimens included seven lower and six upper
277 third molars of *Listriodon* von Meyer 1846 (labelled as *L. splendens*, *L. pentapotamiae* and *L.*
278 *theobaldi*). The listriodontines were treated as one group in the analyses, *Listriodon* spp.

279

280 *Scanning teeth and preparing 3D-scans*

281

282 The 3D-scanning of the teeth was consistently performed with an optical (structured light), hand held
283 PlanScan (Planmeca Oy, Helsinki, Finland) digital impression scanner (by JR and a few fossil
284 specimens from the Turkana Basin by Yoland Savriama). The PlanScan scanner was used together
285 with Planmeca Romexis software (version 3.4.0.R). The scanner software produces aggregated files
286 with output resolution of approximately 0.1 mm. The scans were saved as .STL files in Romexis. The
287 3D-scans were prepared in an open source mesh processing tool MeshLab v1.3.4BETA (Cignoni et
288 al. 2008). All scans were manually orientated so that occlusal surface was perpendicular to Z-axis,
289 and saved as .PLY files.

290 As a conservative choice, all the analysed molars were cropped to have only the first two cusp pairs
291 in order to remove the obvious differences in horizodonty between the species (Fig. 1). In this way,
292 the study focused on the comparable componential topographical differences on the occlusal surface.
293 While horizodonty might be related to increase in chewing efficiency in animals specialized on small

294 items (Souron 2017), it does not affect directly the biomechanical food processing characteristics,
295 which was our focus in this study. The problem that horisodont third molars typically have the mesial
296 and the distal part of the tooth in a different stages of wear was also alleviated by using only the front
297 part of the tooth. The dataset in this study included both brachydont (low-crowned) and hypsodont
298 species. Since the aim was to examine only the surface of the third molars in active occlusion, the
299 still unworn crown height at the time of the death was excluded (Fig. 2). Previous works have cropped
300 the meshes either on the lowest basin on the occlusal surface (M'Kirera and Ungar 2003), from the
301 cervix junction (Boyer et al. 2008) or from the most bulbous part viewed from occlusal perspective
302 (Evans et al. 2007, Karme 2008). For this study the gumline was observed from the extant specimens
303 and images. When seen, colored plaque was used as a marker for the gumline. In this way the cropping
304 was near the root-crown junction in brachydont teeth, but higher in more hypsodont teeth. The
305 knowledge was used to decide the cutting level on each fossil specimen. In addition, the scans were
306 virtually rescanned using 0.05 mm resolution with Rapidform XOS3 (3D Systems Inc., Rock Hill,
307 South Carolina, USA) from occlusal view eliminating all areas over 89 degrees of slope to remove
308 duplicate z values from xy data points (i.e., data was made 2.5D).

309 Cropping of the 3D meshes was done with MeshLab v1.3.4BETA by one person only (JR).

310

311 *Measures of dental topography*

312 Quantitative measures of dental topography were selected to capture two main families of
313 morphology: derivatives of relief and aspects of complexity of the working surface. The derivatives
314 of relief were measured in four ways that capture different aspects of the topography: mean surface
315 slope (MSS), relief index, sharpness index, and Dirichlet Normal Energy (DNE). The aspects of
316 complexity were measured by Orientation Patch Count (OPC) and angularity.

317 In this study R-package “molaR” (Pampush et al. 2016) was used for DNE, OPC and MSS
318 calculations (but not for relief index, because “molaR” uses a relief index function, which is designed
319 for whole tooth (Boyer 2008)), “rgdal” package for MSS and OPC, ArcGIS 10.3 (Esri, Redlands,
320 California, USA) for sharpness (natural breaks method classification) and relief index, and
321 SurferManipulator (Evans 2008) for angularity, MSS and OPC analyses. R-package “rgdal” was used
322 to rasterize the polygon data (shapefile) and convert the raster files to 0.05 mm resolution, or resize
323 them to 50 and 150 data rows. Evans (2007) used 150 data rows as a standard in the first OPC study
324 for a whole tooth row. Other studies have used 50 data rows for one tooth (Smits and Evans 2012,
325 Winchester et al. 2014). For “molaR”, which uses the 3D-meshes instead of raster files, the face count
326 of the mesh was reduced to 10,000 and Laplacian smoothing (3 steps) was done in MeshLab (Boyer
327 2008, Bunn et al. 2011, Pampush et al. 2016, Spradley et al. 2017). JMP Pro 13 (SAS Institute Inc.,
328 Cary, NC) was used to perform the statistical analyses. Complete R-code for analyzing the models
329 can be found in GitHub and the workflow in figure 3.

330 The “molaR”-package uses 3D-meshes whereas the other methods use raster grid data or digital
331 elevation models (2.5D). Thus the MSS and OPC results obtained with “molaR” are different from
332 those obtained with other methods. OPC values obtained from “molaR” are constantly higher than in
333 other methods, but the overall trend is similar, suggesting that OPC is a robust dietary proxy within
334 each implementation. MSS shows a little different pattern in “molaR” than in other methods possibly
335 due to the vertical sides of the teeth, which are affected by the elimination of areas over 89 degrees

336 in 2.5D data. Methods using 2.5D data appear less sensitive to scanning methodology and post-
337 processing, such as cropping height, than methods using full 3D data.

338 Angularity is the second derivative of elevation (or slope of the slope, Fig. 4A) (Ungar et al. 2016).
339 Angularity measures surface jaggedness, as Ungar and M'Kirera (2003) described, the difference
340 between slope and angularity is “analogous to the difference between the sharpness of a knife and its
341 serratedness”. Higher angularity has been associated with insectivore primates when compared to
342 folivores and seed eaters (Winchester et al. 2014, Ungar et al. 2016).

343 MSS from the whole 3D surface represents the steepness of the cusps (Fig. 4B) (Ungar and M'Kirera
344 2003). MSS is measured as the average degree of vertical descend over the tooth surface. As the tooth
345 wears down, MSS usually gets lower (Ungar et al. 2016). Primate species that consume fruits and
346 especially seeds tend to have less sloping crowns while folivores have steeper MSS (Ungar et al.
347 2016).

348 Relief index, the ratio of 3D surface of a tooth to its projected 2D surface, reflects the occlusal relief:
349 the higher the index, the higher the occlusal relief (M'Kirera and Ungar 2003, Ungar and Williams
350 2000). Diet of different primate species have been differentiated with the relief index. Species that
351 eat more leaves have higher relief index than frugivores (Boyer 2008, Boyer et al. 2010).

352 Sharpness index measures the proportion of steeply sloped parts of the surface (Karme 2008, Karme
353 et al. 2010, Ungar et al. 2016), and it is determined by natural breaks method classification. The
354 natural breaks method divides the surface slopes into three categories, which have as small as possible
355 variation within the groups and as high as possible variance between the groups. The relative
356 proportion of the highest slope category is the sharpness index (Karme 2008, Ungar et al. 2016). Seed
357 eaters tend to have low sharpness index (Ungar et al. 2016).

