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RESEARCH ARTICLE

New insights on feeding habits of *Kolpochoerus* from the Shungura Formation (Lower Omo Valley, Ethiopia) using dental microwear texture analysis

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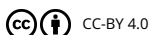
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Abstract

During the Neogene and the Quaternary, African suids show dental morphological changes considered to reflect adaptations to increasing specialization on graminivorous diets, notably in the genus *Kolpochoerus*. They tend to exhibit elongated third molars and some degree of hypsodonty, suggesting increasing consumption of abrasive grasses. However, the most significant morphological changes are observed more than 1 million years after the increased consumption of C₄ plants, such as graminoids. To date, only a few studies have applied dental microwear texture analysis (DMTA) to specimens of *Kolpochoerus*, which provides information on the mechanical properties of the diet, and therefore bring fundamental insights on the mechanical stresses exerted on dental morphologies. In addition, none has yet focused on specimens from the Shungura Formation (Lower Omo Valley, Ethiopia), which is the most complete Late Pliocene to Early Pleistocene record in eastern Africa. To better interpret the dental microwear textures (DMT) of *Kolpochoerus*, we built a modern referential using four genera of extant suids with contrasting diets: the herbivores *Phacochoerus* and *Hylochoerus*, and the omnivores *Potamochoerus* and *Sus*. Our results show that their DMT reflect their different feeding habits. In light of these results, we then studied the DMT of 68 *Kolpochoerus* specimens from the Shungura Formation and dating from about 2.9 Ma to 1.0 Ma. Their DMT differ from extant suids, but some similarities with *Phacochoerus* are observed. In line with previous studies, we propose that their DMT reflect a high consumption of herbaceous plants (graminoids and non-graminoids), with preferences for young, low-abrasive grasses. Yet, while a high intake of such grasses is consistent with both the shift toward increased C₄ feeding and morphological changes, more studies are needed to further understand the temporal offset between the two.

Keywords: abrasion; dietary niche; ecology; paleoenvironment; Plio-Pleistocene; scale-sensitive fractal analysis (SSFA)

INTRODUCTION

Reconstructing past dietary habits among mammals is crucial for a better understanding of the environmental conditions in which extinct species lived, and how they shared ecological resources (Andrews *et al.* 1979; Fortelius *et al.* 2002). It also helps understanding the potential selective pressures that drove the evolution of dental morphologies. Indeed, mammals generally exhibit teeth that are adapted to their diet, optimizing not only efficient processing of food items but also durability against wear (Hiitemae 2000). With the expansion of grasslands during the Neogene and the Quaternary, mammals with dental morphologies adapted to the consumption of large amount of abrasive grasses, such as high-crowned molars in ruminants or equids, have become more and more abundant (Janis 2008). The evolutionary history of African suids, a rapidly evolving group, also show this trend towards dental morphologies that are assumed to be adapted to increasing graminivory (i.e. main consumption of abrasive graminoids, or grasses and sedges). These characteristics appear multiple times in several suid genera, most likely resulting from convergent evolution (Harris & White 1979; Souron *et al.* 2015a). This is particularly observed during the Late Pliocene and the Pleistocene in two suine lineages, *Metridiochoerus-Phacochoerus* and *Kolpochoerus-Hylochoerus*, which are commonly represented in faunal assemblages from eastern Africa (Rannikko *et al.* 2017; Lazagabaster *et al.* 2018). Thus, in addition to their relevance for biostratigraphic correlations (White & Harris 1977; Cooke 2007), suids also have a potential for paleoenvironmental reconstructions (Harris & Cerling 2002; Bishop *et al.* 2006; Lazagabaster 2019). However, the elongated third molars displayed by African suids, with extra cusps in the distal part, contrast with the ones observed among graminivorous ruminants, which rather exhibit hypsodont molars that are relatively short mesio-distally (e.g., Janis 2008; Madden 2014). Although both dental innovations have been linked to increasing graminivory, elongated molars are probably associated with improved efficiency for fragmenting small foods whereas hypsodont molars are rather linked to increased tooth durability against wear (Lucas 2004; Souron 2017; Yang *et al.* 2022).

In addition, changes in third molar length and height are not similar in the different suid clades. In *Kolpochoerus*, we mostly observe an increase in molar length rather than in molar height, whereas in *Metridiochoerus*, molar height increases significantly with length (Harris & White 1979; Cooke 2007). This suggests that different mechanisms influenced the selection of dental morphologies in *Kolpochoerus* and in *Metridiochoerus*, probably due to different ecologies. Moreover, the most significant changes in dental morphologies, notably in *Kolpochoerus*, are observed substantially after the shift in stable carbon isotope compositions

reflecting increasing graminivorous diets (Harris & Cerling 2002; Bibi *et al.* 2013; Souron 2017). In the lineage *Kolpochoerus limnetes*/*Kolpochoerus* aff. *paiceae*, while a the progressive lengthening of third molars from about 2.7 Ma, along with an increasing complexity, has been related to a specialization toward graminivory (Harris & White 1979; Cooke 1985; Kullmer 1999), the shift toward much more derived species with more elongated and hypsodont third molars is described at about 1.5 Ma (Souron 2012). This contrast with the inferred diets that are already strongly dominated by C₄ plants (i.e., mostly graminoids, such as grasses and sedges, and amaranths), since about 3 Ma for most specimens (Harris & Cerling 2002; Bibi *et al.* 2013; Souron 2017; Negash *et al.* 2020). Because there is a temporal offset between the most drastic changes in dental morphologies and the strong dietary shift (as inferred from stable carbon isotopes), further investigation of the paleoecology of *Kolpochoerus* using a multi-proxy approach is needed for better understanding which factors favored the selection of such morphology, and by which mechanisms.

