

1 **Habitudes alimentaires des *Kolpochoerus* de la Formation de Shungura**
2 **(basse vallée de l'Omo, Éthiopie) : apports de l'analyse des textures de**
3 **micro-usure dentaire**

4 **New insights on feeding habits of *Kolpochoerus* from the Shungura**
5 **Formation (Lower Omo Valley, Ethiopia) using dental microwear**
6 **textures**

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27 **Résumé :**

28 Au Néogène et au Quaternaire, les suidés africains présentent des changements
29 morphologiques dentaires considérés comme des adaptations à des alimentations de plus
30 en plus spécialisées sur les graminées, notamment dans le genre *Kolpochoerus*. Ils tendent
31 à présenter des troisièmes molaires allongées et un certain degré d'hypsodontie, suggérant
32 une consommation croissante d'herbes abrasives. Toutefois, les changements
33 morphologiques les plus importants ne sont pas synchrones avec la consommation accrue
34 de plantes en C₄, telles que les graminées. À ce jour, seules quelques études ont appliqué
35 l'analyse des textures de micro-usure dentaire (DMTA), qui renseigne sur les propriétés
36 mécaniques de l'alimentation, à des spécimens de *Kolpochoerus*. En outre, aucune ne
37 s'est intéressée à des spécimens de la Formation de Shungura (basse vallée de l'Omo,
38 Éthiopie), qui constitue l'enregistrement le plus complet du Pliocène récent au Pléistocène
39 ancien en Afrique orientale.

40 Nous avons étudié les textures de micro-usure dentaire (DMT) chez quatre genres
41 de suidés actuels ayant des régimes alimentaires contrastés : les herbivores *Phacochoerus*
42 et *Hylochoerus*, et les omnivores *Potamochoerus* et *Sus*. Nos résultats montrent que leurs
43 DMT reflètent leurs différentes habitudes alimentaires. Nous avons ensuite étudié les
44 DMT de 68 spécimens de *Kolpochoerus* de la Formation de Shungura et datant d'environ
45 2,9 Ma à 1,0 Ma. Leurs DMT diffèrent des suidés actuels, mais certaines similitudes avec
46 *Phacochoerus* sont observées. En lien avec les études précédentes, nous proposons que
47 leurs DMT reflètent une consommation importante de plantes herbacées (graminées ou
48 non), avec des préférences pour les herbacées jeunes et peu abrasives.

49 **Mots-clés :** abrasion, niche alimentaire, écologie, paléo-environnement, Plio-Pléistocène,
50 analyse fractale échelle-dépendante (SSFA)

51 **Abstract:**

52 During the Neogene and the Quaternary, African suids show dental morphological
53 changes considered to reflect adaptations to increasing specialization on graminivorous
54 diets, notably in the genus *Kolpochoerus*. They tend to exhibit elongated third molars and
55 some degree of hypsodonty, suggesting increasing consumption of abrasive grasses.
56 However, the most significant morphological changes are not synchronous with the
57 increased consumption of C₄ plants, such as graminoids. To date, only a few studies have
58 applied dental microwear texture analysis (DMTA), which provides information on the
59 mechanical properties of the diet, to specimens of *Kolpochoerus*. In addition, none has
60 yet focused on specimens from the Shungura Formation (Lower Omo Valley, Ethiopia),
61 which is the most complete Late Pliocene to Early Pleistocene record in eastern Africa.

62 We studied dental microwear textures (DMT) in four genera of extant suids with
63 contrasting diets: the herbivores *Phacochoerus* and *Hylochoerus*, and the omnivores
64 *Potamochoerus* and *Sus*. Our results show that their DMT reflect their different feeding
65 habits. We then studied the DMT of 68 *Kolpochoerus* specimens from the Shungura
66 Formation dating from about 2.9 Ma to 1.0 Ma. Their DMT differ from extant suids, but
67 some similarities with *Phacochoerus* are observed. In line with previous studies, we
68 propose that their DMT reflect a high consumption of herbaceous plants (graminoids and
69 non-graminoids), with preferences for young, low-abrasive grasses.

70 **Keywords:** abrasion, dietary niche, ecology, paleoenvironment, Plio-Pleistocene, scale-
71 sensitive fractal analysis (SSFA)

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73

74 1. INTRODUCTION

75 Reconstructing past dietary habits among mammals is crucial for a better
76 understanding of the environmental conditions in which extinct species lived, and how
77 they shared ecological resources (Andrews *et al.* 1979; Fortelius *et al.* 2002). It also helps
78 to understand the potential selective pressures that drove the evolution of dental
79 phenotypes. Indeed, mammals generally exhibit teeth that are adapted to their diet,
80 optimizing not only efficient processing of food items but also durability against wear
81 (Hiemae 2000). With the expansion of grasslands during the Neogene and the
82 Quaternary, mammals with dental morphologies adapted to the consumption of large
83 amounts of abrasive grasses, such as high-crowned molars, become more abundant (Janis
84 2008). The evolutionary history of African suids, a rapidly evolving group, also show this
85 trend towards dental morphologies that are assumed to be adapted to increasing
86 graminivory (i.e. main consumption of abrasive graminoids, or grasses and sedges).
87 These characteristics appear multiple times in several suid genera, most likely resulting
88 from convergent evolution (Harris & White 1979; Souron *et al.* 2015a). This is
89 particularly observed during the Late Pliocene and the Pleistocene in two suine lineages,
90 *Metridiochoerus-Phacochoerus* (warthogs) and *Kolpochoerus-Hylochoerus* (bushpigs)
91 which are commonly represented in faunal assemblages (Rannikko *et al.* 2017;
92 Lazagabaster *et al.* 2018). Thus, in addition to their relevance for biostratigraphic
93 correlations (White & Harris 1977; Cooke 2007), suids also have a potential for
94 paleoenvironmental reconstructions (Harris & Cerling 2002; Bishop *et al.* 2006;
95 Lazagabaster 2019). However, the elongated molars displayed by African suids, with
96 extra cusps in the distal part, contrast with the ones observed among graminivorous
97 ruminants, which exhibit hypsodont molars that are relatively short mesio-distally (e.g.,

98 Janis 2008; Madden 2014). Although both dental innovations have been linked to
99 increasing graminivory, elongated molars are probably associated with improved
100 efficiency for fragmenting small foods whereas hypsodont molars are rather linked to
101 increased tooth durability against wear (Lucas 2004; Souron 2017; Yang *et al.* 2022).
102 Besides, changes in third molar length and height are not similar nor synchronous in the
103 different suid clades. For example, in *Kolpochoerus*, we mostly observe an increase in
104 molar length rather than in molar height, whereas in *Metridiochoerus*, molar height
105 increases significantly with length (Harris & White, 1979; Cooke, 2007). Moreover,
106 asynchronous changes in dental morphology and stable carbon composition (Harris &
107 Cerling 2002; Bibi *et al.* 2013; Souron 2017), notably in *Kolpochoerus*, highlight the need
108 for further investigation of suid paleoecology using a multi-proxy approach in order to
109 better understand which factors favored the selection of such dental morphologies, and
110 by which mechanisms.

111 The extinct genus *Kolpochoerus* has a promising potential to contribute to a better
112 understanding of the relationships between morphological evolution, dietary changes, and
113 environmental changes among the Suidae. Indeed, it is one of the most abundant suid taxa
114 with a wide geographic distribution, and one of the most diverse, notably in terms of
115 feeding habits (Harris & White 1979; Brunet & White 2001; Bishop *et al.* 2006; Haile-
116 Selassie & Simpson 2013; Souron 2012). Particularly, fossils from the Shungura
117 Formation have played an important role in our understanding of East African
118 environments during the Plio-Pleistocene. The Shungura Formation is located in the
119 Lower Omo Valley in southwestern Ethiopia. It is the most complete stratigraphic and
120 paleontological record from the Late Pliocene to Early Pleistocene in eastern Africa, with
121 sediments deposited almost continuously from ca. 3.75 Ma to ca. 1.0 Ma. It is subdivided

122 into 12 members of sedimentary deposits: Basal, A to H and J to L, whose ages were
123 determined by using radiochronology of interspersed volcanic tuffs and
124 magnetostratigraphy (Heinzelin 1983; Feibel *et al.* 1989; McDougall & Brown 2006,
125 2008; McDougall *et al.* 2012; Kidane *et al.* 2014). Since the early 1930s, the Shungura
126 Formation has been intensively surveyed through several research expeditions by C.
127 Arambourg (Arambourg 1934, 1943), the International Omo Research Expedition (IORE:
128 Howell 1968; Coppens 1975), and the Omo Group Research Expedition (OGRE:
129 Boisserie *et al.* 2008). It has yielded ca. 57,000 fossil vertebrate specimens, as well as
130 numerous lithic assemblages. On average, suids represent 10.3 % of the Shungura faunal
131 remains (Omo database), including a large proportion of *Kolpochoerus*, almost all
132 attributed to the lineage *K. limnetes*/*K. aff. paiceae* (following the same taxonomic
133 framework as described in Bibi *et al.* 2018; Brink *et al.* 2022) and to *K. afarensis* at the
134 base of the sequence (Souron 2012). In the lineage *K. limnetes*/*K. aff. paiceae*, the
135 progressive lengthening of third molars from about 2.7 Ma, along with increasing
136 complexity in occlusal surface morphology (?) has been related to a specialization toward
137 a graminivorous diet (Harris & White 1979; Cooke 1985; Kullmer 1999). Later studies
138 on stable carbon isotopic compositions are congruent with the hypothesis of a strong
139 graminivorous component in the diet (Harris & Cerling 2002; Bibi *et al.* 2013; Negash *et*
140 *al.* 2020). However, these morphological changes are not synchronous with the increasing
141 consumption of C₄ plants, i.e. mostly graminoids (such as grasses and sedges) and
142 amaranths. At Shungura, a notable shift toward a C₄-dominated diet is observed from
143 Member B to Member C (Bibi *et al.* 2013; Negash *et al.* 2020) whereas dental
144 morphological changes are rather progressive, with a shift at about 1.5 Ma to much more
145 derived species with more elongated and hypsodont third molars (Souron 2012). In

146 addition, two recent studies suggested that *Kolpochoerus* more likely had a less abrasive
147 diet than typical graminivorous suids and might have favored more mesic habitats
148 (Rannikko *et al.* 2020; Yang *et al.* 2022). Thus, more studies are needed for a better
149 understanding of *Kolpochoerus* paleoecology.