358 OPC measures the complexity of the tooth surface (Evans et al. 2007). The analysis identifies uniform
359 orientation patches on the tooth surface and calculates their number (Fig. 4C). The first use of OPC

360 was comparing the heterogeneity of carnivoran and rodent teeth (Evans et al. 2007). Highly
361 carnivorous species in both groups showed less patches on the tooth surface than more herbivorous
362 species. Derived method from OPC is OPCR (Orientation Patch Count Rotated), where the OPC
363 calculation is repeated several times from rotating specimen (Evans and Jernvall 2009, Wilson et al.
364 2012, Evans and Janis 2014). In the Equidae (horses) lineage, OPCR reflected the change from
365 mixed-feeding to grazing by increasing complexity (Evans and Janis 2014). Our OPC and OPCR
366 results have high linear correlation (R^2 over 0.98) in both SurferManipulator and “molaR”, thus we
367 used OPC results because we could compare them to the “rgdal” (aspect function) results.

368 DNE measures the deviation of a surface being planar (bending or curving of the surface) (Bunn et
369 al. 2011). DNE is independent of manual orientation and scale (Bunn et al. 2011, Winchester 2016).
370 We found out that DNE is very sensitive to artefactual errors in polygon meshes. DNE might not be
371 useful tool for complex teeth or fossil specimens that have cracks or other taphonomic alteration in
372 their surfaces (Spradley et al. 2017). See DNE results in supplementary material S7.

373 The statistical tests were made with R and JMP Pro 14 (SAS Institute, USA).

374

375 **3. Results**

376 Mean values for each index are shown in Table 1 and all raw values for each teeth are in
377 supplementary material (S10). Tukey-Kramer HSD test (for MSS, relief index and sharpness index)
378 and Steel-Dwass All pairs test (non-parametric version of Tukey’s method, for angularity and OPC)
379 were used to analyse whether the extant species with different diet preferences have significantly
380 (here and later we mean statistically significant) different dental topography (see S8). Alpha level for
381 statistically significant results is set to 0.05.

382 Angularity (Fig. 5) of *Ph. africanus* and *Potamochoerus* is significantly different from the other
383 present-day species ($p = <0.0001$, except for *Potamochoerus* – *Babyrousa* $p = 0.1674$, Steel-Dwass).
384 The highest means are seen for *Ph. africanus*, *M. andrewsi*, *N. scotti* and *N. euilus*. *Kolpochoerus*
385 *heseloni* has a lower mean than the latter, but higher than the other present -day suids. *Potamochoerus*
386 and *Listriodon* have the lowest angularity values.

387 MSS (Fig. 6) of *Ph. africanus* and *H. meinertzhageni* are significantly different from each other and
388 distinct from all other present-day species ($p = <0.0001$, Tukey-Kramer HSD). The extant
389 omnivorous species cannot be distinguished by MSS. *Listriodon* and *H. meinertzhageni* have higher
390 values than the other species, while *N. scotti*, *M. andrewsi* and *Ph. africanus* have lower values, and
391 *N. euilus* and *K. heseloni* have similar values as the present-day omnivorous species.

392 Among the present-day suids *Ph. africanus* and *H. meinertzhageni* have significantly different relief
393 index (Fig. 7) from each other and from all other species ($p = <0.001$, Tukey-Kramer HSD). The
394 present-day omnivorous suids (*Potamochoerus*, *Babyrousa* and *S. scrofa*) cannot be distinguished by
395 relief index. *Listriodon* and *H. meinertzhageni* have higher values than the others, while *N. scotti*, *M.*
396 *andrewsi* and *Ph. africanus* have lower values than the others. *Notochoerus euilus* and *Kolpochoerus*
397 *heseloni* have similar values to the present-day omnivorous species.

398 Sharpness index (Fig. 8) of *Ph. africanus* is lower than of the present-day species ($p = <0.0001$,
399 Tukey-Kramer HSD). *Sus scrofa* and *Potamochoerus* also have significantly different sharpness
400 index from each other ($p = 0.0211$, Tukey-Kramer HSD). *Listriodon* and *H. meinertzhageni* have
401 higher values than the other species, while *N. scotti*, *M. andrewsi* and *Ph. africanus* have lower values
402 than the others. Of the fossils *N. euilus* and *K. heseloni* have similar values to the present-day
403 omnivorous species.

404 OPC values (SurferManipulator, 50 rows, Fig. 9) of *Ph. africanus* are significantly different from all
405 other present-day species ($p = <0.0001$, Steel-Dwass). *Sus scrofa* has significantly higher OPC values

406 than *Potamochoerus* ($p = 0.0205$, Steel-Dwass) and *Babyrousa* ($p = 0.0176$, Steel-Dwass). The
407 highest OPC values are on *Ph. africanus*, *N. scotti*, *N. euilus* and *K. heseloni*, while *Listriodon* has
408 the lowest OPC values. Furthermore, *N. scotti* and *M. andrewsi* have the highest OPC values, whereas
409 *Ph. africanus*, *N. euilus* and *K. heseloni* have lower OPC values than the previous ones, but higher
410 than the other suids. OPC values between SurferManipulator and “rgdal” have high linear correlation
411 with 50 rows ($r = 0.93$). Linear correlations between SurferManipulator, “rgdal” and “molaR” can
412 be found in supplementary material S9.

413 Principal component analysis (PCA) with angularity (SurferManipulator), mean surface slope (MSS,
414 SurferManipulator), relief index (ArcGIS), sharpness index (ArcGIS) and OPC (50 rows,
415 SurferManipulator) is shown in figure 10. Principal component 1 (PC1) accounts 78.4% of the total
416 variation and principal component 2 (PC2) accounts for 14.1% of the total variation. All variables
417 contribute more strongly and equally to the PC1: angularity and OPC have a negative effect while
418 mean surface slope, sharpness and relief index have a positive effect. The measures of surface
419 complexity (angularity and OPC) and the derivatives of relief (mean surface slope, sharpness and
420 relief index) are positively correlated within the groups and negatively correlated between the groups.
421 Angularity, relief index and OPC contribute more on the PC2 than mean surface slope and sharpness
422 index. Figure 11 depicts a box plot of the PC1 and PC2 for each group.

423 DNE does not seem to give a meaningful dietary signal, we report the results in S7, but exclude it
424 from the dietary analysis and interpretation.

425

426 **4. Discussion**

427 The results show that the full spectrum of diet preferences of present-day suids can be captured by a
428 combination of 3D dental topography parameters. The PCA analysis shows that diets are
429 discriminated between grazing, omnivory and mixed-feeding: high surface complexity and low relief

430 discriminates grazers from mixed feeders of which have low surface complexity and high relief, while
431 omnivores are between the two. However, the variation is quite large within the diet groups, which
432 depicts the versatile diet of all suids.

433 The grazing suid *Ph. africanus*, as expected by its different diet, is distinct from other present-day
434 suids in all parameters, this provides a reliable baseline for interpreting fossil suid teeth.
435 *Phacochoerus africanus* has lower mean surface slope, relief index and sharpness index and higher
436 angularity and OPC compared to the other tested present-day suids. The herbivorous mixed-feeder
437 *H. meinertzhageni* has higher mean surface slope, relief index and sharpness index compared to the
438 other tested present-day suids. A previous analysis of 3D microwear texture analysis on the enamel
439 surfaces has demonstrated similar results: omnivorous taxa (*S. scrofa* and *Potamochoerus* sp.) were
440 distinguished from the herbivorous taxa (*Ph. africanus* and *H. meinertzhageni*) in terms of
441 complexity, and heterogeneity distinguished specialized diet of *Ph. africanus* from the other taxa
442 (Souron et al. 2015b). In addition, the results of this study demonstrates that the omnivorous suids
443 from the tropics, *Potamochoerus* and *Babyrousa*, differ from the generalist *Sus scrofa* by their lower
444 OPC.