Most commonly used dietary proxies record different aspects of the diet and over different timescales. Therefore, it is not surprising that dental morphology and enamel stable carbon composition do not reflect similar dietary habits (Davis & Pineda Munoz 2016). As already pointed out for extinct African suids (Souron 2017), it is crucial to have a more integrative approach combining different and complementary paleoecological proxies to improve inferences of past diets, and then to better understand the relationships between feeding habits, morphology, and environmental constraints. Among paleoecological proxies, dental microwear is highly dependent on the physical properties of masticated food items and thus provides insights on mechanical pressures exerted on the feeding system (e.g., Lucas *et al.* 2013, 2014; Daegling *et al.* 2016; Merceron *et al.* 2016). It records the diet over a short timescale, few weeks or months before death (Teaford & Oyen 1989; Teaford *et al.* 2017, 2021; Winkler *et al.* 2020). In recent years, Dental Microwear Texture Analysis (DMTA) has proved its efficiency in detecting dietary differences between species (e.g., R. S. Scott *et al.* 2006, 2012; J. R. Scott 2012; Schulz *et al.* 2013; Merceron *et al.* 2021; Hullot *et al.* 2021), as well as small variations within species or populations (Merceron *et al.* 2010, 2014; Berlioz *et al.* 2017; Percher *et al.* 2017). Thus, this methodology has been widely employed to infer past dietary habits (e.g., Ungar *et al.* 2008, 2017; Berlioz *et al.* 2018; Blondel *et al.* 2018, 2022; Martin *et al.* 2018; Merceron *et al.* 2018, 2021; Hullot *et al.* 2021). Nevertheless, to date, only few studies have applied DMTA on extant or extinct suids (Souron *et al.* 2015b; Ungar *et al.* 2017; Yamada *et al.* 2018, 2021; Lazagabaster 2019; Louail *et al.* 2021, 2022) and none has yet focused on DMT of *Kolpochoerus* from the Shungura Formation.

The extinct genus *Kolpochoerus* has a promising potential to contribute to a better understanding of the relationships between morphological evolution, dietary changes, and environmental changes. Indeed, it is one of the most abundant suid taxa in Plio-Pleistocene localities and with a wide geographic distribution, suggesting an adaptability to a variety of environmental conditions. Widespread in eastern Africa (e.g., Harris & White 1979; White 1995; Suwa *et al.* 2003, 2014; Bishop 2011; Haile-Selassie & Simpson 2013; Souron *et al.* 2015a), specimens of *Kolpochoerus* have been recovered from northern to southern Africa, including central Africa (e.g., Broom 1931; Hendeby & Cooke 1985; Brunet & White 2001; Geraads *et al.* 2004). Some specimens have even been described from the Middle East (Geraads *et al.* 1986) and possibly from the Siwaliks in eastern Himalaya (Chavasseau 2008; Pickford 2012). The genus *Kolpochoerus* is also one of the most diverse, notably in terms of dental morphologies and feeding habits (Harris & White 1979; Brunet & White 2001; Bishop *et al.* 2006; Haile-Selassie & Simpson 2013; Souron 2012). Fossils from the Shungura Formation have played an important role in our understanding of African environments in the Omo Valley during the Plio-Pleistocene. The Shungura Formation is located in the Lower Omo Valley in southwestern Ethiopia. It is the most complete stratigraphic and paleontological record from the Late Pliocene to Early Pleistocene in eastern Africa, with sediments deposited almost continuously from ca. 3.75 Ma to ca. 1.0 Ma. It is subdivided into 12 members of sedimentary deposits: Basal, A to H and J to L, whose ages were determined by using radiochronology of interspersed volcanic tuffs and magnetostratigraphy (Heinzelin 1983; Feibel *et al.* 1989; McDougall & Brown 2006, 2008; McDougall *et al.* 2012; Kidane *et al.* 2014). Since the early 1930s, the Shungura Formation has been intensively surveyed through several research expeditions by C. Arambourg (Arambourg 1934, 1943), the International Omo Research Expedition (IORE: Howell 1968; Coppens 1975), and the Omo Group Research Expedition (OGRE: Boisserie *et al.* 2008). It has yielded ca. 57,000 fossil vertebrate specimens, as well as numerous lithic assemblages. On average, suids represent 10.2 % of the Shungura faunal remains (Omo Database - fossil specimen database for Shungura and Usno formations including full IORE and OGRE collections, maintained by OGRE), including about 32 % of *Kolpochoerus*, almost all attributed to the lineage *K. limnetes*/*K. aff. paiceae* (following the same taxonomic framework as described in Bibi *et al.* 2018; Brink *et al.* 2022) and to *Kolpochoerus afarensis* at the base of the sequence (Souron 2012).

To fill the gap regarding inferences on the mechanical properties of food materials consumed by *Kolpochoerus* from the Shungura Formation, we propose here the first study that measures the DMT variations on specimens of *Kolpochoerus* from Member C to Member L (about ca.

2.9 Ma to 1.0 Ma). As such, our study also complements two recent ones, focusing on relative abundances within the family Suidae (Rannikko *et al.* 2020) and on functional occlusal traits (Yang *et al.* 2022), which have suggested that *Kolpochoerus* might have had a less abrasive diet than typical graminivorous suids. To better interpret the DMT of *Kolpochoerus*, we expand the baseline developed by Souron *et al.* (2015b) and Lazagabaster (2019) by including larger samples of African suids (particularly *Hylochoerus*) with different dietary habits encompassing the full spectrum from herbivorous to omnivorous. We also discussed inter-specific differences within *Phacochoerus* and *Potamochoerus* genera, as well as intra-specific differences in Eurasian wild *Sus scrofa*. Then, considering the patterns observed on extant suids, we explored DMT variations in specimens attributed to the lineage *K. limnetes*/*K. aff. paiceae* through the Shungura sequence to propose inferences regarding their past dietary habits.