150 Because dietary proxies record the diet over different timescales, it is not
151 surprising that dental morphology and enamel stable carbon composition do not reflect
152 similar dietary habits (Davis & Pineda Munoz 2016). As already pointed out for extinct
153 African suids (Souron 2017), it is crucial to have a more integrative approach combining
154 different and complementary paleoecological proxies to improve inferences of past diets,
155 to better understand the relationships between feeding habits, morphology, and
156 environmental constraints. Among paleoecological proxies, dental microwear is highly
157 dependent on the physical properties of masticated food items (e.g., Lucas *et al.* 2013,
158 2014; Daegling *et al.* 2016; Merceron *et al.* 2016), and records the diet over a short
159 timescale, few weeks or months before death (Teaford & Oyen 1989; Teaford *et al.* 2017,
160 2021; Winkler *et al.* 2020). In recent years, Dental Microwear Texture Analysis (DMTA)
161 has proved its efficiency in detecting dietary differences between species (e.g., R. S. Scott
162 *et al.* 2006, 2012; J. R. Scott 2012; Schulz *et al.* 2013; Merceron *et al.* 2021; Hullot *et al.*
163 2021), as well as small variations within species or populations (Merceron *et al.* 2010,
164 2014; Berlioz *et al.* 2017; Percher *et al.* 2017). Thus, this methodology has been widely
165 employed to infer past dietary habits (e.g., Ungar *et al.* 2008, 2017; Berlioz *et al.* 2018;
166 Blondel *et al.* 2018, 2022; Martin *et al.* 2018; Merceron *et al.* 2018, 2021; Hullot *et al.*
167 2021). Nevertheless, to date, only few studies have applied DMTA on extant or extinct
168 suids (Souron *et al.* 2015b; Ungar *et al.* 2017; Yamada *et al.* 2018, 2021; Lazagabaster

169 2019; Louail *et al.* 2021, 2022) and none has yet focused on DMT of *Kolpochoerus* from
170 the Shungura Formation.

171 This is the first study that measures the DMT variations on a large sample of extant
172 suids and extinct *Kolpochoerus* from the Shungura Formation, including specimens from
173 Member C to Member L. We expand the extant DMT baseline developed by Souron *et*
174 *al.* (2015b) and Lazagabaster (2019) by including larger samples of African suids
175 (particularly *Hylochoerus*) with different dietary habits. We also discuss inter-specific
176 differences within *Phacochoerus* and *Potamochoerus* genera, as well as intra-specific
177 differences in Eurasian wild *Sus scrofa*. Then, considering the patterns observed on extant
178 suids, we explore the DMT variations in specimens attributed to the lineage *Kolpochoerus*
179 *limnetes*/*K. aff. paiceae* through the Shungura sequence to contribute to our knowledge
180 of their past dietary habits.

181

182 **2. MATERIAL AND METHODS**

183 **2.1. Sample and dietary habits of extant suids**

184 We considered a total of 102 extant wild specimens, belonging to four suid genera
185 and six species: *Hylochoerus* (*H. meinertzhageni*, n = 21), *Phacochoerus* (n = 23; n = 9
186 for *Ph. africanus* and n = 14 for *Ph. aethiopicus*), *Potamochoerus* (n = 33; n = 15 for *Po.*
187 *porcus* and n = 18 for *Po. larvatus*) and *Sus* (*S. scrofa*, n = 25). For *Sus*, we used two wild
188 boar populations from France (n = 6) and from the Białowieża Forest in Poland (n = 19).
189 Both areas are closed mixed forest, but the former is characterized by an oceanic climate
190 whereas the latter has a much more continental climate with limited human impact. The
191 specimens are housed in the following institutions: Musée Royal de l’Afrique Centrale,

192 Tervuren, Belgium (MRAC); Polish Academy of Sciences in Białowieża, Poland (MRI
193 PAS); The Ethiopian Heritage Authority, collections of comparative anatomy, Addis
194 Ababa, Ethiopia (MCA); Museo Zoologico dell'Università di Firenze, Italy (MZUF);
195 Naturhistorisches Museum Basel, Switzerland (NMB), Laboratory Paleontology
196 Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM) and Institut National de
197 Recherche pour l'Agriculture, l'Alimentation et l'Environnement, France (INRAE
198 Occitanie-Toulouse).

199 Taxonomic identifications at the specific level were verified both based on the
200 craniomandibular and dental morphology of the specimens and on their geographical
201 origin. This step is crucial as museum labels frequently indicate incorrect identifications
202 at the specific level, resulting from previous taxonomic practices. Indeed, the extant
203 species of *Phacochoerus* and *Potamochoerus* were long lumped into single species,
204 respectively called *Ph. aethiopicus* and *Po. porcus* (Oliver 1993; Grubb & d'Huart 2010)
205 and the confusion remains pervasive in the current literature and museum collections. The
206 two extant species of *Phacochoerus* are sympatric in some parts of Ethiopia, Somalia,
207 and especially in Kenya (de Jong *et al.* 2023) but they are easily distinguished from each
208 other by several discrete and continuous morphological characters of the cranium,
209 mandible, and dentition (e.g., d'Huart & Grubb 2005; Groves & Grubb 2011; Souron
210 2012, 2015, 2016). The two extant *Potamochoerus* species are overall geographically
211 well separated but possibly sympatric in some parts of Democratic Republic of Congo,
212 Burundi, and Rwanda (Leslie, Jr. & Huffman 2015). They are morphologically more
213 similar to each other than the two species of warthogs and are mostly distinguished based
214 on shape and size differences of the skull and differences in first upper premolar



215 prevalence (Souron 2012; Boisserie *et al.* 2014). Specimen numbers and their geographic
216 proveniences are provided in the Supplementary Material (ESM1, Table S1).

217 None of the extant suid specimens are associated to individual dietary data (such
218 as stomach contents or field observations), but the dietary habits of these extant taxa have
219 been largely investigated – although the giant forest hog (*H. meinertzhageni*) and the
220 desert warthog (*Ph. aethiopicus*) are less known. Extant wild *Sus scrofa* and the two
221 species of *Potamochoerus* are generalized omnivores that eat a wide array of food items
222 such as fruits, seeds, leaves, grasses, barks, underground storage organs (USOs), fungi,
223 animal matter, agricultural crops, feces, as well as human garbage or inorganic matter.
224 Their dietary habits vary greatly depending on the geographic area, seasonality, and food
225 availability (*Sus scrofa*: Giménez-Anaya *et al.* 2008; Keuling *et al.* 2017; *Potamochoerus*
226 *porcus* and *Po. larvatus*: Skinner *et al.* 1976; Breytenbach & Skinner 1982; Seydack
227 1990, 2017; Harris & Cerling 2002; Melletti *et al.* 2017). These omnivorous species
228 display molars that are bunodont and brachyodont, in contrast to the two species of
229 *Phacochoerus* and *Hylochoerus meinertzhageni*. The former has very elongated and
230 hypsodont third molars with numerous cusps or pillars, and the latter displays a
231 bunolophodont pattern and moderately hypsodont molars (e.g., Owen 1850; Harris &
232 White 1979; Souron *et al.* 2015a; Souron 2017; Lazagabaster *et al.* 2021; see also Fig. 1).

233 Few extant wild suid species are considered as herbivorous: the two species of
234 *Phacochoerus* and, to a lesser extent, *H. meinertzhageni*. These taxa mainly feed on
235 fibrous vegetal matter, such as grasses (graminoids) and forbs (non-graminoids), and
236 incorporate fruits and roots in their diet to a lesser extent (*Ph. africanus* and *Ph.*
237 *aethiopicus*: Harris & Cerling 2002; Treydte *et al.* 2006; Butynski & de Jong 2017; de
238 Jong & Butynski 2017; Edossa *et al.* 2021; *H. meinertzhageni*: d’Huart 1978; Harris &

239 Cerling 2002; Cerling & Viehl 2004; d’Huart & Kingdon 2013; Reyna-Hurtado *et al.*
240 2017). Species of *Phacochoerus* are the most specialized, feeding mostly on short, green,
241 tropical grasses and consuming all plant parts, including underground storage organs.
242 *Hylochoerus meinertzhageni* has been less studied than the three other genera, but
243 previous work suggests it is more likely an herbivorous mixed feeder (e.g. d’Huart &
244 Kingdon 2013; Souron *et al.* 2015b; Mekonnen *et al.* 2018). In contrast to other suids, the
245 rooting behavior in this species is strongly reduced and the portion of subterranean foods
246 in its diet is low.

247

248 **2.2. Sample of *Kolpochoerus* from Shungura**

249 We analyzed a total of 68 specimens from the Shungura Formation that belong to
250 the extinct genus *Kolpochoerus* and that do not show any apparent alteration (see section
251 3.2). All specimens are attributed to the lineage *K. limnetes*/*K. aff. paiceae*. The sample
252 includes specimens from members C (n = 12), E (n = 13), F (n = 8), G (n = 15), H (n =
253 4), J (n = 4), and L (n = 12), representing a time period from ca. 2.76 Ma to 1.0 Ma. We
254 discarded members B, D, and the upper sequence of Member G for which only one or
255 two specimens were available for the study. Specimen numbers and their stratigraphic
256 provenance are provided in the Supplementary Material (ESM1, Table S2).

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258 **2.3. Surface acquisition and processing**

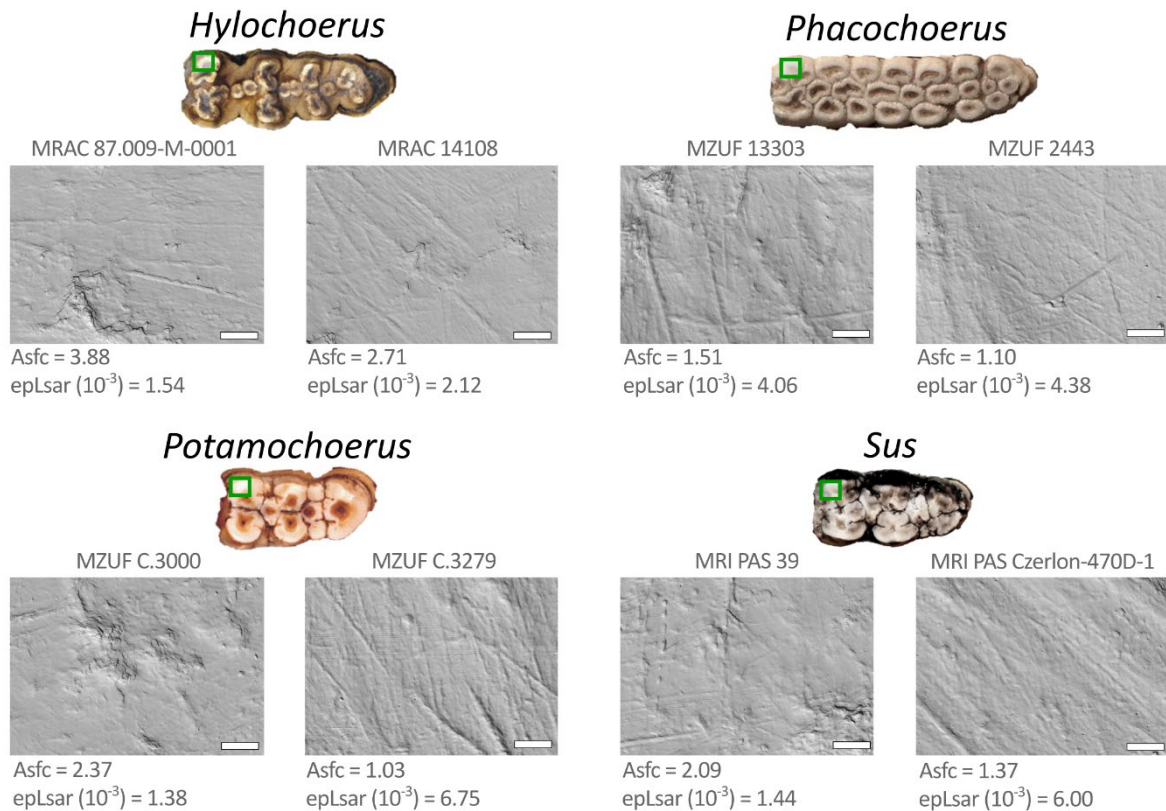
259 We considered wear facets associated with the shearing phase I of mastication.
260 All suitable upper and lower first, second and third molars were included in this study.
261 Each facet was molded with polyvinylsiloxane (Regular Body President, ref. 6015 - ISO