445 Until now, 3D dental topography analyses have been used mostly for primate teeth, and were tailored
446 to distinguish between frugivorous, omnivorous, folivorous and insectivorous diets (Boyer et al.
447 2008, Bunn et al. 2011). Folivorous primates have sharp edges for cutting and shearing leaves (Kay
448 1981, Ungar and M'Kirera 2003) while frugivorous species have thick enamel, low occlusal relief
449 and round cusps to process fruit flesh and hard seeds, which need less slicing (Kay 1981, Ungar et al.
450 2016). This template is difficult to apply to suids, which have different dietary categories, molar
451 shapes and wear patterns. Despite these differences, the parameters capture patterns that are
452 reasonable *a priori*: herbivorous mixed-feeder *H. meinertzhageni* and the browser *Listriodon* show
453 higher means surface slope and relief index like folivorous primates, while the omnivorous and
454 frugivorous suids show low mean surface slope and relief index like frugivorous primates (Kay 1981,

455 Boyer et al. 2008). With a few exceptions (e.g., *Theropithecus* and some hominins) primates lack the
456 grass eating end of the diet spectrum, which we see in the warthog and in the hypsodont African suids
457 of the Plio-Pleistocene. However, OPCR analysis can capture differences between mixed-feeding and
458 grazing equids (Evans and Janis 2014) and our results show similar trend in that the grazing suids
459 have higher OPC values than the mixed-feeding and omnivorous suids. In addition, angularity, which
460 reflects the surface jaggedness (Ungar and M'Kirera 2003), is higher in *Ph. africanus* and in the
461 hypsodont Turkana Basin fossil suids. Therefore, to describe a full spectrum of suid, diets we need
462 two somewhat complementary dimensions. Complexity or heterogeneity increases from browsers to
463 mixed-feeders towards grazers. Topographical height of the elements goes the other way around: it
464 increases from grazers towards mixed-feeders and browsers. Intuitively this is sensible, since grazers
465 tend to have high-crowned teeth that wear flat due to abrasion of food and grit. Thus, large facets,
466 which are born in attrition, are replaced by smaller and more random facets, which increases
467 heterogeneity of the occlusal surface. Realized differences in relief among grazers perhaps come from
468 enamel-dentine boundaries, which appear as basins as softer dentine wears a bit ahead of enamel.
469 This difference in enamel-dentine wear has been used to infer realized diets in elephants (Saarinen et
470 al. 2015). Since grazing suid teeth are too small for reliable angle measurements by hand as can be
471 done for elephants (Saarinen et al. 2015), topographic steepness indices of grazing suids may have a
472 potential for similar mesowear analyses.

473 From meat eaters to omnivores and herbivores, mammals have been observed to increase the
474 complexity of their occlusal surfaces (Evans et al. 2007). There are several ways to increase the
475 complexity, such as making individual structures more complex, for example by folding the enamel,
476 or multiplying the existing pattern, for example by adding cusp pairs and making the occlusal surface
477 longer (horizodonty). The multiplying increases the absolute amount of tools on the occlusal surface,
478 while making different structures increases the variety of different tools on the occlusal surface. The
479 Turkana Basin suids have highly folded enamel bands with relatively deep enamel rings, while *Ph.*

480 *africanus* has developed a large number of round cusps and cusplets instead of keeping the highly
481 folded enamel.

482 The results of the PCA verify that besides the warthog, other suids do not have easily distinguishable
483 diet. Even the warthog that is the most dedicated to grass eating consumes a variety of food items.
484 Thus, even though the suids are mostly herbivorous, separating the suids into a diet categories like
485 grazers, browsers, frugivores or insectivores does not work well. In addition, as the suids are very
486 flexible to consume foods that are found in their own environment, individuals might have divergent
487 diets. In this study, *Sus scrofa*, *Potamochoerus* and *Babyrousa* have been considered as omnivorous
488 suids. They are all found mostly in the closed habitats and have remained bunodont (Seydack 2017,
489 Melletti et al. 2017, Macdonald 2017, Sheherazade et al. 2017). However, *Sus scrofa* has higher OPC
490 than the other two, and higher angularity than *Potamochoerus*, suggesting that it has more versatile
491 tools for processing greater variety of food items. *Sus scrofa* might face greater seasonal variation in
492 food availability and a need for fallback foods in mid-latitudes because of the winter-summer cycle
493 (Marshall and Wrangham 2007, Ungar et al. 2016). Dental microwear texture analysis has shown
494 differences between the two *Potamochoerus* species and it has been considered to be possibly because
495 of divergence in seasonality, food availability and soil composition in their respective habitats
496 (Lazagabaster 2019). Our study includes both species clustered together, but it could be worth
497 analyzing the species separately with larger sample size and investigate whether *Po. larvatus*
498 resembles more *Sus scrofa* in terms of the dental topography.

499 Mixed-feeder *H. meinertzhageni* and browser *Listriodon* have similar high relief pattern in the
500 analyses. However, *H. meinertzhageni* has higher OPC values pointing towards more heterogeneous
501 dental surfaces. This could indicate that *H. meinertzhageni* has a more abrasive diet. Compared to
502 other extant suids, *H. meinertzhageni* has a peculiar moderately hypsodont, almost lophodont tooth
503 morphology and lacking extra cusplets. In addition, Ewer (1970) described *Hylochoerus* chewing
504 being similar to the sideway action of *Ph. africanus*, but less extensive. The morphology and chewing

505 motion might be a result of adapting a grazer tooth, instead of an omnivore tooth, to the needs of
506 browsing. The ancestors of *H. meinertzhageni* are argued to be *Kolpochoerus phillipi* and *K. majus*
507 who have less derived teeth than for example *K. heseloni* (Souron et al. 2015a). However, stable
508 isotope analyses of *K. majus* and *K. phillipi* indicate exclusive C₄ diet (Bedaso et al. 2010,
509 Lazagabaster et al. 2018).

510 The fossil suids analysed in this study are all found in the Turkana Basin. *Notochoerus euilus* is the
511 earliest species, living around 4-2.5 Ma. Grasslands were already started to spread in the eastern
512 Africa before the appearance of *N. euilus* (Levin et al. 2004). *Notochoerus scotti* was possibly a
513 successor for *N. euilus*. It occurred around 3.5-1.5 Ma (Bishop 2010). *Kolpochoerus heseloni* has
514 been found from localities dated from 3.26 to 0.7 Ma and *Metridiochoerus andrewsi* from 3.4 to 1.66
515 Ma (Bishop 2010). Therefore, *N. euilus*, *N. scotti*, *K. heseloni* and *M. andrewsi* coexisted at the end
516 of the Pliocene and in the Pleistocene.