MATERIAL AND METHODS

SAMPLE AND DIETARY HABITS OF EXTANT SUIDS

We considered a total of 102 extant wild specimens, belonging to four suid genera and six species: *Hylochoerus* (*Hylochoerus meinertzhageni* or giant forest hog, n = 21), *Phacochoerus* (n = 23; n = 9 for *Phacochoerus africanus* or common warthog, and n = 14 for *Phacochoerus aethiopicus* or desert warthog), *Potamochoerus* (n = 33; n = 15 for *Potamochoerus porcus* or red river hog, and n = 18 for *Potamochoerus larvatus* or bushpig) and *Sus* (*Sus scrofa* or wild boar, n = 25). For *Sus*, we used two wild boar populations from France (n = 6) and from the Białowieża Forest in Poland (n = 19). Both areas are closed mixed forest but the former is characterized by an oceanic climate whereas the latter has a much more continental climate with limited human impact. The specimens are housed in the following institutions: Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Polish Academy of Sciences in Białowieża, Poland (MRI PAS); The Ethiopian Heritage Authority, collections of comparative anatomy, Addis Ababa, Ethiopia (MCA); Museo Zoologico dell'Università di Firenze, Italy (MZUF); Naturhistorisches Museum Basel, Switzerland (NMB), Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM) and Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement, France (INRAE Occitanie-Toulouse).

Taxonomic identifications at the specific level were verified for extant taxa both based on the craniomandibular and dental morphology of the specimens and on their geographical origin.

This step is all the more crucial that museum labels frequently indicate incorrect identifications at the specific level, resulting from previous taxonomic practices. Indeed, the extant species of *Phacochoerus* and of *Potamochoerus* were long lumped into single species, respectively called *Ph. aethiopicus* and *Po. porcus* (Oliver 1993; Grubb & d'Huart 2010) and the confusion remains pervasive in the current literature and museum collections. The two extant species of *Phacochoerus* are sympatric in some parts of Ethiopia, Somalia, and especially in Kenya (de Jong *et al.* 2023) but they are easily distinguished from each other by several discrete and continuous morphological characters of the cranium, mandible, and dentition (e.g., d'Huart & Grubb 2005; Groves & Grubb 2011; Souron 2012, 2015, 2016). The two extant *Potamochoerus* species are overall geographically well separated but possibly sympatric in some parts of Democratic Republic of Congo, Burundi, and Rwanda (Leslie, Jr. & Huffman 2015). They are morphologically more similar to each other than the two species of warthogs and are mostly distinguished based on shape and size differences of the skull and differences in first upper premolar prevalence (Souron 2012; Boisserie *et al.* 2014). Specimen numbers, tooth positions, and their geographic proveniences are provided in the Supplementary Material (ESM1: Table S1).

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

Few extant wild suid species are considered as herbivorous: the two species of *Phacochoerus* and, to a lesser extent, *H. meinertzhageni*. These taxa mainly feed on fibrous vegetal matter, such as grasses (graminoids) and forbs (non-graminoids), and incorporate fruits and roots in

their diet to a lesser extent (*Ph. africanus* and *Ph. aethiopicus*: Harris & Cerling 2002; Treydte *et al.* 2006; Butynski & de Jong 2017; de Jong & Butynski 2017; Edossa *et al.* 2021; *H. meinertzhageni*: d’Huart 1978; Harris & Cerling 2002; Cerling & Viehl 2004; d’Huart & Kingdon 2013; Reyna-Hurtado *et al.* 2017). Species of *Phacochoerus* are the most specialized, feeding mostly on short, green, tropical grasses and consuming all plant parts, including underground storage organs. *Hylochoerus meinertzhageni* has been less studied than the three other genera, but previous work suggests it is more likely an herbivorous mixed feeder (e.g., d’Huart & Kingdon 2013; Souron *et al.* 2015b; Mekonnen *et al.* 2018). In contrast to other suids, the rooting behavior in this species is strongly reduced and the portion of subterranean foods in its diet is low.

SAMPLE OF *KOLPOCHOERUS* FROM SHUNGURA

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

SURFACE ACQUISITION AND PROCESSING

We considered wear facets associated with the shearing phase I of mastication, which are located on the lingual and labial enamel bands (facets 1 to 8, contrary to crushing facets 9 to 13 located on the labial and lingual sides of the occlusal basin on lower and upper molars, respectively; see Miyamoto *et al.* 2022 and Figure 2 in their study; see also Tausch *et al.* 2015). We did not consider crushing facets because they are reduced in some taxa (such as *Phacochoerus*) and are no longer apparent on molars with heavily worn occlusal basin. All suitable worn upper and lower first, second and third molars were included in this study (ESM1: Tables S1 and S2). While it might increase the variability in microwear patterns, studies by Schulz *et al.* (2010) and Ramdarshan *et al.* (2017) showed non-significant variations in microwear textures between cheek teeth along the tooth row, and between upper and lower cheek teeth, when considering homologous wear facets (see also ESM1: Table S3 showing no significant difference between tooth positions within taxon). Each facet was molded with

polyvinylsiloxane (Regular Body President, ref. 6015 - ISO 4823, medium consistency, polyvinylsiloxane addition-type, Coltene Whaledent). For each specimen, all suitable non-overlapping worn areas on shearing facets were scanned in order to encompass intra-facet variations. We scanned one to fourteen surfaces for each specimen (ESM1: Tables S1 and S2). Each surface was scanned as flat as possible using “TRIDENT”, a white-light confocal profilometer Leica DCM8 with a 100× objective housed at the PALEVOPRIM lab, CNRS and University of Poitiers, France (Numerical aperture = 0.90; Working distance = 0.9 mm; Leica Microsystems). Each scanned surface was pre-processed using LeicaMap v8.0 (Leica Microsystems; MountainsMap, Digital Surf). Non-measured points (< 3 %) were filled with a smooth shape (Laplacian filter) calculated from neighboring points. We applied a morphological filter to remove artifacts such as aberrant peaks (Merceron *et al.* 2016) and surfaces were then leveled. A 140 × 100 μm (1086 × 776 pixels) leveled area was automatically generated at the center of each surface. In case of adhering dirt particles, the extracted area was shifted aside to get the particles out of the field of selection. In the worst cases (9 % of surfaces in extant suids and 2 % in *Kolpochoerus*), we manually erased the particles using a user-defined contour and replaced with a smooth shape calculated from neighboring points.