262 4823, medium consistency, polyvinylsiloxane addition-type, Coltene Whaledent). For
263 each specimen, all suitable non-overlapping worn areas on shearing facets were scanned
264 in order to encompass intra-facet variations. We scanned one to fourteen surfaces for each
265 specimen (Tables S1 and S2). Each surface was scanned as flat as possible using
266 “TRIDENT”, a white-light confocal profilometer Leica DCM8 with a 100× objective
267 housed at the PALEVOPRIM lab, CNRS and University of Poitiers, France (Numerical
268 aperture = 0.90; Working distance = 0.9 mm; Leica Microsystems). Each scanned surface
269 was pre-processed using LeicaMap v8.0 (Leica Microsystems; MountainsMap, Digital
270 Surf). Non-measured points (< 3 %) were filled with a smooth shape (Laplacian filter)
271 calculated from neighboring points. We applied a morphological filter to remove artifacts
272 such as aberrant peaks (Merceron *et al.* 2016) and surfaces were then leveled. A 140 ×
273 100 μm (1086 × 776 pixels) leveled area was automatically generated at the center of
274 each surface. In case of adhering dirt particles, the extracted area was shifted aside to get
275 the particles out of the field of selection. In the worst cases (9 % of surfaces in extant
276 suids and 2 % in *Kolpochoerus*), we manually erased the particles using a user-defined
277 contour and replaced with a smooth shape calculated from neighboring points.

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279 **2.4. Procedure for selecting wear surfaces of fossil specimens**

280 We explored the diversity of surface textures among extant suid taxa as a baseline
281 for selecting wear surfaces of specimens of *Kolpochoerus* without apparent, or potential,
282 taphonomic alterations. Fig. 1 shows the variations in surface textures within extant suid
283 taxa, being more or less complex and more or less anisotropic (see 3.3. for details on
284 texture parameters).



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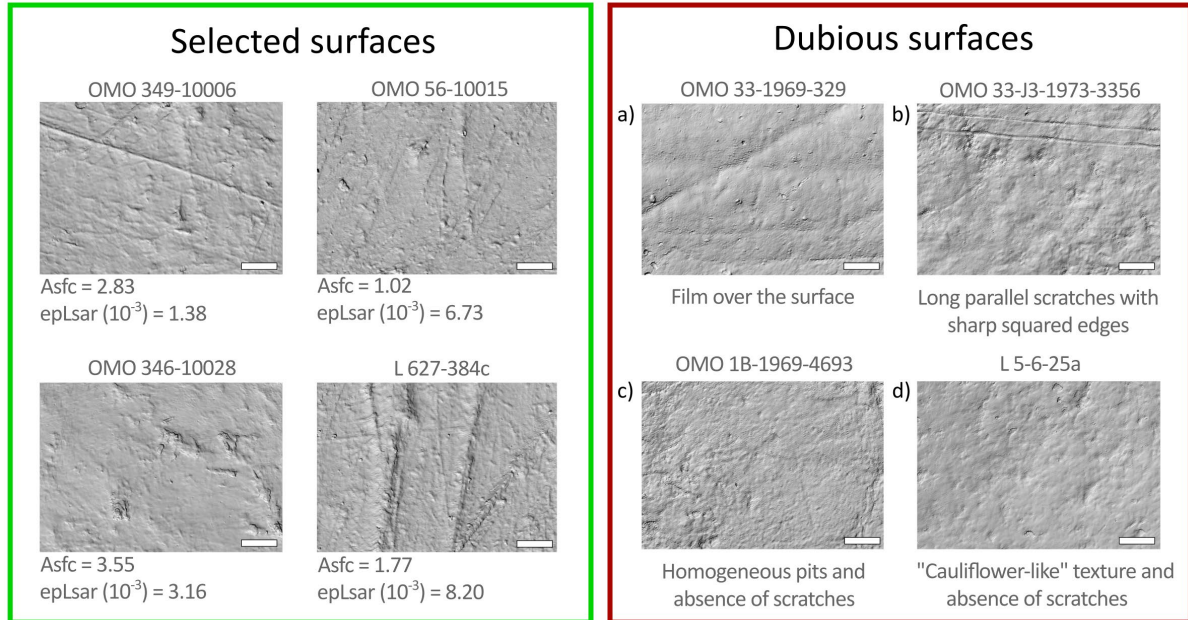
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Fig. 1. Photosimulations of shearing facets on extant suid genera illustrating the diversity within taxa in terms of complexity (Asfc) and anisotropy (epLsar). The green squares on molars of each taxon indicate the location of a shearing facet on a right lower third molar. Scalebar: 20 μ m.

Moreover, potentially altered surfaces of *Kolpochoerus* were identified, and discarded, using the following characteristics (see also Weber *et al.* 2021): a) presence of a thin film over the surface that masks the microwear marks; b) long and parallel scratches that run over the surface and with sharp squared edges; c) textures with homogeneous small pits and no visible scratch; and/or d) homogeneous texture with a “cauliflower-like” appearance and no visible scratch. Fig. 2 shows an example of each of these characteristics, as well as the variations in unaltered surfaces within *Kolpochoerus*. Photosimulations and false color elevation maps of all the surfaces included in this study are provided in the Supplementary Material (ESM2, ESM3).

Kolpochoerus



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Fig. 2. Photosimulations of shearing facets on *Kolpochoerus*. Selected surfaces (left) show relatively heterogeneous texture with pits and scratches of different sizes and different orientations. Dubious surfaces (right) were discarded when they show: a) a thin film over the surface that masks the dietary marks; b) long and parallel scratches that run over the surface and with sharp squared edges; c) a homogeneous texture with pits of similar size and an absence of scratch; d) a texture showing a “cauliflower-like” aspect and an absence of scratch. The green square on the molar of *Kolpochoerus* indicates the location of a shearing facet. Scalebar: 20 μm .

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2.5. Acquisition of textural parameters

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Prior to the acquisition of textural parameters, a second-order least square polynomial surface (PS2) was subtracted from each surface to remove the concavity or convexity of dental facets. We considered three Scale Sensitive Fractal Analysis (SSFA) parameters for this study (calculated using LeicaMap v8.0): Area-scale fractal complexity (Asfc), exact proportion of Length-scale anisotropy of relief (epLsar (Sfrax) in LeicaMap v8.0), and Heterogeneity of Area-scale fractal complexity (HAsfc36, calculated through

315 6×6 blocks in this study). We also computed HAsfc9 and HAsfc81 (calculated through
316 3×3 and 9×9 blocks, respectively) for each surface, but they were discarded because
317 less discriminative than HAsfc36 (see Tables S3 and S8). Complexity (Asfc) measures
318 the surface roughness at a given scale. Anisotropy (epLsar) quantifies the orientation
319 concentration of surface roughness. Heterogeneity of complexity (HAsfc36) measures the
320 variation of complexity of subsampled parts of the surface. Detailed descriptions of these
321 parameters can be found in Scott *et al.* (2006). For each parameter, we considered the
322 mean value of all scanned surfaces per individual (see Tables S1 and S2). As a
323 complement to the figures presented in the main text, we provide boxplots of SSFA
324 parameters for each sample of extant suids and *Kolpochoerus* as Supplementary (ESM1,
325 Fig. S1 to S3).

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327 **2.6. Stable carbon isotopic values of extant suids and *Kolpochoerus* from Shungura**

328 All stable carbon isotopic values on enamel bioapatite of extant African suids and
329 extinct *Kolpochoerus* from the Shungura Formation were compiled from the literature.
330 We used the recently published compilation on extant African suids from Lazagabaster
331 *et al.* (2021), which is available online as supplementary material (see references herein).
332 To our knowledge, no data are available on modern wild and/or free-ranging *Sus scrofa*.
333 All data on *Kolpochoerus* from the Shungura Formation were compiled using two recent
334 studies by Bibi *et al.* (2013) and Negash *et al.* (2020). From this latter study, we only
335 included stable carbon isotopic values of specimens for which element identification is
336 documented in the Omo Database and attributed to a M2 or a M3.

337

338 2.7. Statistical analyses

339 All statistical analyses were conducted in the R statistical environment (R Core
340 Team, 2020, v4.0.3). We performed analyses of variance (one-way ANOVAs) on each
341 SSFA parameter to detect significant differences between extant taxa and *Kolpochoerus*
342 by members (Table S3). The data were box-cox transformed prior to the analyses to meet
343 the assumptions of homoscedasticity and normal distributions of the residual errors. Then,
344 we conducted two post-hoc tests for multiple comparisons (package “agricolae”) to
345 determine the sources of significant variations: Tukey’s Honest Significant Difference
346 (HSD) and Fisher’s Least Significant Difference (LSD, less conservative than HSD) tests
347 (Tables S4 and S5). An alternative non-parametric Kruskal-Wallis test was run for one
348 parameter (epLsar) that did not meet the assumptions of normality of residuals (Table
349 S6), and followed with a post-hoc Dunn’s test (package “dunn.test”; Table S7). We also
350 conducted an ANOVA to detect significant differences between extant *H.*
351 *meinertzhageni*, *Ph. africanus*, *Ph. aethiopicus*, *Po. larvatus*, *Po. porcus* and the two
352 populations of *Sus scrofa* (see Table S8 for descriptive statistics and Table S9 for
353 ANOVA results), followed with both HSD and LSD post-hoc tests (Tables S10 and S11).