517 Fossil suids *N. scotti* and *M. andrewsi* have similar low dental relief and high complexity as *Ph.*
518 *africanus*. While *M. andrewsi* might be a relative of *Ph. africanus* and, thus, share a similar hypsodont
519 morphology via ancestry (Cooke 1978, Kullmer 1999), the tetraconodontine *N. scotti* developed a
520 similar morphology from a bunodont ancestry independently. Low relief and complex dental surface
521 indicate that *M. andrewsi* and *N. scotti* were both dedicated grazers. They were large suids compared
522 to present-day *Ph. africanus* (Harris and White 1979, Pickford 2013), indicating that they might have
523 been bulk-feeders, unlike *Ph. africanus*, which is a selective feeder (Ewer 1958). However, as seen
524 in the PCA a few specimens of *M. andrewsi* does not go in the same space with warthogs. They are
525 not temporally older than the other specimens, but two of them come from the same area. This could
526 indicate that some individuals consumed less grasses depending on their environment. Earlier work
527 of the authors (Rannikko et al. 2017) suggests that *N. scotti* might have been a dry shrubland
528 specialist. Unfortunately, the dental topography analyses had very low sample size of *N. scotti* and
529 they fall within the same space than *Phacochoerus* in the PCA.

530 *Kolpochoerus heseloni* and *Notochoerus euilus* resemble *Sus scrofa* in the terms of relief index, mean
531 surface slope, angularity and sharpness index, even considering the relative disproportion of upper
532 and lower teeth in the samples, which suggests that they were also generalists. However, the results
533 of the PCA demonstrates that they in fact are quite different by their dental surface topography
534 because of their higher OPC. The higher OPC values points towards a more abrasive herbivorous diet
535 and thus probably higher proportion of grazing.

536 Post-cranial studies (Bishop 1999, Bishop et al. 2006) have suggested that *N. euilus* and *K. heseloni*
537 had a limb morphology for a closed or intermediately wooded environment. The specimens of *K.*
538 *heseloni* in our analysis were from strata dated between 2.0-1.5 Ma. Stable carbon isotopes indicates
539 that at least the latest *K. heseloni* in the Turkana Basin was mostly grazing (Harris and Cerling 2002,
540 Cerling et al. 2015, Patterson et al. 2017), but the earlier *Kolpochoerus* that dispersed into Africa and
541 to the Turkana Basin might have been more like most of the extant suids, adapted to omnivorous diet
542 and closed habitats. Our results support the interpretation that *N. euilus* and *K. heseloni* favored more
543 closed environments, but still included grasses to their diets. As seen from the PCA, they do not
544 overlap well with either extant grazing *Phacochoerus* or omnivorous suids. The difference might
545 indicate that the diets of *N. euilus* and *K. heseloni* were less abrasive than the diet of a warthog. For
546 example, if they inhabited closer environments than *Phacochoerus*, the amount of ingested dust or
547 other mineral particles could have been smaller. However, Lazagabaster et al. (2019) demonstrate
548 that *N. euilus* from Hadar have similar dental microwear texture than *Phacochoerus* suggesting high
549 amounts of grasses in their diet. Without an analysis that include specimens from larger geographical
550 area and longer geological time periods, we cannot evaluate if the results reflect local adaptations due
551 to different environmental settings rather than larger evolutionary trend. In addition, the different
552 methods used to evaluate diets might not in fact depict the same reasons or they are biased and thus
553 fail to agree the true conditions of the different populations.

554 Both pull and push factors are potentially available in the setting of the Turkana Basin during the
555 Plio-Pleistocene. The study of Cerling et al. (2011) demonstrated that the Turkana Basin's landscape was
556 relatively open in the late Miocene and followed by an increase in the woody cover in the middle Pliocene.
557 Open environments returned by 1.8 Ma, and the time afterwards was a culmination of the long-term trend of
558 shrinking woodlands (Cerling et al. 2011). Wet-dry cycled seasonality was possibly increasing from the
559 end of the Pliocene and introduced seasonally arid grasslands (Bobe and Eck 2001, Bobe and
560 Behresmeyer 2004), and grass was an abundant and attractive food source for species that could cope
561 with the abrasiveness of grass and fast throughput digestion of cellulose.

562 Finally, it is important to consider that at any given time in the evolutionary history of a lineage there
563 might not be a perfect fit between morphology and ecology (Lister 2013, Souron 2017). A dental
564 topography analysis is done from worn teeth and, thus, is connected to the specimen's actual diet.
565 However, the morphology of the teeth can affect how the teeth is worn even though the diet varies.
566 In our study, the dental topography is analysed from a limited set of specimens. Thus, the ecology of
567 the animal might have been changed, but the morphology of the animal fit for the earlier diet remains.

568

569 **5. Conclusions**

570 In this study 3D dental topography methodologies were successfully extended to present-day and
571 fossil suids. Grazing *Ph. africanus* had low relief and higher number of orientation patches in occlusal
572 surface, while mixed-feeder *H. meinertzhageni* had higher relief and less patches, and omnivorous
573 suids had intermediate relief and orientation patch count, generalist *Sus scrofa* having more patches
574 than the omnivorous mostly tropical suids, *Potamochoerus* and *Babyrousa*. The Miocene browser,
575 *Listriodon*, had the highest relief and least patches. The Turkana Basin suids *N. scotti* and *M. andrewsi*
576 had similar dental topography with *Ph. africanus* while *N. euilus* and *K. heseloni* had similarities with
577 *Ph. africanus* and with the present-day omnivorous suids. The morphological changes could be

578 ancestral, and thus might not correlate with the environment where one particular specimen lived.
579 However, it will hint the environmental conditions of the lineage further in the past. The results
580 indicated that *N. scotti* and *M. andrewsi* were most probably adapted mainly to grazing, while *N.*
581 *euilus* and *K. heseloni* were not dedicated grazers or were inhabiting a more closed environment and
582 consumed less abrasive diet.

583

584

585

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597

598 **Authors' contributions**

599

600 JR, AK, HA, MF and IZ conceived the ideas and designed the study; JR collected the data; HA, AK
601 and JR analysed the data; JR, AK, MF and IZ interpret the results; JR led the writing of the
602 manuscript; all authors contributed critically to the drafts and gave final approval for publication.

603

604 **Data accessibility**

605

606 The scanned data that support the findings of this study are available from the corresponding author
607 upon reasonable request. The data that supports the findings of this study are available in the
608 supplementary material of this article and R code in GitHub.

609

610 **There are no conflicts of interest.**

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892 Captions

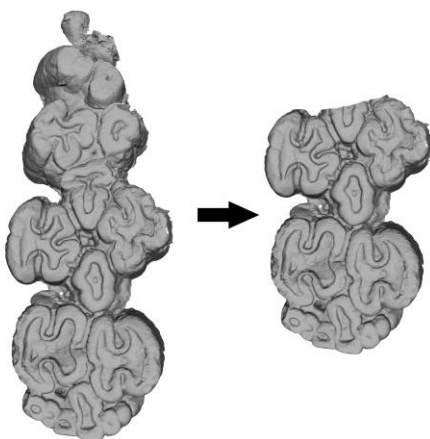
Table 1. Means for every genus/species from the analyses. Mean surface slope (MSS) analysed with R-package “rgdal” and SurferManipulator (SM), relief index with ArcGIS, angularity with SM, sharpness index with ArcGIS, Dirichlet normal energy (DNE) with R-package “molaR”, orientation patch count (OPC) with SM (50 rows), “rgdal”(50 rows) and “molaR”. M3 = upper third molar, m3 = lower third molar.