PROCEDURE FOR SELECTING WEAR SURFACES OF FOSSIL SPECIMENS

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

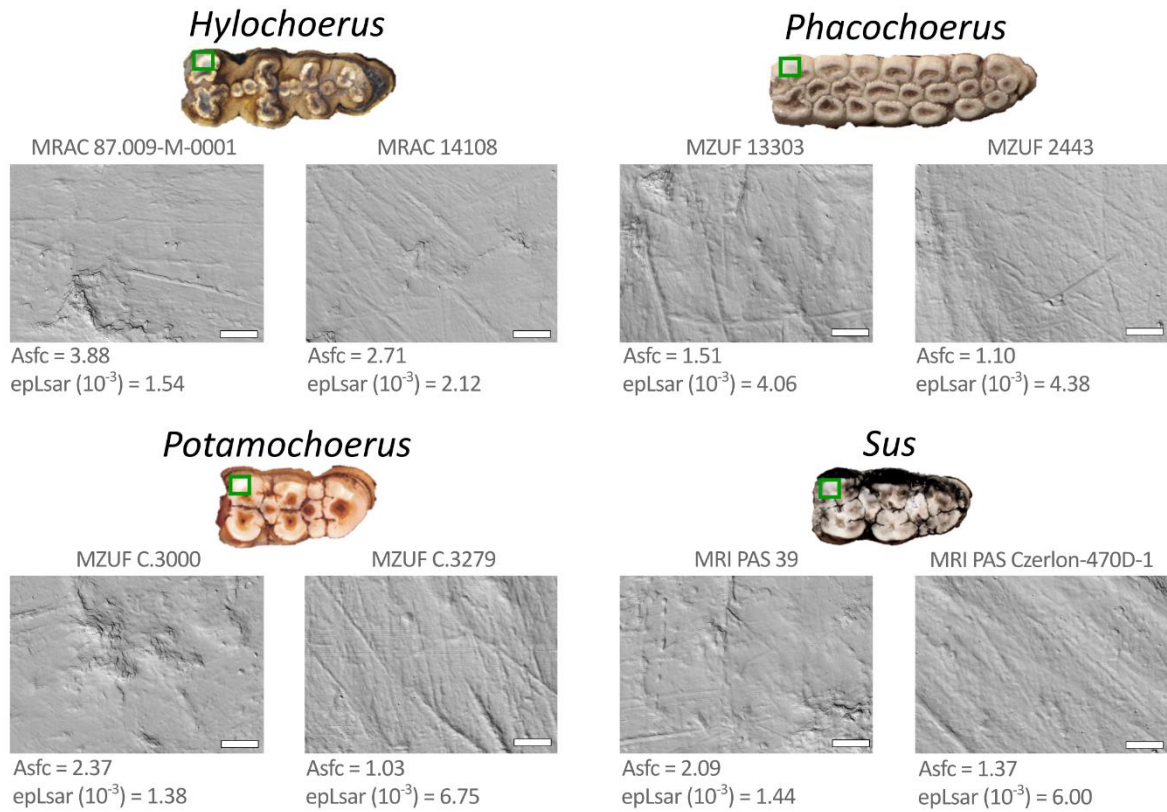


FIG. 1. – Photosimulations of shearing facets on extant suid genera illustrating the diversity within taxa in terms of complexity (Asfc) and anisotropy (epLsar). The green squares on molars of each taxon indicate the location of a shearing facet on a right lower third molar. Scalebar: 20 μ m.

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

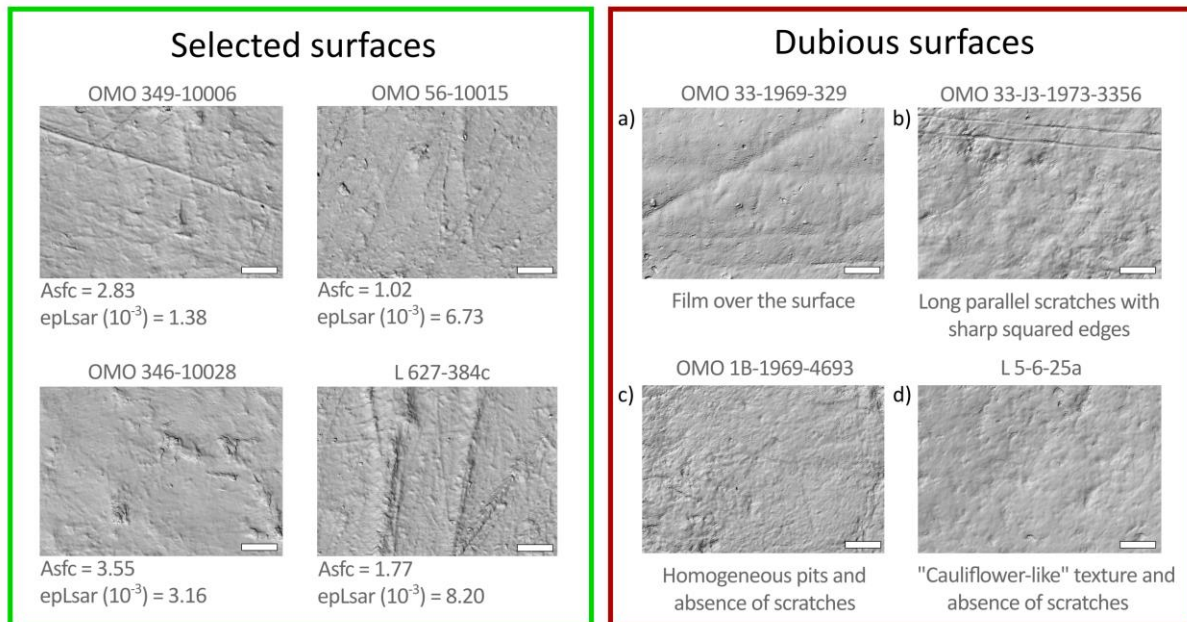
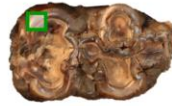


FIG. 2. – Photosimulations of shearing facets on *Kolpochoerus*. Selected surfaces (left) show relatively heterogeneous texture with pits and scratches of different sizes and different orientations. Dubious surfaces (right) were discarded when they show: a) a thin film over the surface that masks the 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 .