354

355 3. ABBREVIATIONS

DMT	Dental microwear textures
DMTA	Dental microwear texture analysis
USO	Underground storage organ
PS2	2 nd -order polynomial surface
SSFA	Scale-sensitive fractal analysis

epLsar	Anisotropy, or exact proportion of Length-scale anisotropy of relief
Asfc	Complexity, or Area-scale fractal complexity
HAsfc	Heterogeneity of area-scale fractal complexity
ANOVA	Analysis of variance
LSD	Least-significant difference, or Fisher's posthoc test
HSD	Honest significant difference, or Tukey's posthoc test

356

357 4. RESULTS

358 4.1. DMTA of extant suid taxa

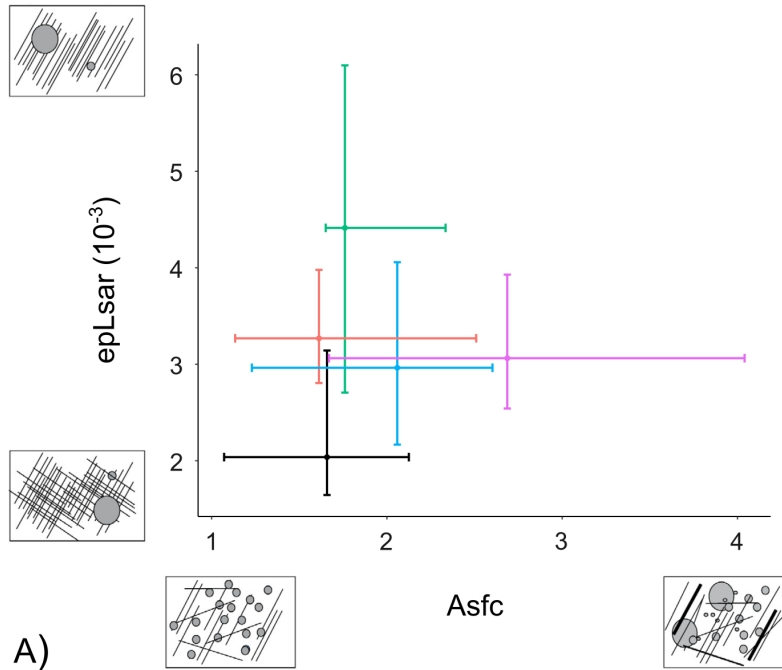
359 At the generic level, *Phacochoerus* exhibits the most anisotropic surfaces when
360 compared to other extant suid taxa (Fig. 3A, Tables 1, 2 and S5). Its mean and median
361 epLsar values are significantly higher than in omnivorous *Potamochoerus* and *Sus* ($p <$
362 0.02 , Tables 2 and S5), but *Phacochoerus* does not significantly differ from *Hylochoerus*.
363 *Potamochoerus* and *Sus* are similar in anisotropy and include the lowest values. In terms
364 of complexity, we observe that *Sus* shows the highest values among our sample of extant
365 suids. However, significant differences with the three other taxa are identified with LSD
366 post-hoc tests ($p < 0.03$, Tables 2 and S6), not HSD tests. *Potamochoerus* tends to exhibit
367 shearing surfaces that are slightly more complex than *Hylochoerus* and *Phacochoerus*.
368 When looking at the heterogeneity of complexity (here, HAsfc₃₆; Fig. 3), we observe that
369 *Phacochoerus* is significantly lower than all other taxa ($p < 0.03$, Tables 2 and S7), and
370 strongly differs from *Sus* ($p < 0.001$, Table 2 and S7). *Hylochoerus* and *Potamochoerus*
371 tend to show intermediate HAsfc₃₆ values between *Sus* and *Phacochoerus*, but do not

372 significantly differ from our *Sus* sample. Summary statistics for the extant suid genera
373 analyzed in this study and compared to are presented in Table 1.

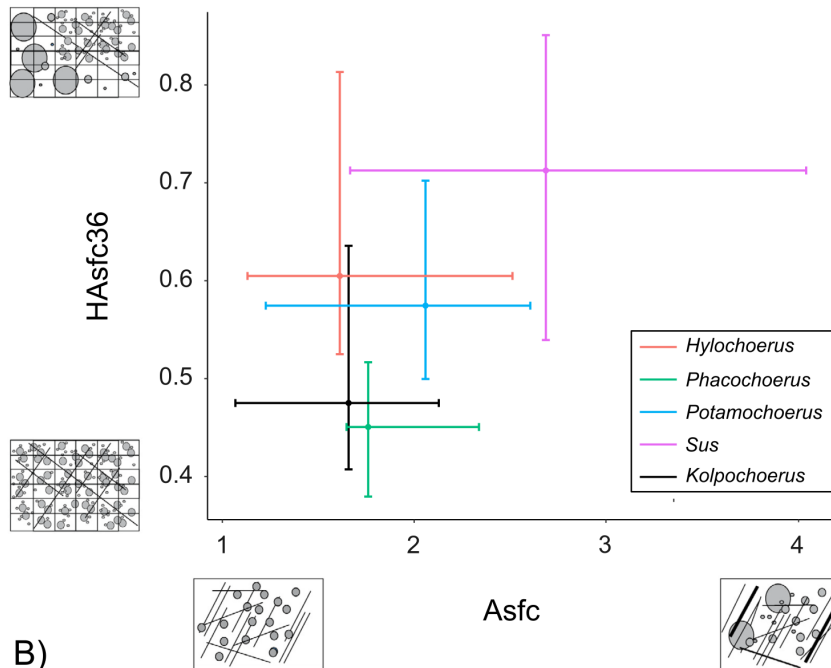
374 **Table 1.** Descriptive statistics (mean, SD: standard deviation, median, Q1: first quartile, Q3: third quartile, range) of dental microwear texture parameters for extant suid
 375 taxa and *Kolpochoerus* through the Shungura sequence (members C, E, F, lower part of G, H, J and L).

	Extant genera				<i>Kolpochoerus</i>							
	<i>Hylochoerus</i> (N = 21)	<i>Phacochoerus</i> (N = 23)	<i>Potamochoerus</i> (N = 33)	<i>Sus</i> (N = 25)	Total (N = 68)	Member C (N = 12)	Member E (N = 13)	Member F (N = 8)	Member G (N = 15)	Member H (N = 4)	Member J (N = 4)	Member L (N = 12)
Asfc												
Mean	2.26	2.20	2.34	3.46	1.78	2.10	1.37	1.46	1.70	2.48	1.75	2.00
(SD)	(1.95)	(1.37)	(1.45)	(2.48)	(1.00)	(1.05)	(0.63)	(0.93)	(0.85)	(2.04)	(0.71)	(1.09)
Median	1.61	1.76	2.06	2.69	1.66	1.83	1.36	1.26	1.82	1.70	1.84	1.82
(Q1, Q3)	(1.13, 2.51)	(1.65, 2.34)	(1.23, 2.60)	(1.67, 4.04)	(1.07, 2.13)	(1.54, 2.55)	(0.87, 1.63)	(0.84, 1.67)	(1.05, 2.08)	(1.12, 3.06)	(1.48, 2.11)	(1.36, 2.20)
Range	0.55 - 8.55	0.85 - 6.50	0.82 - 5.77	1.08 - 10.48	0.63 - 5.42	0.78 - 4.68	0.69 - 2.84	0.66 - 3.51	0.63 - 3.43	1.07 - 5.43	0.82 - 2.52	0.90 - 5.00
epLsar (x10⁻³)												
Mean	3.60	4.39	3.17	3.12	2.45	2.41	2.12	2.35	3.19	2.15	2.48	2.07
(SD)	(1.21)	(1.77)	(1.42)	(1.20)	(1.25)	(1.26)	(1.07)	(1.23)	(1.49)	(0.10)	(1.70)	(0.90)
Median	3.27	4.41	2.96	3.06	2.04	2.14	2.05	2.19	2.81	1.79	1.83	1.89
(Q1, Q3)	(2.81, 3.98)	(2.71, 6.10)	(2.17, 4.06)	(2.54, 3.93)	(1.65, 3.14)	(1.35, 3.27)	(1.26, 2.43)	(1.67, 3.06)	(2.29, 3.99)	(1.68, 2.26)	(1.63, 2.69)	(1.74, 2.57)
Range	1.61 - 6.61	1.83 - 7.28	0.76 - 5.94	1.19 - 5.89	0.51 - 6.10	0.88 - 4.69	0.90 - 4.56	0.56 - 4.05	0.67 - 6.10	1.41 - 3.63	1.26 - 4.98	0.51 - 3.99
HAsfc36												
Mean	0.65	0.46	0.63	0.75	0.53	0.46	0.49	0.65	0.64	0.42	0.42	0.53
(SD)	(0.21)	(0.13)	(0.21)	(0.30)	(0.19)	(0.22)	(0.15)	(0.19)	(0.20)	(0.09)	(0.15)	(0.13)
Median	0.61	0.45	0.58	0.71	0.48	0.41	0.45	0.67	0.57	0.41	0.37	0.49
(Q1, Q3)	(0.53, 0.81)	(0.38, 0.52)	(0.50, 0.70)	(0.54, 0.85)	(0.41, 0.64)	(0.35, 0.47)	(0.43, 0.49)	(0.46, 0.77)	(0.50, 0.78)	(0.35, 0.48)	(0.34, 0.44)	(0.46, 0.57)
Range	0.33 - 1.13	0.28 - 0.79	0.33 - 1.17	0.36 - 1.67	0.25 - 1.09	0.25 - 1.09	0.27 - 0.84	0.44 - 0.95	0.37 - 1.07	0.33 - 0.51	0.31 - 0.63	0.38 - 0.80

376



A)



B)