Genus/species	n (M3/ m3)	MSS (rgdal)	MSS (SM)	MSS (molaR)	Relief index (ArcGIS)	Angularity (SM)	Sharpness index (ArcGIS)	DNE (molaR)	OPC 50 (SM)	OPC 50 (rgdal)	OPC (molaR)
<i>Listriodon</i>	6/7	43.7	46.8	56.4	2.37	87.5	0.36	300	47	41	117
<i>N. euilus</i>	6/0	38	38.8	54.8	2.19	88.3	0.27	878	101	82	275
<i>N. scotti</i>	2/1	33.4	34	47.1	1.87	88.4	0.21	1470	101	121	368
<i>K. heseloni</i>	6/1	35.8	37	52.1	2.17	88.1	0.26	553	108	87	253
<i>M. andrewsi</i>	5/4	31.5	32.2	54.1	1.93	88.5	0.18	1025	113	98	320
<i>Ph. africanus</i>	15/15	29.2	31.3	45.2	1.76	88.4	0.23	293	113	97	270
<i>Potamochoerus</i>	15/15	37.5	39.8	50.2	2.12	87.5	0.29	307	67	56	152
<i>S. scrofa</i>	15/15	36.9	38.6	51.5	2.11	87.9	0.27	656	80	63	185
<i>Babyrousa</i>	5/5	34.9	38.6	46.9	2.01	87.7	0.28	249	62	49	140
<i>H. meinertzhageni</i>	4/4	42.3	45.5	58.8	2.48	87.8	0.34	366	67	59	143

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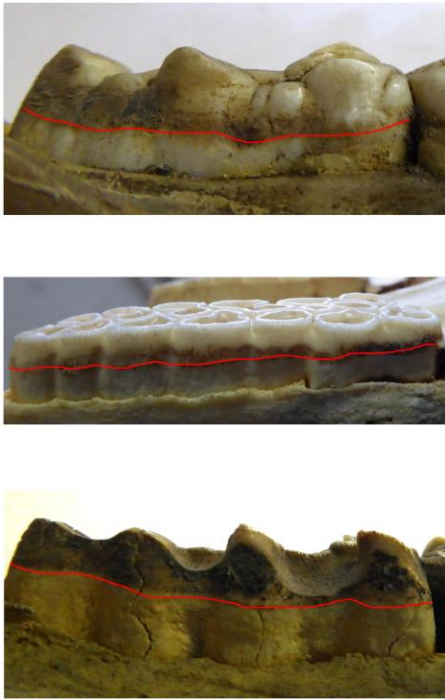
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898 Figure 1. Cropping was done immediately after the second cusp pair, going from the mesial towards
 899 the distal direction.

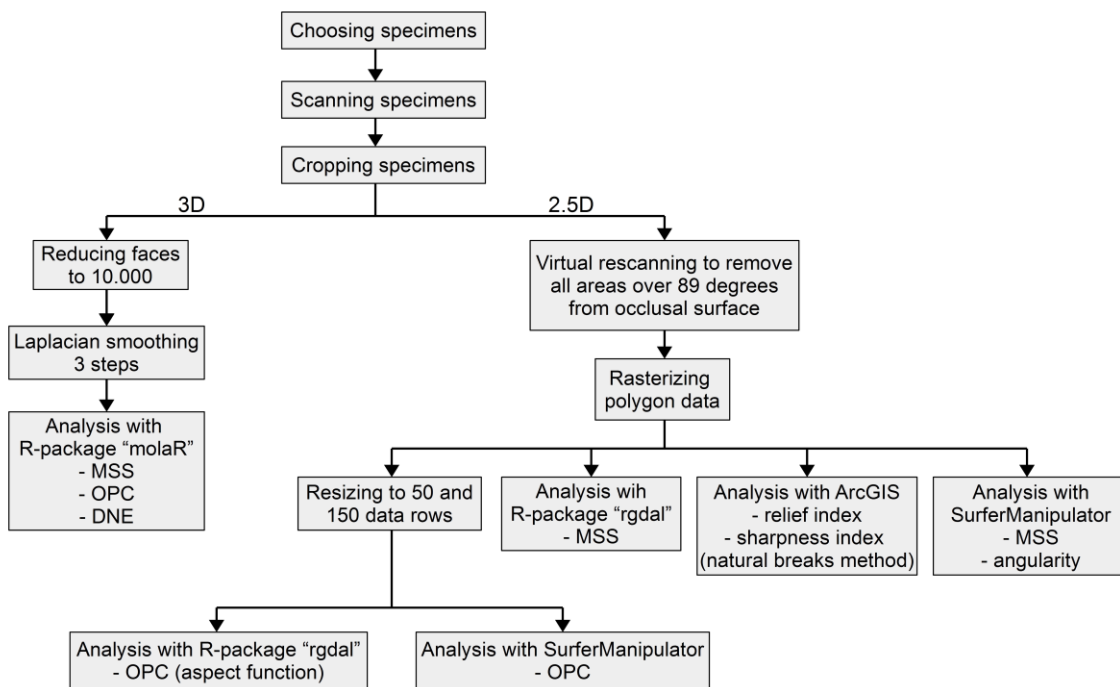
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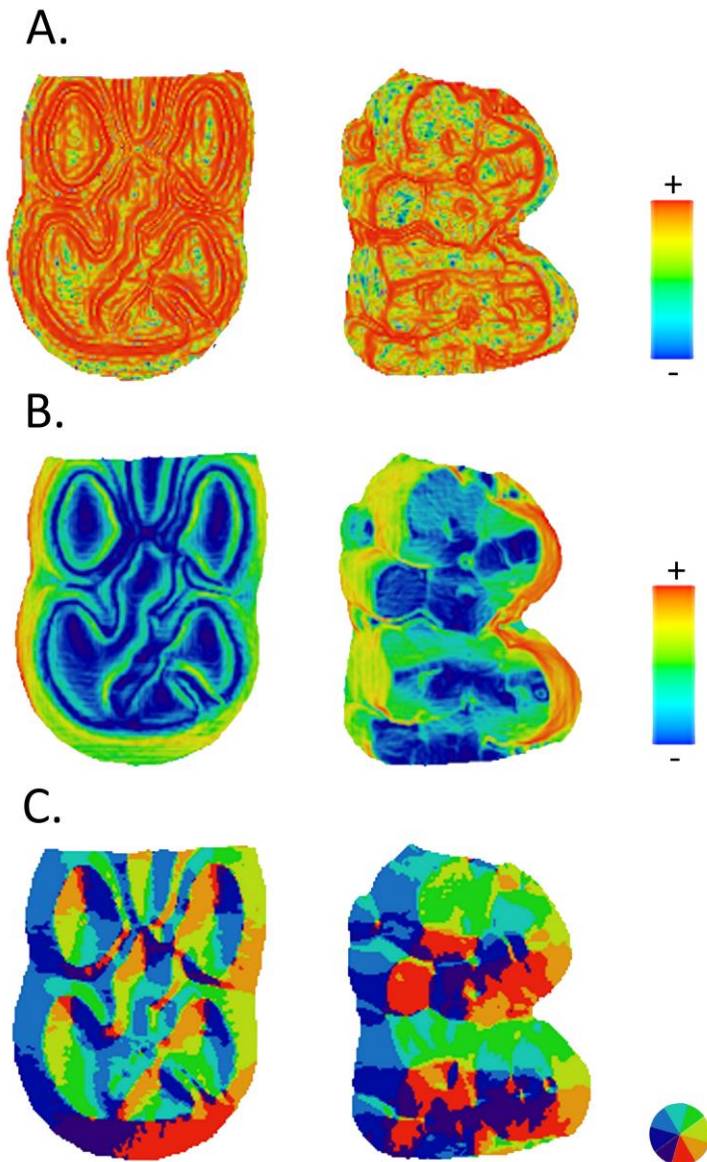
Figure 2. Cropping tooth surface under the coloured plaque.