ACQUISITION OF TEXTURAL PARAMETERS

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 6×6 blocks in this study). We also computed HASfc9 and HASfc81 (calculated through 3×3 and 9×9 blocks, respectively) for each surface, but they were discarded because less discriminative than HASfc36 (ESM1: Tables S4 and S9). Complexity (Asfc) measures the surface roughness at a given scale. Anisotropy (epLsar) quantifies the orientation concentration of surface roughness. Heterogeneity of complexity (HASfc36) measures the variation of complexity of subsampled parts of the surface. Detailed descriptions of these parameters can be found in Scott *et al.* (2006). For each

parameter, we considered the mean value of all scanned surfaces per individual (ESM1: Tables S1 and S2). As a complement to the figures presented in the main text, we provide biplots showing individual data points (ESM1: Fig. S1), as well as boxplots of SSFA parameters for each sample of extant suids and *Kolpochoerus* as Supplementary (ESM1: Fig. S2 to S4).

STABLE CARBON ISOTOPE VALUES OF EXTANT SUIDS AND *KOLPOCHOERUS* FROM SHUNGURA

All stable carbon isotopic values on enamel bioapatite of extant African suids and extinct *Kolpochoerus* from the Shungura Formation were compiled from the literature. We used the recently published compilation on extant African suids from Lazagabaster *et al.* (2021), which is available online as supplementary material (see references herein). To our knowledge, no data on enamel bioapatite is available on modern wild and/or free-ranging *Sus scrofa* (but see Hu *et al.* 2009; Russo *et al.* 2017; Balasse *et al.* 2018; Vedel *et al.* 2022 on other biological tissues and/or on archeological specimens). All data on *Kolpochoerus* from the Shungura Formation were compiled using two recent studies by Bibi *et al.* (2013) and Negash *et al.* (2020). From this latter study, we only included stable carbon isotopic values of specimens for which element identification is documented in the Omo Database, and attributed to a M2 or a M3.

STATISTICAL ANALYSES

All statistical analyses were conducted in the R statistical environment (R Core Team 2020, v4.0.3). We performed analyses of variance (one-way ANOVAs) on each SSFA parameter to detect significant differences between extant taxa and *Kolpochoerus* by members (ESM1: Table S4). The data were box-cox transformed prior to the analyses to meet the assumptions of homoscedasticity and normal distributions of the residual errors. Then, we conducted two post-hoc tests for multiple comparisons (package “agricolae”) to determine the sources of significant variations: Tukey’s Honest Significant Difference (HSD) and Fisher’s Least Significant Difference (LSD, less conservative than HSD) tests (ESM1: Tables S5 and S6). An alternative non-parametric Kruskal-Wallis test was run for one parameter (epLsar) that did not meet the assumptions of normality of residuals (ESM1: Table S7), and followed with a post-hoc Dunn’s test (package “dunn.test”; ESM1: Table S8). We also conducted an ANOVA to detect significant differences between extant *H. meinertzhageni*, *Ph. africanus*, *Ph. aethiopicus*, *Po. larvatus*, *Po. porcus* and the two populations of *Sus scrofa* (see ESM1: Table S9 for descriptive statistics and Table S10 for ANOVA results), followed with both HSD and LSD post-hoc tests (ESM1: Tables S11 and S12).

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

RESULTS

DMTA OF EXTANT SUID TAXA

At generic level, *Phacochoerus* exhibits the most anisotropic surfaces when compared to other extant suid taxa (Fig. 3A, Tables 1 and 2, ESM1: Table S8). Its mean and median epLsar values are significantly higher than in omnivorous *Potamochoerus* and *Sus* ($p < 0.02$, Table 2, ESM1: Table S8), but *Phacochoerus* does not significantly differ from *Hylochoerus*. *Potamochoerus* and *Sus* are similar in anisotropy and include the lowest values. In terms of complexity, we observe that *Sus* shows the highest values among our sample of extant suids. However, significant differences with the three other taxa are identified with LSD post-hoc tests ($p < 0.03$, Table 2, ESM1: Table S5), not HSD tests. *Potamochoerus* tends to exhibit shearing surfaces that are slightly more complex than *Hylochoerus* and *Phacochoerus*. When looking at the heterogeneity of complexity (here, HAsfc36; Fig. 3), we observe that *Phacochoerus* is significantly lower than all other taxa ($p < 0.03$, Table 2, ESM1: Table S6), and strongly differs from *Sus* ($p < 0.001$, Table 2, ESM1: Table S6). *Hylochoerus* and *Potamochoerus* tend to show intermediate HAsfc36 values between *Sus* and *Phacochoerus*, but do not significantly differ from our *Sus* sample. Summary statistics for the extant suid genera analyzed in this study are presented in Table 1.