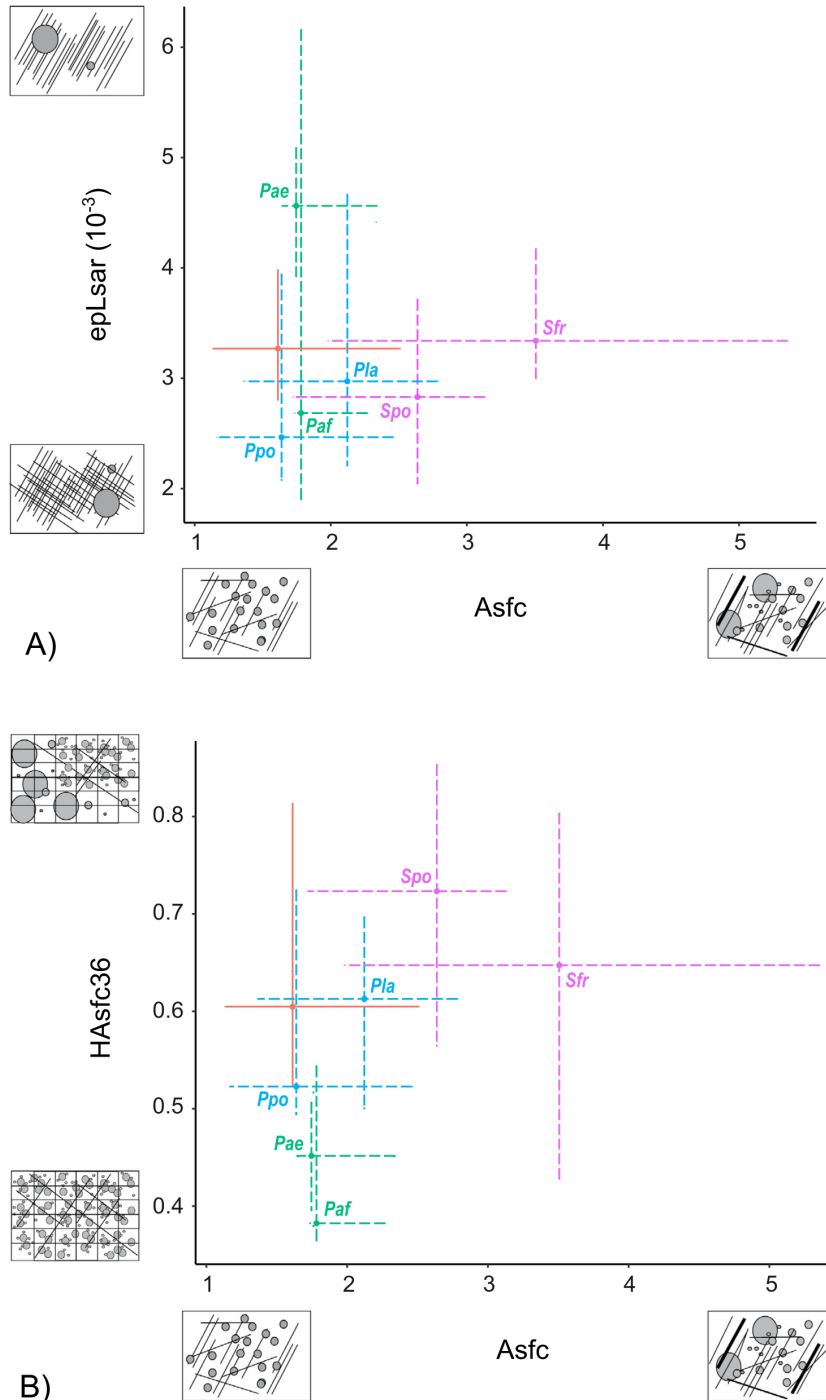
378

379 **Fig. 3.** Biplots of SSFA parameters on extant suid genera *Phacochoerus* (n = 23, green), *Hylochoerus* (n =
 380 21, orange), *Potamochoerus* (n = 33, blue) and *Sus* (n = 25, pink), and *Kolpochoerus* (n = 68, black). A)
 381 Biplot of complexity (Asfc) and anisotropy (epLsar); B) Biplot of complexity (Asfc) and heterogeneity of
 382 complexity (HAsfc36). Median values are indicated and bars represent the inter-quartile range.

383

384 We also observe some differences within the genera *Potamochoerus* and *Phacochoerus*,
385 as well as intra-specific differences within *Sus scrofa* (Fig. 4A). These differences concern the
386 anisotropy (epLsar) and the heterogeneity (HASfc36) of surface textures, not the complexity
387 (Asfc; Table S9). Notably, common warthogs (*Ph. africanus*) exhibit a large share of wear
388 surfaces being much less anisotropic than those of desert warthogs (*Ph. aethiopicus*), as shown
389 by the median value of the former being 1.5 times lower than for the latter (Fig. 4). However, the
390 two samples of warthogs do not significantly differ (Table S10). Common warthogs even exhibit
391 a median epLsar value below the ones measured for the two populations of *Sus scrofa* and the one
392 of *Po. larvatus*. Still, they show the highest inter-quartile range with specimens that present more
393 anisotropic surfaces than all other omnivores, and no significant difference is identified between
394 them and the other suid samples (Table S10). Regarding HASfc36, although desert warthogs tend
395 to show higher values than common warthogs, they do not significantly differ, and both species
396 tend to display more homogeneous wear surfaces than omnivorous and less-specialized suids (p
397 < 0.04 with LSD test only; Table S11). Species of *Potamochoerus* slightly differ, *Po. larvatus*
398 showing more anisotropic, more complex and more heterogeneous surfaces than *Po. porcus* (Fig.
399 4), but differences are not significant (Tables S10 and S11). At last, the two wild boar populations
400 also slightly differ (though not significantly; Tables S10 and S11), the boars from France showing
401 more complex, more anisotropic and less heterogeneous wear surfaces than boars from the
402 Białowieża Forest in Poland (Fig. 4).

403



404

405 **Fig. 4.** Biplots of SSFA parameters on extant *Phacochoerus* (green dotted lines), *Hylochoerus* (orange solid
 406 line), *Potamochoerus* (blue dotted lines) and *Sus* (pink dotted lines) showing inter- and intra-specific
 407 variations: *Ph. aethiopicus* (*Pae*, n = 14), *Ph. africanus* (*Paf*, n = 9), *Po. larvatus* (*Pla*, n = 18), *Po. porcus*
 408 (*Ppo*, n = 15), *S. scrofa* from Poland (*Spo*, n = 19), *S. scrofa* from France (*Sfr*, n = 6). A) Biplot of
 409 complexity (*Asfc*) and anisotropy (*epLsar*); B) Biplot of complexity (*Asfc*) and heterogeneity of complexity
 410 (*HASfc36*). Median values are indicated and bars represent the inter-quartile range.

411

412 **4.2. Comparisons between *Kolpochoerus* from Shungura and extant suids**

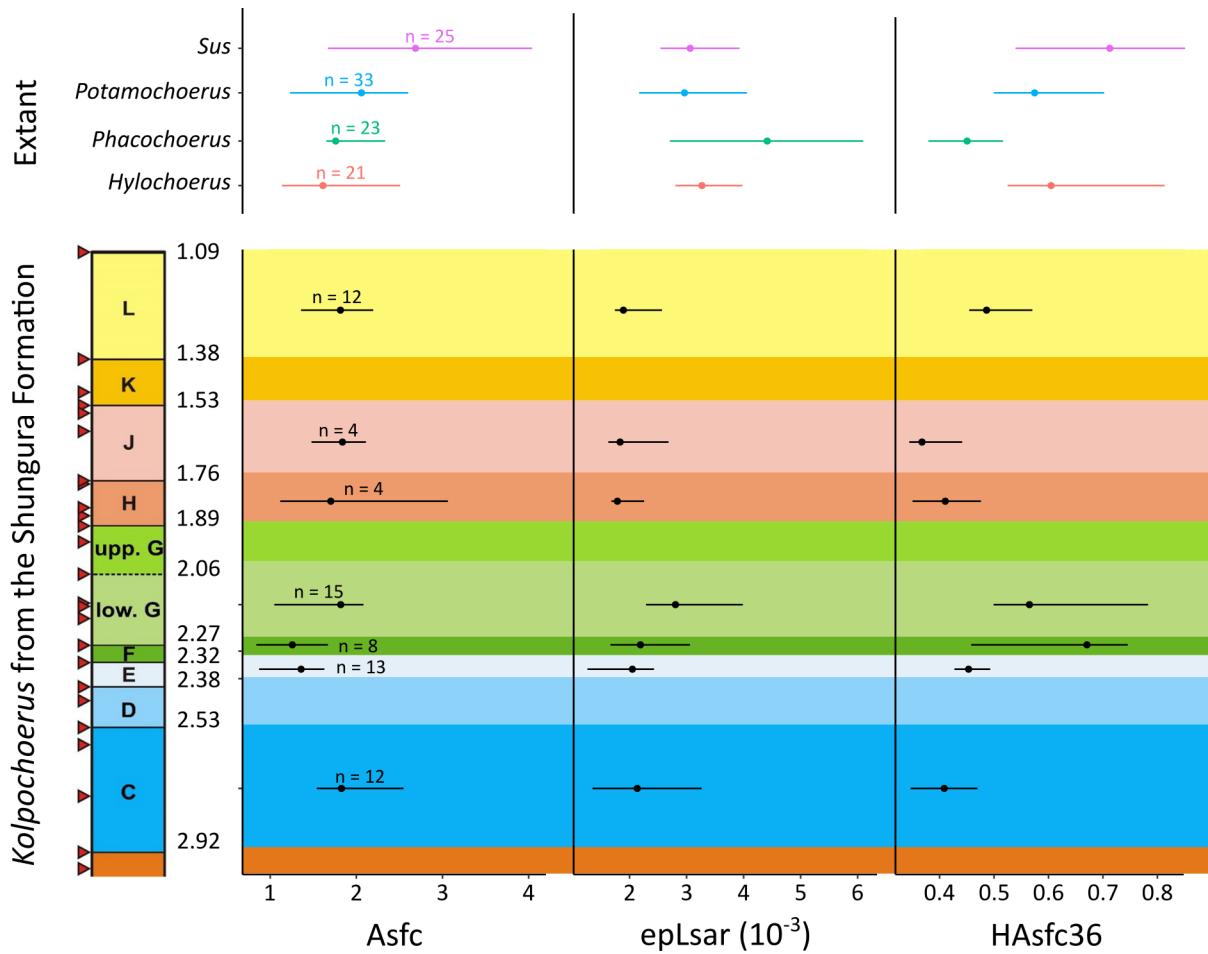
413 Specimens of *Kolpochoerus* from Shungura show low values of complexity, being
414 more similar to herbivorous genera *Phacochoerus* and *Hylochoerus*, and clearly distinct
415 from *Sus* (Fig. 3, Tables 2 and S6). Regarding anisotropy, specimens of *Kolpochoerus*
416 show the lowest values and only partly overlap with the values observed on extant suids
417 (Fig. 3A, Tables 1 and 2). Indeed, about half of the specimens of *Kolpochoerus* show
418 anisotropy values that are lower than the first quartile of each extant suid samples (Fig.
419 3A). They are well distinct from *Phacochoerus* (Fig. 3A, Tables 2 and S5). When looking
420 at the heterogeneity of complexity, *Kolpochoerus* also tend to show low mean and median
421 values and are similar to *Phacochoerus* (Fig. 3B, Table 1). However, while *Phacochoerus*
422 strongly differs from the three other extant genera, *Kolpochoerus* show some surfaces
423 that are more heterogeneous than *Phacochoerus* and overlap with the three other taxa.
424 Still, *Kolpochoerus* differs from *Sus*, which has the highest values (Fig. 3B, Tables 2 and
425 S7). Summary statistics of the total sample of *Kolpochoerus* are provided in Table 1.