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Figure 3. Workflow chart. MSS = mean surface slope, OPC = orientation patch count, DNE = Dirichlet normal energy.

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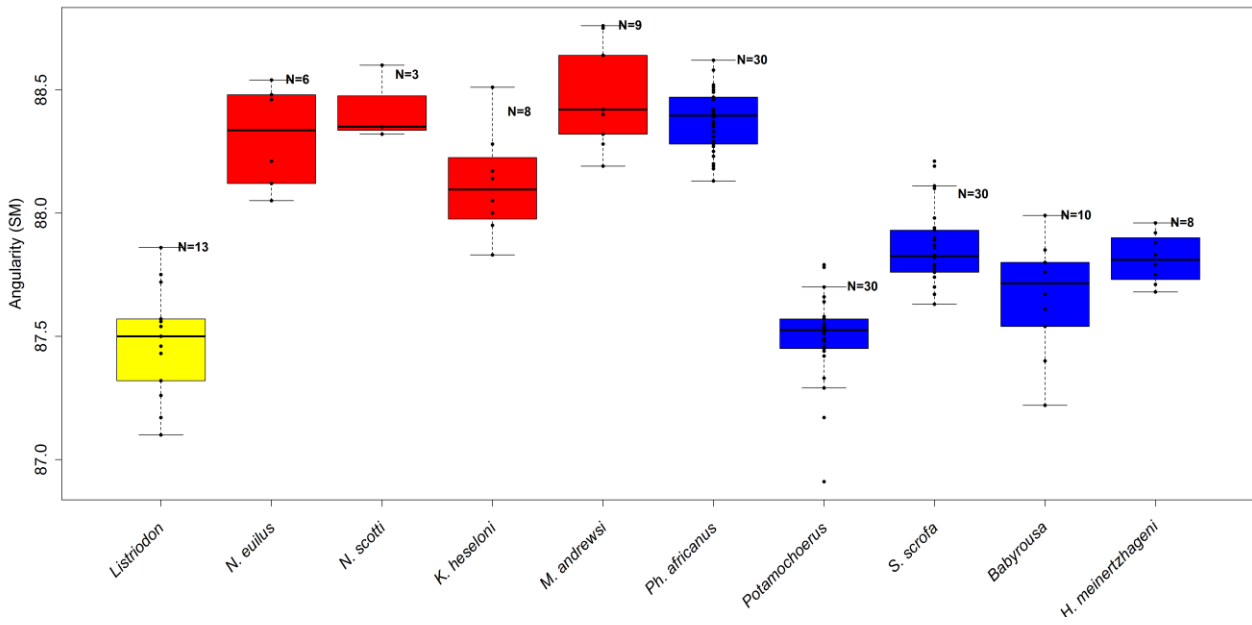
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914 Figure 4. Visual representation of A. angularity, B. mean surface slope and C. orientation patch
 915 count. In A. and B. colors represent low values in blue to high values in red. In C. colors represent
 916 different directions according to the pie legend. Teeth on the left are *Ph. africanus* and on the right
 917 *Potamochoerus*.

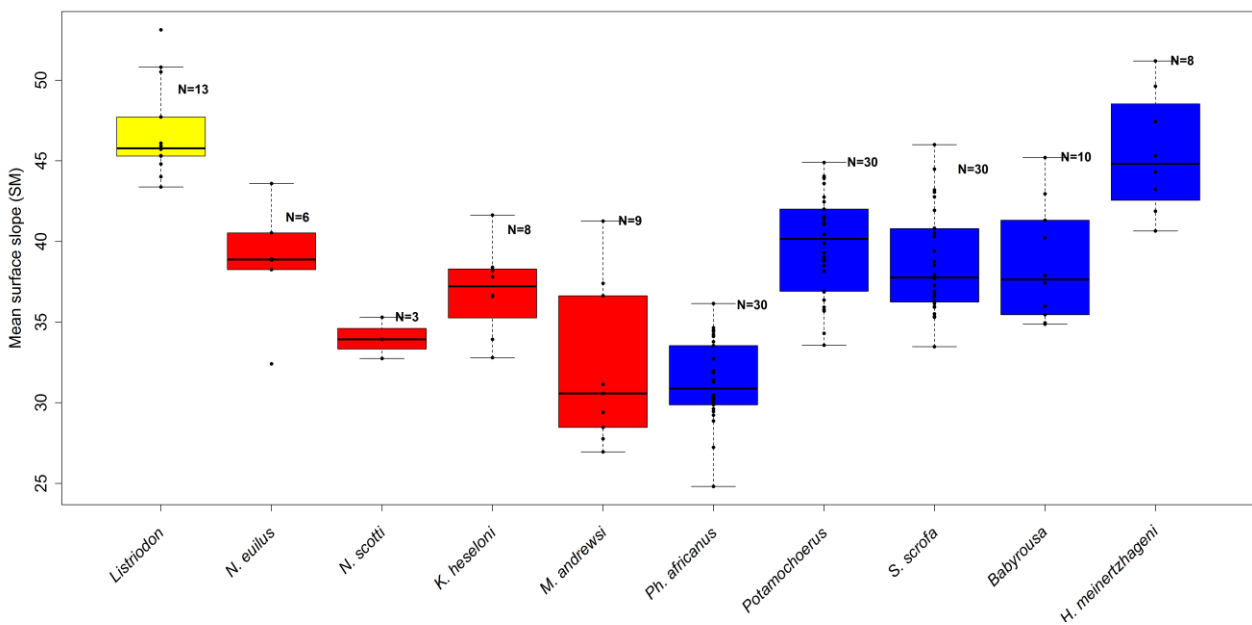
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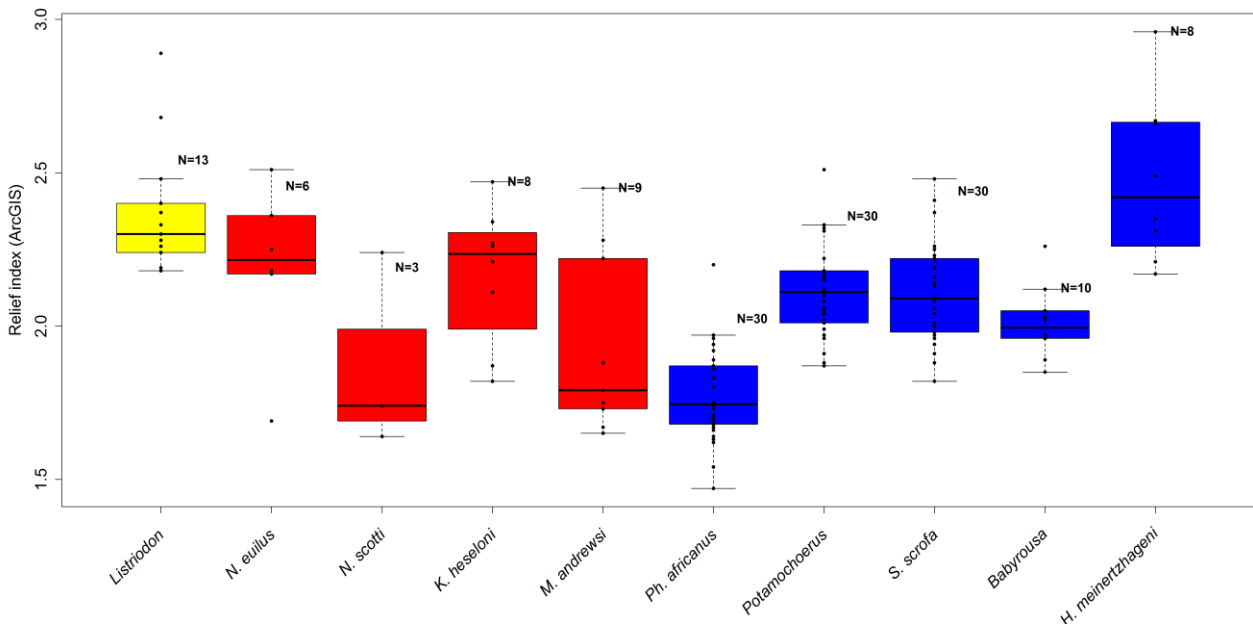
Figure 5. Angularity analysed with SurferManipulator. In the box plots, the lowest boundary of the box indicates the 25th percentile, a black line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the maximum and minimum values. Points above and below the whiskers indicate possible outliers. N indicates the number of specimens. In colour version: yellow = Miocene suids, red = the Turkana Basin suids, blue = extant suids.