TABLE 1. – Descriptive statistics (mean, SD: standard deviation, median, Q1: first quartile, Q3: third quartile, range) of dental microwear texture parameters for extant suid 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

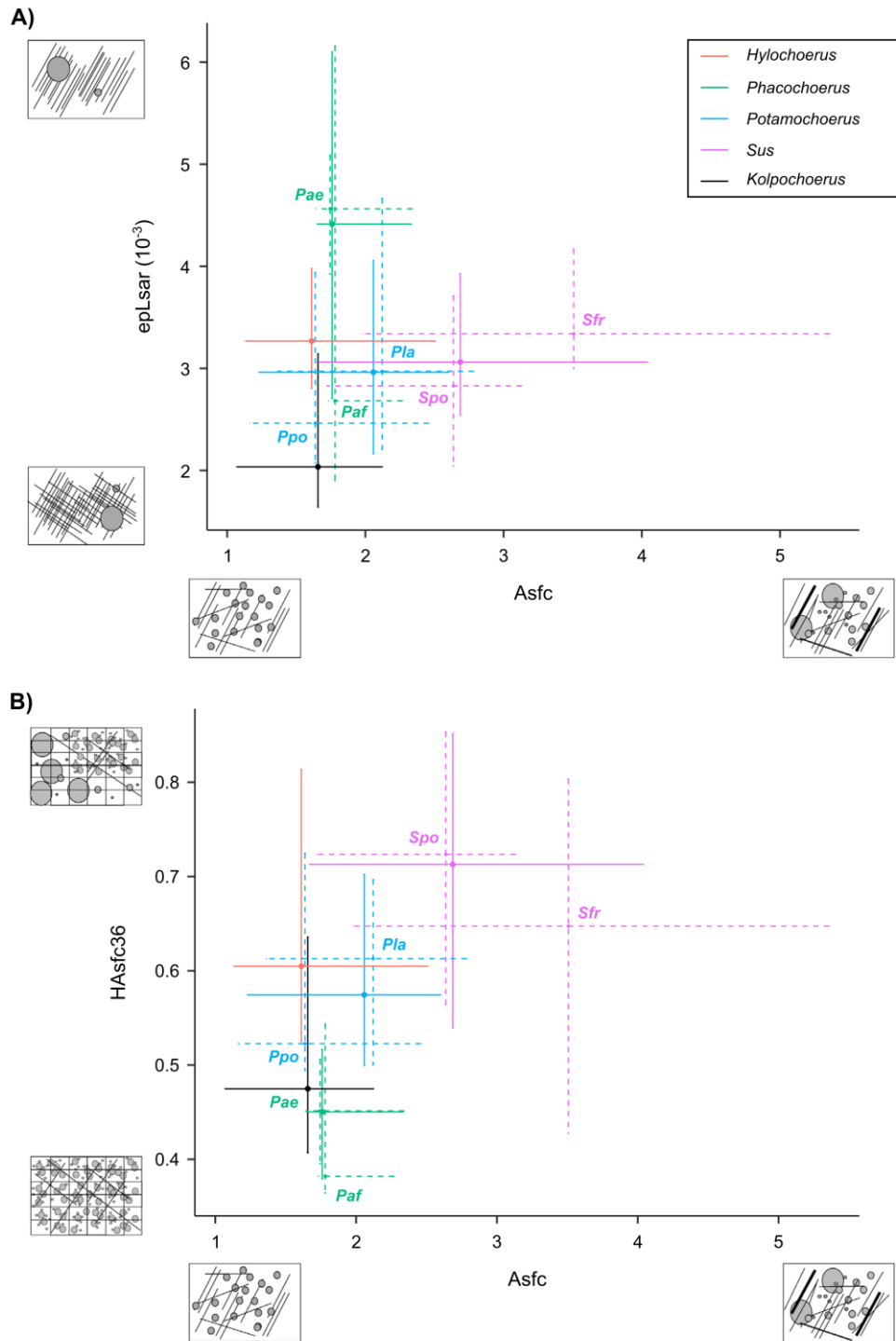


FIG. 3. – Biplots of SSFA parameters on extant *Phacochoerus* (n = 23, green), *Hylochoerus* (n = 21, orange), *Potamochoerus* (n = 33, blue), *Sus* (n = 25, pink) and *Kolpochoerus* (n = 68, black). Inter- and intra-specific variations within extant genera are shown (dotted lines): *Ph. aethiopicus* (*Pae*, n = 14), *Ph. africanus* (*Paf*, n = 9), *Po. larvatus* (*Pla*, n = 18), *Po. porcus* (*Ppo*, n = 15), *S. scrofa* from Poland (*Spo*, n = 19), *S. scrofa* from France (*Sfr*, n = 6). **A**, Biplot of complexity (Asfc) and anisotropy (epLsar); **B**, biplot of complexity (Asfc) and heterogeneity of complexity (HAsfc36). Median values are indicated and bars represent the inter-quartile ranges.

We also observe differences within the genera *Potamochoerus* and *Phacochoerus*, as well as intra-specific differences within *Sus scrofa* (Fig. 3A). These differences concern the anisotropy (epLsar) and the heterogeneity (HAsfc36) of surface textures, not the complexity (Asfc; ESM1: Tables S5, S6 and S8). Notably, common warthogs (*Ph. africanus*) exhibit wear surfaces less anisotropic than those of desert warthogs (*Ph. aethiopicus*), as shown by the median value of the former being 1.5 times lower than for the latter (Fig. 3, ESM1: Table S9). However, the two samples of warthogs do not significantly differ (ESM1: Table S11). Common warthogs even exhibit a median epLsar value below the ones measured for the two populations of *Sus scrofa* and the one of *Po. larvatus*. Still, they show the highest inter-quartile range with specimens that present more anisotropic surfaces than all other omnivores, and no significant difference is identified between them and the other suid samples (ESM1: Table S11). Regarding HAsfc36, although desert warthogs tend to show higher values than common warthogs, they do not significantly differ, and both species tend to display more homogeneous wear surfaces than omnivorous and less-specialized suids ($p < 0.04$ with LSD test only; ESM1: Table S12). Species of *Potamochoerus* slightly differ, *Po. larvatus* showing more anisotropic, more complex and more heterogeneous surfaces than *Po. porcus* (Fig. 3), but differences are not significant (ESM1: Tables S11 and S12). At last, the two wild boar populations also slightly differ (though not significantly; ESM1: Tables S11 and S12), the boars from France showing more complex, more anisotropic and less heterogeneous wear surfaces than boars from the Białowieża Forest in Poland (Fig. 3).