426

427 **4.3. DMTA among *Kolpochoerus* through the Shungura sequence**

428 Through the sequence, the complexity of wear surfaces of *Kolpochoerus* seems
429 stable, except for specimens from members E and F that tend to display less complex
430 surfaces (Fig. 5, Tables 1 and 2). Nevertheless, no significant difference between
431 members is detected with both post-hoc tests. Compared to extant suids, specimens from
432 members E, F and G show significantly less complex surfaces than *Sus* ($p < 0.03$ with
433 both post-hoc tests, Tables 2 and S6). Regarding the anisotropy, mean and median values
434 are stable within the sequence, although specimens from the lower part of Member G are

435 slightly more anisotropic (Fig. 5, Tables 1 and 2), but they significantly differ from
436 members E and L only ($p < 0.02$). Compared to extant taxa, *Kolpochoerus* from all
437 members except G strongly differ from herbivorous *Phacochoerus* ($p < 0.02$, Tables 2
438 and S5). They also show less anisotropic surfaces than *Hylochoerus*, except in members
439 G and J ($p < 0.02$, Tables 2 and S5). Only specimens from members E and L show
440 significantly less anisotropic surfaces than omnivorous genera *Sus* and *Potamochoerus*
441 ($p < 0.02$, Tables 2 and S5). When looking at HAsfc36, we observe increasing values
442 from Member C to Member F, then a decrease from Member F to Member J, and again
443 higher values in Member L. The most heterogeneous surfaces are found in members F
444 and G (Fig. 5, Tables 1 and 2). Overall, no significant difference between members was
445 identified using both post-hoc tests. When compared to extant suids, *Kolpochoerus* are
446 generally more similar to *Phacochoerus* in HAsfc36. Nonetheless, it is worth noting that
447 specimens of *Kolpochoerus* from members F and G have less homogeneous surfaces than
448 those of *Phacochoerus*, even though significant differences are only identified with LSD
449 post-hoc test. In Member C, specimens of *Kolpochoerus* significantly differ from the
450 three other extant genera ($p < 0.03$ with both post-hoc tests, Tables 2 and S7). In members
451 E and J, they significantly differ from *Sus* only ($p < 0.05$ with both post-hoc tests, Tables
452 2 and S7). Altogether, even though DMTA parameters do not reveal substantial changes
453 between members, our results suggest some variations in terms of food mechanical
454 properties in *Kolpochoerus* within the sequence.



455

456 **Fig. 5.** Dental microwear texture SSFA parameters (Asfc: complexity, epLsar: anisotropy, and HASfc36:
 457 heterogeneity of complexity) on *Kolpochoerus* (black) through the different members of the Shungura
 458 Formation. Median values are indicated and bars represent the inter-quartile range. Data on extant suid
 459 genera *Phacochoerus* (green), *Hylochoerus* (orange), *Potamochoerus* (blue) and *Sus* (pink) are indicated
 460 for comparison.

461 **Table 2.** Combined Tukey's HSD and Fisher's LSD post-hoc tests following one-way ANOVAs. Parameters in bold are significant ($p < 0.05$) with both post-hoc tests.
 462 The parameter *epLsar* is given in italic when significant with a Dunn's test.

		Extant genera				<i>Kolpochoerus</i>						
		<i>Hylochoerus</i>	<i>Phacochoerus</i>	<i>Potamochoerus</i>	<i>Sus</i>	C	E	F	G	H	J	L
Extant	<i>Hylochoerus</i>											
	<i>Phacochoerus</i>	HAsfc36										
	<i>Potamochoerus</i>		<i>epLsar</i> ; HAsfc36									
	<i>Sus</i>	Asfc	Asfc; <i>epLsar</i> ; HAsfc36	Asfc								
<i>Kolpochoerus</i>	C	<i>epLsar</i> ; HAsfc36	<i>epLsar</i>	HAsfc36	Asfc; HAsfc36							
	E	<i>epLsar</i> ; HAsfc36	Asfc; <i>epLsar</i>	Asfc; <i>epLsar</i> ; HAsfc36	Asfc; <i>epLsar</i> ; HAsfc36	Asfc						
	F	<i>epLsar</i>	Asfc; <i>epLsar</i> ; HAsfc36	Asfc	Asfc	HAsfc36	HAsfc36					
	G		HAsfc36		Asfc	HAsfc36	<i>epLsar</i> ; HAsfc36					
	H	HAsfc36	<i>epLsar</i>	HAsfc36	HAsfc36				HAsfc36	HAsfc36		
	J	HAsfc36	<i>epLsar</i>	HAsfc36	HAsfc36				HAsfc36	HAsfc36		
	L	<i>epLsar</i>	<i>epLsar</i>	<i>epLsar</i>	Asfc; <i>epLsar</i> ; HAsfc36				<i>epLsar</i>			

463

464 5. DISCUSSION

465 5.1. Dental microwear textures and dietary habits in extant suid taxa

466 Overall, this study shows that DMT variations among extant suid taxa, despite
467 overlapping data, reflect differences in dietary habits as documented by field studies and
468 previous ecological studies based on dental microwear or stable isotopes. These
469 differences are mirrored in three commonly used SSFA parameters that describe the
470 heterogeneity of orientation of wear scratches, the surface roughness and the
471 heterogeneity of surface roughness: anisotropy (epLsar), complexity (Asfc) and
472 heterogeneity of complexity (HAsfc36), respectively.

473 In our analysis, the herbivorous taxon *Phacochoerus* strongly differs from the
474 omnivorous *Sus*, showing the highest anisotropy values, and the lowest in heterogeneity
475 of complexity, along with low surface complexity. High anisotropy values and low
476 complexity have been documented among graminivorous mammals in previous studies
477 (Ungar *et al.* 2007; J. R. Scott 2012; Merceron *et al.* 2014). Thus, the DMT patterns
478 observed on *Phacochoerus* reflect the large amount of fibrous items in its diet, mainly
479 herbaceous monocots (Cumming 1975, 2013; Harris & Cerling 2002; Treydte *et al.* 2006;
480 Butynski & de Jong 2017; de Jong & Butynski 2017). In addition, both common and
481 desert warthogs show homogeneous surfaces compared to other suids, which might
482 reflect their rather monotypic diets on herbaceous plants. These results are congruent with
483 previous dental microwear studies (Souron *et al.* 2015b; Lazagabaster 2019). In the
484 common warthogs, the large dispersion of anisotropy values (see 1st and 3rd quartiles on
485 Fig. 4) could reflect the seasonality of the diet, as it has been suggested that *Ph. africanus*
486 may feed more on roots, barks and rhizomes during the dry season (Cumming 1975, 2013;

487 Souron *et al.* 2015b; but see Treydte *et al.* 2006 showing little evidence for such seasonal
488 variations). Even though *Ph. africanus* show highly dispersed anisotropy values, the
489 median value is much lower than the one of desert warthogs (*Ph. aethiopicus*; Fig. 4).
490 Although the ecology of the desert warthog is largely unknown, these dissimilarities in
491 DMT patterns likely reflect subtle differences in feeding habits and/or habitat between
492 the two species. A different timing of third molar root development in desert warthogs
493 (i.e. late-forming roots allowing enamel columns to continue growing, thus extending
494 tooth durability) might reflect an adaptation to a more abrasive diet and/or more
495 exogenous particles than common warthogs (Grubb & d’Huart 2013). Such a diet could
496 explain the higher values of anisotropy in *Ph. aethiopicus*. In *Ph. africanus*, the low
497 epLsar median value could reflect feeding preferences on short and fresh (i.e., less
498 abrasive) graminoid and non-graminoid herbs (Butynski & de Jong 2017; see also
499 Francisco *et al.* 2018).

500 In contrast, the omnivorous *Sus scrofa* shows low anisotropy values and high
501 values of complexity and heterogeneity of complexity. This probably reflects the lesser
502 amount of fibrous plants in its diet and greater proportion of fruits, USOs, animal matter,
503 and fungi. Wild boars show significantly higher values in heterogeneity of complexity
504 than *Phacochoerus*. Although the impact of diet on HAsfc remains poorly understood,
505 previous studies have suggested that a more diversified diet leads to heterogeneous wear
506 surfaces (Scott *et al.* 2012; Souron *et al.* 2015b; Ramdarshan *et al.* 2016; Merceron *et al.*
507 2018). Here, our results tend to support this hypothesis, but there is no doubt that the link
508 between dietary diversity and surface heterogeneity is not that straightforward, notably
509 considering the similarity between *Potamochoerus* and *Hylochoerus*. Differences in
510 heterogeneity could also partly relate to other factors, such as grit ingestion and/or

511 seasonal variations (Souron *et al.* 2015b; Louail *et al.* 2022). Highly dispersed complexity
512 values, along with high values of heterogeneity, might reflect the intra-specific dietary
513 variations among *Sus scrofa*, as well as seasonal variations in the diet (e.g., Keuling *et al.*
514 2017). Moreover, highly dispersed values most likely reflect the fact that our sample
515 includes specimens from two different geographic areas in Poland and France, with
516 different climates (continental and oceanic, respectively) and slaughtering periods (spring
517 and winter, respectively) as well as differences in the access to agricultural crops or other
518 anthropogenic food supplies. The Białowieża Forest in Poland is one of the best-
519 preserved forest in Europe with limited human impact, and the Polish specimens contrast
520 with the few individuals from France. Notably, the latter show tend to show more
521 complex surfaces compared to specimens from Poland (Fig. 4). This could be partly
522 related to a greater consumption of agricultural crops or other by-products of human
523 activities, as previously observed in wild/free-ranging and stall-fed populations of *Sus*
524 (Yamada *et al.* 2018; Louail *et al.* 2021, 2022). However, we cannot further test this due
525 to the lack of precise data on feeding habits and habitat.

526 The other omnivorous taxon *Potamochoerus* is similar to *Sus* in terms of
527 anisotropy, but intermediate between *Phacochoerus* and *Sus* when looking at complexity
528 and heterogeneity of complexity. Although a previous study observed more similar DMT
529 patterns between *Potamochoerus* and *Sus scrofa* (Souron *et al.* 2015b; Table S12), our
530 results are not directly comparable because these authors used an interferometry-based
531 microscope with a 50× objective whereas we used a confocal profilometer with a 100×
532 objective. Moreover, some of the specimens of *Potamochoerus* and *Sus scrofa* that we
533 studied were not included in Souron *et al.* (2015b). In the present study, some specimens
534 of *Po. larvatus* come from a more open environment (specimens from MZUF, Table S1)

535 than what typically characterizes this genus. Some of them show low complexity values,
536 which might contribute to the differences between Souron *et al.* (2015b) and the present
537 study at the generic level. Moreover, the use of different modules for extracting SSFA
538 parameters might also contribute to differences between the two previous DMTA studies
539 on extant suids (Souron *et al.* 2015b; Lazagabaster 2019; Table S12) and the present one
540 (i.e. use of Toothfrax module and, here, use of MountainsMap module; see Calandra *et*
541 *al.* 2022). In his study, Lazagabaster (2019) observed different DMT patterns between
542 *Po. larvatus* and *Po. porcus*, the former showing more anisotropic, less complex and less
543 heterogeneous wear surfaces than the latter (Table S12). The author suggested this could
544 relate to differences in habitats, *Po. larvatus* inhabiting in general more open areas than
545 *Po. porcus*. Here, we observe that *Po. larvatus* tend to show more anisotropic but also
546 more complex and more heterogeneous wear surfaces than *Po. porcus*. These disparities
547 between Lazagabaster's study (2019) and the present one could also be due to differences
548 in geographic provenance or slaughtering periods of specimens sampled. In addition, two
549 specimens identified as *Po. porcus* in Lazagabaster's study come from localities where
550 only *Po. larvatus* is known and one specimen is impossible to identify to specific level
551 without further study of its morphology as it comes from a region where both species
552 occur. This implies a reduction of the sample size of *Po. porcus* in Lazagabaster (2019)
553 from six to three specimens (and an increase of the sample size of *Po. larvatus* from 23
554 to 25 specimens), which makes robust statistical comparisons between the two species
555 difficult. More studies are needed to further investigate variations in dietary habits within
556 and between the two species. Overall, our results show that the DMT patterns of
557 *Potamochoerus* reflect the distinct dietary habits between them and herbivorous
558 *Phacochoerus*. Dissimilarities with wild boars could reflect a less versatile diet in terms

559 of physical and mechanical properties than in wild boars, which might face greater
560 seasonal variation in food availability in mid-latitudes than *Potamochoerus* (see also
561 differences in dental topographies documented by Rannikko *et al.* 2020). Observed
562 similarities with *Hylochoerus* (notably in anisotropy and heterogeneity of complexity)
563 could partly relate to their common preference for forested or ecotone areas (Reyna-
564 Hurtado *et al.* 2017), although *Potamochoerus* probably have a more diversified diet than
565 *Hylochoerus* in terms of physical and mechanical properties.