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Figure 6. Mean surface slope (MSS) analysed with SurferManipulator. In the box plots, the lowest boundary of the box indicates the 25th percentile, a black line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the maximum and minimum values. Points above and below the whiskers indicate possible outliers. N indicates the number of specimens. In colour version: yellow = Miocene suids, red = the Turkana Basin suids, blue = extant suids.

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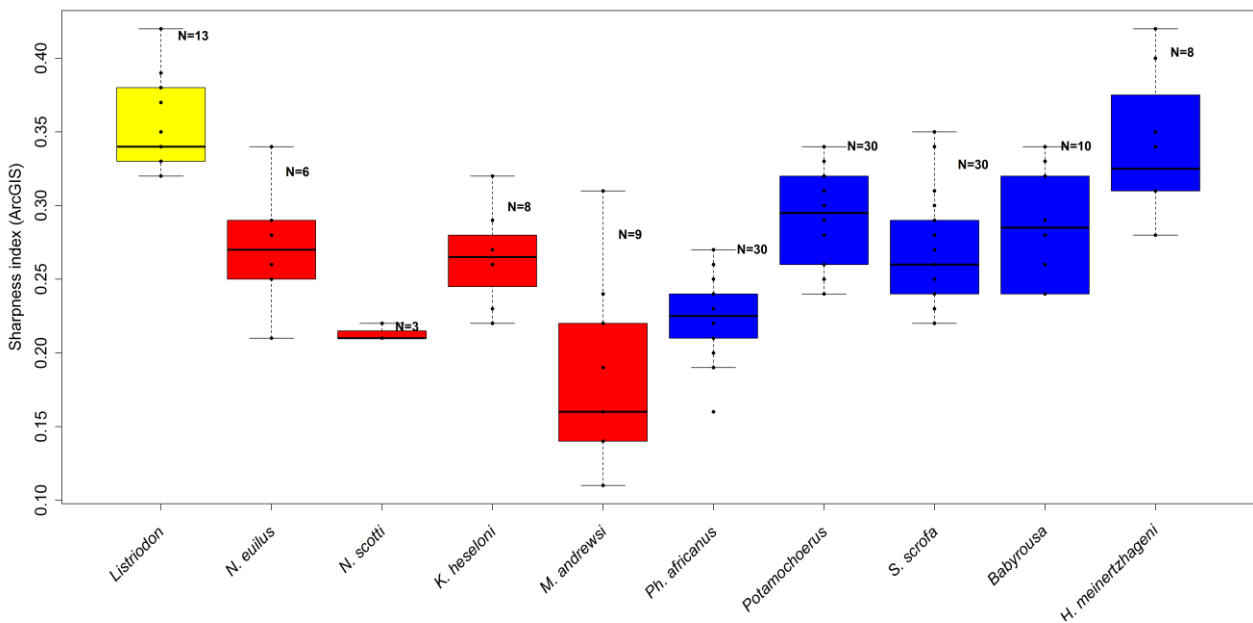
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Figure 7. Relief index analysed with ArcGIS. In the box plots, the lowest boundary of the box indicates the 25th percentile, a black line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the maximum and minimum values. Points above and below the whiskers indicate possible outliers. N indicates the number of specimens. In colour version: yellow = Miocene suids, red = the Turkana Basin suids, blue = extant suids.