COMPARISONS BETWEEN *KOLPOCHOERUS* FROM SHUNGURA AND EXTANT SUIDS

Specimens of *Kolpochoerus* from Shungura show low values of complexity, being more similar to herbivorous genera *Phacochoerus* and *Hylochoerus*, and clearly distinct from *Sus* (Fig. 3, Table 2, ESM1: Table S5). Regarding anisotropy, specimens of *Kolpochoerus* show the lowest values and only partly overlap with the values observed on extant suids (Fig. 3A, Tables 1 and 2). Indeed, about half of the specimens of *Kolpochoerus* show anisotropy values that are lower than the first quartile of each extant suid samples (Fig. 3A). They are well distinct from *Phacochoerus* (Fig. 3A, Table 2, ESM1: Table S8). When looking at the heterogeneity of complexity, *Kolpochoerus* also tend to show low mean and median values and are similar to *Phacochoerus* (Fig. 3B, Table 1). However, while *Phacochoerus* strongly differs from the three other extant genera, *Kolpochoerus* show some surfaces that are more heterogeneous than *Phacochoerus* and overlap with the three other taxa. Still, *Kolpochoerus* differs from *Sus*, which has the highest values (Fig.

3B, Table 2, ESM1: Table S6). Summary statistics of the total sample of *Kolpochoerus* are provided in Table 1.

DMTA AMONG *KOLPOCHOERUS* THROUGH THE SHUNGURA SEQUENCE

Through the sequence, no significant difference in the complexity of wear surfaces of *Kolpochoerus* is detected between members with both post-hoc tests, as well as in the heterogeneity of complexity. The complexity seems stable, except for specimens from members E and F that tend to display less complex surfaces (Fig. 4, Tables 1 and 2). Compared to extant suids, specimens from members E, F and G show significantly less complex surfaces than *Sus* ($p < 0.03$ with both post-hoc tests, Table 2, ESM1: Table S5). When looking at HASfc36, we observe increasing values from Member C to Member F, then a decrease from Member F to Member J, and again higher values in Member L. The most heterogeneous surfaces are found in members F and G (Fig. 4, Tables 1 and 2). When compared to extant suids, *Kolpochoerus* are generally more similar to *Phacochoerus* in HASfc36. Nonetheless, it is worth noting that specimens of *Kolpochoerus* from members F and G have less homogeneous surfaces than those of *Phacochoerus*, even though significant differences are only identified with LSD post-hoc test. In Member C, specimens of *Kolpochoerus* significantly differ from the three other extant genera ($p < 0.03$ with both post-hoc tests, Table 2, ESM1: Table S6). In members E and J, they significantly differ from *Sus* only ($p < 0.05$ with both post-hoc tests, Table 2, ESM1: Table S6). Regarding the anisotropy, mean and median values are stable within the sequence. Specimens from the lower part of Member G are slightly more anisotropic (Fig. 4, Tables 1 and 2), but they significantly differ from members E and L only ($p < 0.02$, ESM1: Table S8). Compared to extant taxa, *Kolpochoerus* from all members except G strongly differ from herbivorous *Phacochoerus* ($p < 0.02$, Table 2, ESM1: Table S8). They also show less anisotropic surfaces than *Hylochoerus*, except in members G and J ($p < 0.02$, Table 2, ESM1: Table S8). Only specimens from members E and L show significantly less anisotropic surfaces than omnivorous genera *Sus* and *Potamochoerus* ($p < 0.02$, Table 2, ESM1: Table S8). Altogether, even though DMTA parameters do not reveal substantial changes between members, our results highlight some variations in dental microwear textures of *Kolpochoerus* within the sequence.

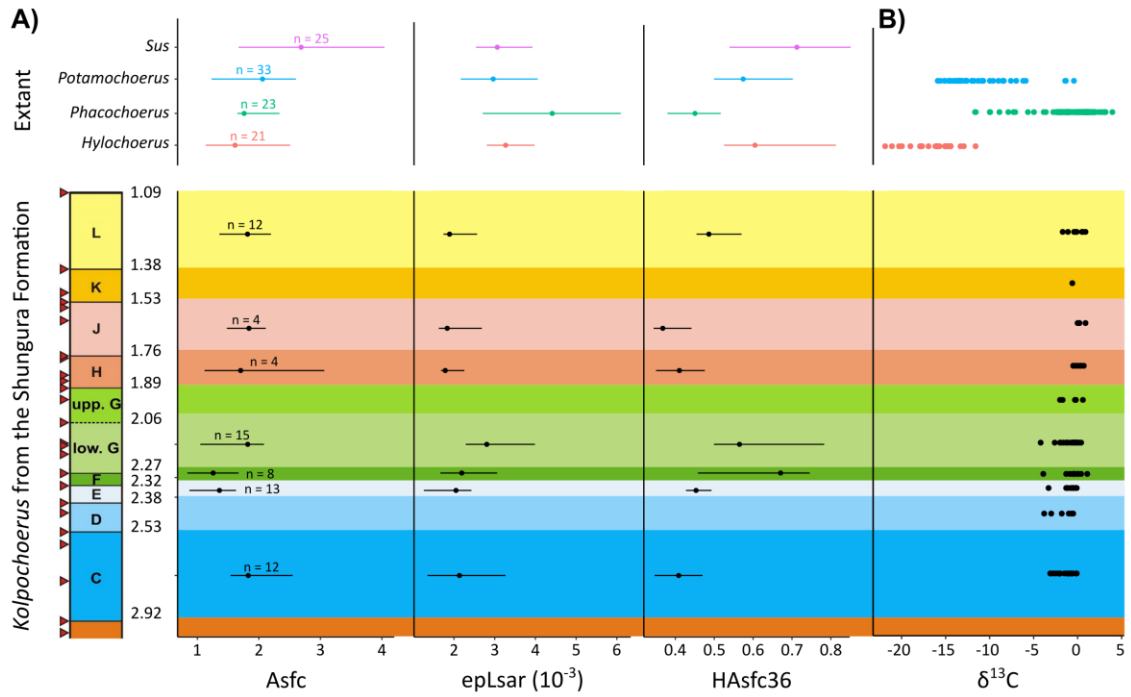


FIG. 4. – **A**, Dental microwear texture parameters on extinct *Kolpochoerus* (black) through the different members of the Shungura Formation (Asfc: complexity, epLsar: anisotropy, and HASfc36: heterogeneity of complexity). Median values are indicated and bars represent inter-quartile ranges. Data on 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 ($\delta^{13}\text{C}$ ‰ 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).