566 Our results on DMT patterns of *Hylochoerus* are quite surprising because they do
567 not reflect the strong herbivory component in their diet, as observed in previous dental
568 microwear studies (Souron *et al.* 2015b; Lazagabaster 2019; Table S12). Nonetheless, in
569 addition to differences in methodological approaches (see above) that could explain these
570 incongruities, it is worth noting that Souron *et al.* (2015b) and Lazagabaster (2019) only
571 included 5 and 3 specimens (respectively) of *Hylochoerus*, whereas 21 specimens were
572 included in the present study. Here, specimens of *Hylochoerus* also exhibit low
573 complexity surfaces similarly to herbivorous *Phacochoerus*, but they show in average
574 less anisotropic surfaces. They also exhibit more heterogeneous surfaces than
575 *Phacochoerus*, but the difference between them is reduced compared to previous
576 observations in Souron *et al.* (2015b) and Lazagabaster (2019) (HASfc9 and HASfc81;
577 see Table S8). Our results on a larger sample of *Hylochoerus* are congruent with less
578 abrasive grasses in its diet than *Phacochoerus*, as documented by field studies, but this
579 could also be partly explained by differences in mastication biomechanics between the
580 two species. As suggested by Souron *et al.* (2015b), the more heterogeneous surfaces
581 could also be related to less frequent rooting behaviors (see also Louail *et al.* 2022) than
582 in *Phacochoerus*. Even though the feeding ecology of *Hylochoerus* remains largely

583 unknown, several studies have highlighted that this taxon does not feed predominantly on
584 grasses and should rather be considered as an herbivorous mixed feeder (Harris & Cerling
585 2002; d’Huart & Kingdon 2013; Souron *et al.* 2015b). Notably, a previous work on stable
586 carbon isotope composition of forest hog hair has shown that they consume very little C₄
587 grasses during the year, reaching only up to 20% grass in the diet at the beginning of the
588 rainy season (Cerling & Viehl 2004). Although it is unclear why DMT patterns of
589 *Hylochoerus* are that similar to those of the omnivorous *Potamochoerus*, it is likely that
590 they reflect a diet consisting of various herbaceous vegetation in closed, forested habitats,
591 probably including soft browse along with low-abrasive herbaceous plants (grasses and
592 forbs), as reflected by low complexity and low anisotropy. Overall, this microwear pattern
593 is coherent with much less abrasive foods in *Hylochoerus* diet than in *Phacochoerus*.

594 We need further investigations for a better understanding of the relationships
595 between feeding ecology and dental microwear textures among extant suids. This implies
596 the development of more precise comparative framework, with detailed data that are
597 directly related to each population. Nonetheless, our study shows that microwear patterns
598 among extant suids reflect differences in dietary habits, which validates their use as an
599 extant dental microwear baseline for comparisons with fossil data.

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601 **5.2. Dental microwear textures of *Kolpochoerus* from Shungura: dietary** 602 **perspectives**

603 We investigated dental microwear texture variations on extinct *Kolpochoerus*
604 from the Shungura Formation. The total sample of *Kolpochoerus* shows DMT
605 characterized by relatively low values of complexity, anisotropy and heterogeneity of

606 complexity compared to most extant taxa. Thus, they tend to differ from all extant taxa.
607 Although they resemble *Phacochoerus* in Asfc and HAsfc, more specimens have lower
608 Asfc and higher HAsfc values than in the warthog sample. More particularly, they
609 strongly differ from *Phacochoerus* having the lowest anisotropy values. These
610 differences between *Phacochoerus* and *Kolpochoerus* are expected considering that the
611 former is highly specialized. Still, our results appear to contrast with previous studies on
612 dental morphology and stable carbon isotopic compositions of *Kolpochoerus*, which have
613 related dental morphological changes, mainly molar enlargement, to increasing
614 consumption of abrasive grasses. The following paragraphs will discuss the unlikeness
615 that our dental microwear results for *Kolpochoerus* reflect a taphonomic alteration, and
616 the likelihood that DMT preserved a dietary signal reflecting a significant proportion of
617 low-abrasive herbaceous plants (grasses and forbs).

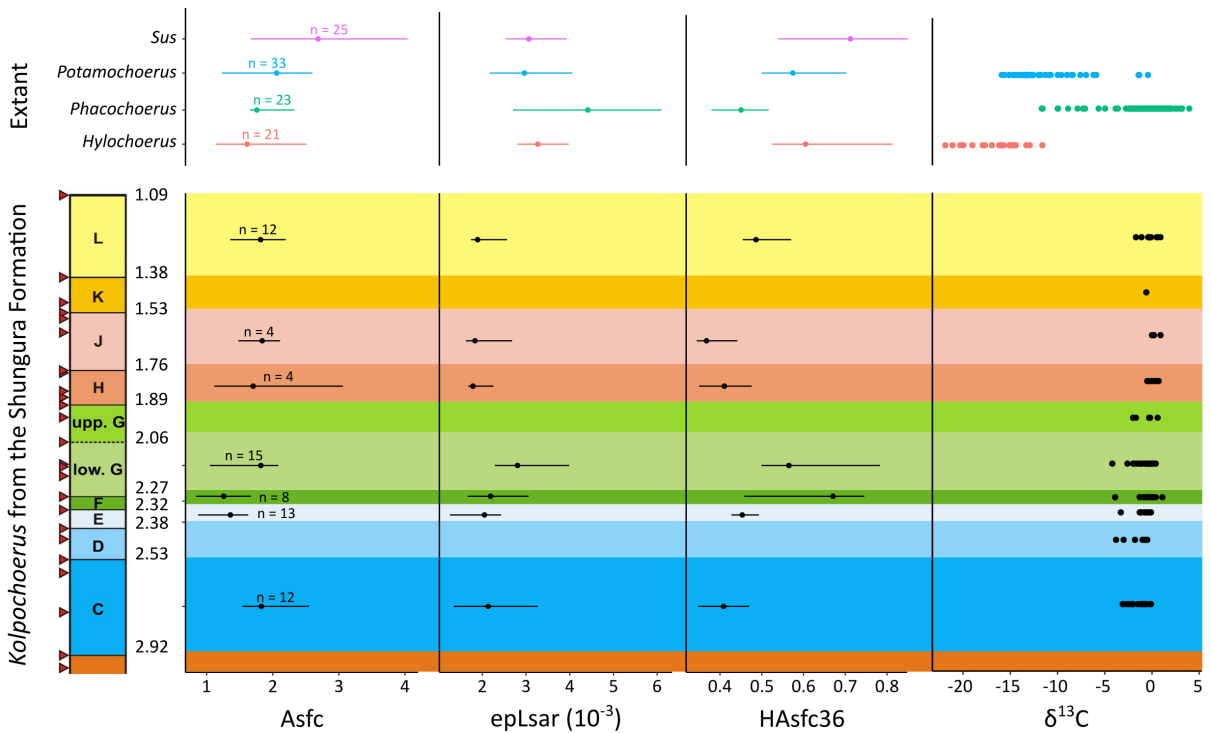
618 The question of potential taphonomic alterations in our sample of *Kolpochoerus*
619 arises because their DMT patterns differ from all extant suid taxa in their very isotropic
620 wear surfaces. Notably, samples from members E (n = 13) and L (n = 12) significantly
621 differ from all other extant taxa in this parameter (Tables 1 and 2, Fig. 5). Unfortunately,
622 the impact of taphonomic alterations (mechanical or chemical) on dental microwear
623 remains largely unknown, as only few studies have investigated this issue (Gordon 1983,
624 1984; King *et al.* 1999; Böhm *et al.* 2019; Uzunidis *et al.* 2021; Weber *et al.* 2022). Only
625 three of them have been conducted on non-human mammal teeth (Böhm *et al.* 2019;
626 Uzunidis *et al.* 2021; Weber *et al.* 2022), and only two have considered standard and
627 commonly used DMTA parameters (Böhm *et al.* 2019; Weber *et al.* 2022). Overall, all
628 these studies observed slightly polished wear surfaces following tumbling experiments,
629 but showed that the dietary signal is still preserved. One recent study pointed out that new

630 abrasion marks following a tumbling experiment have a more isotropic distribution
631 (Uzunidis *et al.* 2021). However, these authors used 2D low-magnification microwear
632 analysis and not standard 3D textural parameters, and this trend is not confirmed by the
633 other studies (Böhm *et al.* 2019; Weber *et al.* 2022). Further studies are needed to better
634 understand how texture parameters, notably epLsar, might be influenced by post-mortem
635 alterations, particularly fluvial transport in sediments. To date, none of these works can
636 be used to validate or invalidate the hypothesis of potential taphonomic alterations in our
637 sample. In contrast, several elements strengthen our assumption that wear surfaces used
638 in this study have preserved their dietary signal. Indeed, we first conducted a meticulous
639 selection of fossil surfaces and discarded all specimens with evident post-mortem
640 alterations, as well as dubious ones (see Fig. 2 and Weber *et al.* 2021). We also calculated
641 the mean values of several scanned microwear areas on the same (or similar) facet, which
642 avoids including extreme values in our analysis. Overall, DMT parameters measured on
643 *Kolpochoerus* specimens are still within the range of our extant suid baseline. Finally,
644 although Lazagabaster (2019) focused on Pliocene specimens, his published DMT data
645 on *Kolpochoerus* from the Hadar Formation also show this trend towards lower
646 anisotropy than in his extant sample, except for *Po. porcus*, a situation nearly similar to
647 our observations. Knowing that fossil preservation and depositional conditions
648 (predominantly lacustrine) are quite different between Shungura and the Hadar
649 Formation, this parallel situation in DMT signals reinforces our assumption that these low
650 anisotropy values in Shungura *Kolpochoerus* are not the results of a taphonomic process,
651 but reflect dietary habits.