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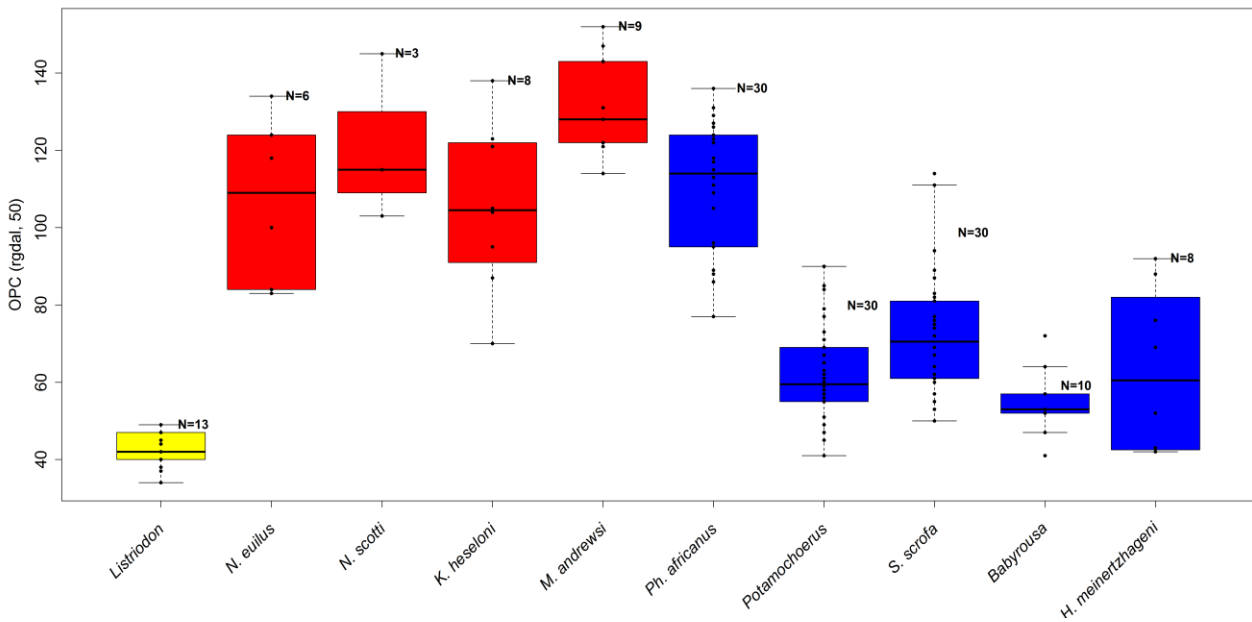
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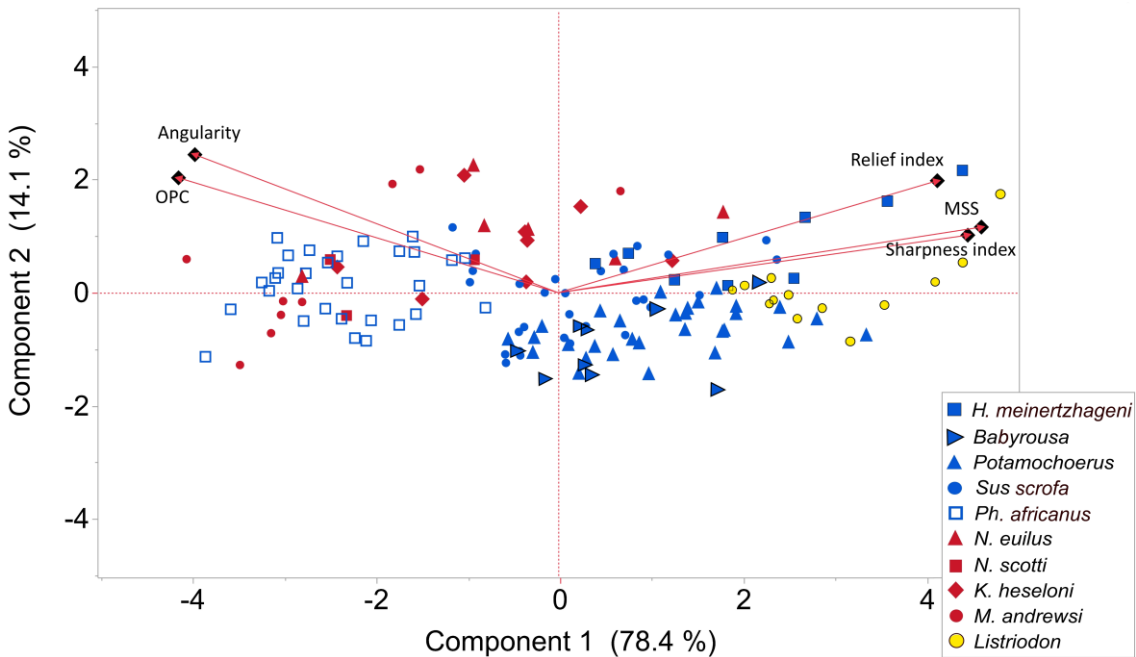
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Figure 8. Sharpness index analysed with ArcGIS (natural breaks method). In the box plots, the lowest boundary of the box indicates the 25th percentile, a black line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the maximum and minimum values. Points above and below the whiskers indicate

951 possible outliers. N indicates the number of specimens. In colour version: yellow = Miocene suids,
 952 red = the Turkana Basin suids, blue = extant suids.
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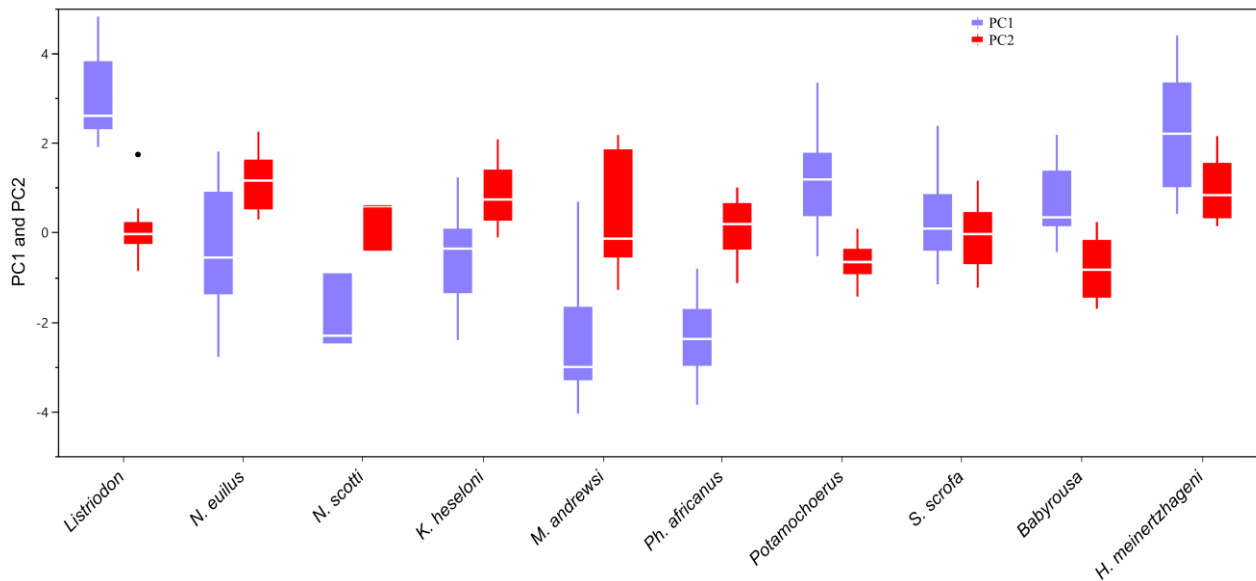


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 955 Figure 9. Orientation patch count (OPC) for 50 data rows, analysed with SurferManipulator. In the
 956 box plots, the lowest boundary of the box indicates the 25th percentile, a black line within the box
 957 marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above
 958 and below the box indicate the maximum and minimum values. Points above and below the
 959 whiskers indicate possible outliers. N indicates the number of specimens. In colour version: yellow
 960 = Miocene suids, red = the Turkana Basin suids, blue = extant suids.
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 964 Figure 10. Principal component analysis (PCA) with angularity (SurferManipulator), mean surface
 965 slope (MSS, SurferManipulator), relief index (ArcGIS), sharpness index (ArcGIS) and OPC (50

966 rows, SurferManipulator). In colour version extant specimens have blue markers, the Turkana Basin
 967 specimens red markers and Miocene specimens yellow markers.
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972 Figure 11. Principal component 1 (PCA1) and 2 (PCA2) values for each suid group analysed. In the
 973 box plots, the lowest boundary of the box indicates the 25th percentile, a white line within the box
 974 marks the median, and the upper boundary of the box indicates the 75th percentile. Line ends above
 975 and below the box indicate the maximum and minimum values. Points above and below the line
 976 ends indicate possible outliers.
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