652 The DMT patterns of *Kolpochoerus* analyzed in this study suggest substantial
653 differences in dietary habits from extant suid taxa. They do not reflect the consumption

654 of fibrous, abrasive plants as in herbivorous *Phacochoerus*, nor the consumption of hard
655 or brittle foods as among omnivorous taxa. Although we observe a progressive increase
656 in anisotropy from Member E to Member G (both differ significantly; Fig. 4, Table S5),
657 values are still much lower than among *Phacochoerus* through all the sequence (except
658 in Lower G). Nonetheless, regarding the heterogeneity of complexity (which is the only
659 texture parameter that strongly distinguish the highly specialized species from the other
660 suids), *Kolpochoerus* appear similar to *Phacochoerus*, having on average low values (Fig.
661 3). Although *Kolpochoerus* display more heterogeneous surfaces in members F and G
662 (and L to a lesser extent; Fig. 4, Table S7), this similarities with extant *Phacochoerus*
663 could reflect a rather monotypic diet. At the species level, *Kolpochoerus* spp. from
664 Shungura appear more similar to some specimens of common warthogs (*Ph. africanus*)
665 that show low anisotropy values (Fig. 3 and 4). Differences in dietary habits between the
666 two warthogs species need to be further investigated, but this resemblance between
667 *Kolpochoerus* and common warthogs might reflect a less abrasive and specialized diet
668 than in desert warthogs. Thus, we suggest their overall DMT patterns likely reflect the
669 consumption of non-fibrous herbaceous plants with lowabrasion It could explain the
670 overall isotropic wear surfaces in *Kolpochoerus*, conversely to the highly specialized
671 *Phacochoerus*. Indeed, we have highlighted that numerous specimens of common
672 warthogs have more isotropic wear surfaces (Fig. 5), which might reflect their dietary
673 preference for fresh, short, low-abrasive grasses. Moreover, preliminary observations by
674 M.L. on controlled-fed pigs suggest that increasing consumption of low-abrasive
675 herbaceous plants leads to decreasing anisotropy. Thus, our results appear in line with the
676 hypothesis of *Kolpochoerus* having feeding preferences for fresh grass shoots, probably
677 in more mesic habitats compared to other extinct suid taxa (Harris & Cerling 2002;

678 Rannikko *et al.* 2017, 2020; Yang *et al.* 2022). We propose that this dietary niche is
679 reflected, at Shungura, in the combination of a progressive enlargement and complexity
680 of third molars, a strong C₄ signal, together with DMT patterns reflecting low-abrasive
681 foods (Fig. 6).



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Fig. 6. A) Dental microwear texture parameters on extinct *Kolpochoerus* (black) through the different members of the Shungura Formation (Asfc: complexity, epLsar: anisotropy, and HASfc36: heterogeneity of complexity). Median values are indicated and error bars represent first and third quartiles. Data on extant suid genera *Phacochoerus* (green), *Hylochoerus* (orange), *Potamochoerus* (blue) and *Sus* (pink) are indicated for comparison. B) Enamel stable carbon isotopic compositions on *Kolpochoerus* through the same members of the Shungura Formation and on modern African suids (δ¹³C ‰ VPDB; data compiled from Bibi *et al.* 2013 and Negash *et al.* 2020 for *Kolpochoerus* and from the compilation available in Lazagabaster *et al.* 2021 for extant suids).

In *Kolpochoerus*, as previously pointed out, the elongation of third molars might be related to increasing chewing efficiency as it multiplies the number of chewing sites (Souron 2017; Yang *et al.* 2022). Whereas hypsodonty would be more associated to the abrasiveness of the grasses, molar enlargement would be more related to the size of food items and mouthfuls. It would thus give an advantage, among herbivorous suids that do not have a specialized digestive physiology such as *Kolpochoerus*, for reducing as much as possible short grasses (Lucas 2004; Souron 2017). Thus, dental morphological changes

700 are still in line with feeding preferences on short, low-abrasive grasses, as reflected by
701 their DMT patterns. In addition, even if the strong C₄ signal observed in *Kolpochoerus*
702 resemble that of extant warthogs (Fig. 6), it does not necessarily reflect the consumption
703 of abrasive grasses. It is largely assumed that grasses possessing the C₄ photosynthetic
704 pathway are high accumulators of silicon (Si), and consequently are more abrasive than
705 C₃ grasses or browse. However, a recent study has shown that Si concentrations in C₃ and
706 C₄ grasses are related to growth conditions (hot and dry conditions promoting higher Si
707 accumulation), not the photosynthetic pathway (Brightly *et al.* 2020). Other studies have
708 investigated the factors of Si accumulation in grasses, and they all highlight a substantial
709 role of growth conditions (e.g., Katz *et al.* 2014, 2018; Quigley *et al.* 2017). Thus, while
710 a strong C₄ signal likely reflects the consumption of herbaceous plants (mostly
711 graminoids), it does not indicate the abrasiveness of the diet, whereas DMT does. Past
712 environmental conditions, such as humidity and insolation, might have more impacted
713 the physical properties of the vegetation. Several studies have highlighted that while
714 Pliocene and Pleistocene eastern African sites show a general trend toward more open
715 landscapes dominated by C₄ resources, the Lower Omo Valley was composed of a mosaic
716 of closed and wooded habitats, riverine forests and open grasslands (e.g., Levin *et al.*
717 2011; Barr 2015; Negash *et al.* 2015, 2020). This implies that the Lower Omo Valley
718 would have provided a diversity of habitats to exploit, with the persistence of mesic
719 conditions. All studies that analyzed stable oxygen isotopes in *Kolpochoerus* in eastern
720 African sites have shown low $\delta^{18}\text{O}$ values compared to other extinct suid taxa, notably at
721 Shungura (Harris & Cerling 2002; Bedaso *et al.* 2010, 2013; Bibi *et al.* 2013; Negash *et*
722 *al.* 2020). Moreover, *Kolpochoerus* tend to show lower values than contemporaneous
723 *Metridiochoerus* from the same sites (Harris & Cerling 2002; Patterson *et al.* 2019; see

724 also Negash *et al.* 2020), which might indicate they were more water dependent. This is
725 supported by other studies that focused on relative abundances and dental topography of
726 Plio-Pleistocene suids in the Turkana basin (Rannikko *et al.* 2017, 2020). Altogether, the
727 combination of these different paleoecological proxies tend to support the hypothesis that
728 *Kolpochoerus* favored more mesic and/or woody habitats, such as at Shungura, with
729 significant consumption of herbaceous plants but dietary preferences for short, soft and
730 low-abrasive ones.

731

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763

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765 The authors declare they have no financial conflicts of interest in relation to the content
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1185

1186 **Figure and Table captions**

1187

1188 **Fig. 1.** Photosimulations of shearing facets on extant suid genera illustrating the diversity within taxa in
1189 terms of complexity (Asfc) and anisotropy (epLsar). The green squares on molars of each taxon indicate
1190 the location of a shearing facet. Scalebar: 20 μm .

1191

1192 **Fig. 2.** Photosimulations of shearing facets on *Kolpochoerus*. Selected surfaces (left) show relatively
1193 heterogeneous texture with pits and scratches of different sizes and different orientations. Dubious
1194 surfaces (right) were discarded when they show: a) a thin film over the surface that masks the dietary
1195 marks; b) long and parallel scratches that run over the surface and with sharp squared edges; c) a
1196 homogeneous texture with pits of similar size and an absence of scratch; d) a texture showing a
1197 “cauliflower-like” aspect and an absence of scratch. The green square on the molar of *Kolpochoerus*
1198 indicates the location of a shearing facet. Scalebar: 20 μm .

1199

1200 **Fig. 3.** Biplots of SSFA parameters on extant suid genera *Phacochoerus* (n = 23, green), *Hylochoerus* (n =
1201 21, orange), *Potamochoerus* (n = 33, blue) and *Sus* (n = 25, pink), and *Kolpochoerus* (n = 68, black). A)
1202 Biplot of complexity (Asfc) and anisotropy (epLsar); B) Biplot of complexity (Asfc) and heterogeneity of
1203 complexity (HASfc36). Median values are indicated and bars represent the range between first and third
1204 quartiles.

1205

1206 **Fig. 4.** Biplots of SSFA parameters on extant *Phacochoerus* (green dotted lines), *Hylochoerus* (orange solid
1207 line), *Potamochoerus* (blue dotted lines) and *Sus* (pink dotted lines) showing inter- and intra-specific
1208 variations: *Ph. aethiopicus* (*Pae*, n = 14), *Ph. africanus* (*Paf*, n = 9), *Po. larvatus* (*Pla*, n = 18), *Po. porcus*
1209 (*Ppo*, n = 15), *S. scrofa* from Poland (*Spo*, n = 19), *S. scrofa* from France (*Sfr*, n = 6). A) Biplot of
1210 complexity (Asfc) and anisotropy (epLsar); B) Biplot of complexity (Asfc) and heterogeneity of complexity
1211 (HASfc36). Median values are indicated and bars represent the range between first and third quartiles.

1212

1213 **Fig. 5.** Dental microwear texture SSFA parameters (Asfc: complexity, epLsar: anisotropy, and HASfc36:
1214 heterogeneity of complexity) on *Kolpochoerus* (black) through the different members of the Shungura
1215 Formation. Median values are indicated and bars represent the range between first and third quartiles. Data
1216 on extant suid genera *Phacochoerus* (green), *Hylochoerus* (orange), *Potamochoerus* (blue) and *Sus* (pink)
1217 are indicated for comparison.

1218

1219 **Fig. 6.** A) Dental microwear texture parameters on extinct *Kolpochoerus* (black) through the different
1220 members of the Shungura Formation (Asfc: complexity, epLsar: anisotropy, and HASfc36: heterogeneity
1221 of complexity). Median values are indicated and error bars represent first and third quartiles. Data on extant
1222 suid genera *Phacochoerus* (green), *Hylochoerus* (orange), *Potamochoerus* (blue) and *Sus* (pink) are

1223 indicated for comparison. B) Enamel stable carbon isotopic compositions on *Kolpochoerus* through the
1224 same members of the Shungura Formation and on modern African suids ($\delta^{13}\text{C}$ ‰ VPDB; data compiled
1225 from Bibi *et al.* 2013 and Negash *et al.* 2020 for *Kolpochoerus* and from the compilation available in
1226 Lazagabaster *et al.* 2021 for extant suids).

1227

1228 **Table 1.** Descriptive statistics (mean, SD: standard deviation, median, Q1: first quartile, Q3: third quartile,
1229 range) of dental microwear texture parameters for extant suid taxa and *Kolpochoerus* through the Shungura
1230 sequence (members C, E, F, lower part of G, H, J and L).

1231

1232 **Table 2.** Combined Tukey's HSD and Fisher's LSD post-hoc tests following one-way ANOVAs.
1233 Parameters in bold are significant ($p < 0.05$) with both post-hoc tests. The parameter *epLsar* is given in
1234 italic when significant with a Dunn's test.

1235