TABLE 2. – Combined Tukey’s HSD and Fisher’s LSD post-hoc tests following one-way ANOVAs (for Asfc and HAsfc36), and Dunn’s test (for epLsar). Parameters in bold are significant ($p < 0.05$) with both post-hoc tests. 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	<i>Asfc</i> ; <i>epLsar</i> ; HAsfc36
<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>

DISCUSSION

DENTAL MICROWEAR TEXTURES AND DIETARY HABITS IN EXTANT SUID TAXA

This study shows that DMT variations among extant suid taxa, despite overlapping data, reflect differences in dietary habits. These differences are mirrored in three commonly used SSFA parameters that describe the heterogeneity of orientation of wear scratches, the surface roughness and the heterogeneity of surface roughness: anisotropy (epLsar), complexity (Asfc) and heterogeneity of complexity (HAsfc36), respectively. Omnivorous wild boars show the most complex and heterogeneous wear surfaces, and dissimilarities with omnivorous *Potamochoerus* might reflect less variable diet in the latter taxon than in *Sus*. Graminivorous warthogs show the most anisotropic surfaces, as expected for a taxon mainly feeding on abrasive grasses, and the less heterogeneous ones. Microwear patterns of *Hylochoerus* likely reflect their mixed diet including much less abrasive foods than in *Phacochoerus*. These findings are congruent with observations from field studies and previous ecological studies based on dental microwear or stable isotopes (Skinner *et al.* 1976; d’Huart 1978; Breytenbach & Skinner 1982; Seydack 1990, 2017; Harris & Cerling 2002; Cerling & Viehl 2004; Treydte *et al.* 2006; Giménez-Anaya *et al.* 2008; d’Huart & Kingdon 2013; Souron *et al.* 2015b; Butynski & de Jong 2017; de Jong & Butynski 2017; Keuling *et al.* 2017; Melletti *et al.* 2017; Reyna-Hurtado *et al.* 2017; Mekonnen *et al.* 2018; Lazagabaster 2019; Edossa *et al.* 2021; Lazagabaster *et al.* 2021). Overall, we not only expand the extant DMT baseline developed by Souron *et al.* (2015b) and Lazagabaster (2019), but also highlight inter- and intra-specific differences in extant suids, which most likely reflect variations in food mechanical properties.

In our analysis, the herbivorous taxon *Phacochoerus* strongly differs from the omnivorous *Sus*, showing the highest anisotropy values, and the lowest in heterogeneity of complexity, along with low surface complexity (Fig. 3, Tables 1 and 2, ESM1: Tables S4 to S12. High anisotropy values and low complexity have been documented among graminivorous mammals in previous studies (Ungar *et al.* 2007; J. R. Scott 2012; Merceron *et al.* 2014). Thus, the DMT patterns observed on *Phacochoerus* likely reflect the large amount of fibrous items in its diet, mainly herbaceous monocots (Cumming 1975, 2013; Harris & Cerling 2002; Treydte *et al.* 2006; Butynski & de Jong 2017; de Jong & Butynski 2017). In addition, both common and desert warthogs show homogeneous surfaces compared to other suids, which might reflect their rather monotypic diets on herbaceous plants. These results are congruent with previous dental microwear studies (Souron *et al.* 2015b; Lazagabaster 2019). In the common warthogs, the large dispersion of anisotropy values (see 1st and 3rd quartiles on Fig. 3) could reflect the

seasonality of the diet, as it has been suggested that *Ph. africanus* may feed more on roots, barks and rhizomes during the dry season (Cumming 1975, 2013; Souron *et al.* 2015b; but see Treydte *et al.* 2006 showing little evidence for such seasonal variations). Even though *Ph. africanus* show highly dispersed anisotropy values, the median value is much lower than the one of desert warthogs (*Ph. aethiopicus*; Fig. 3). Although the ecology of the desert warthog is largely unknown, these dissimilarities in DMT patterns likely reflect subtle differences in feeding habits and/or habitat between the two species. A different timing of third molar root development in desert warthogs (i.e. late-forming roots allowing enamel columns to continue growing, thus extending tooth durability) might reflect an adaptation to a more abrasive diet and/or more exogenous particles than common warthogs (Grubb & d'Huart 2013). Such a diet could explain the higher values of anisotropy in *Ph. aethiopicus*. In *Ph. africanus*, the low epLsar median value could reflect feeding preferences on young, fresh (i.e., less abrasive) graminoid and non-graminoid herbs (Butynski & de Jong 2017; see also Francisco *et al.* 2018).

In contrast, the omnivorous *Sus scrofa* shows low anisotropy values and high values of complexity and heterogeneity of complexity (Fig. 3, Tables 1 and 3, ESM1: Tables S4 to S12). This probably reflects the lesser amount of fibrous plants in its diet and greater proportion of fruits, USOs, animal matter, and fungi. Wild boars show significantly higher values in heterogeneity of complexity than *Phacochoerus*. Although the impact of diet on HAsfc remains poorly understood, previous studies have suggested that a more diversified diet leads to heterogeneous wear surfaces (Scott *et al.* 2012; Souron *et al.* 2015b; Ramdarshan *et al.* 2016; Merceron *et al.* 2018). Here, our results tend to support this hypothesis, but there is no doubt that the link between dietary diversity and surface heterogeneity is not that straightforward, notably considering the similarity between *Potamochoerus* and *Hylochoerus*. Differences in heterogeneity could also partly relate to other factors, such as grit ingestion and/or seasonal variations (Souron *et al.* 2015b; Louail *et al.* 2022). Highly dispersed complexity values, along with high values of heterogeneity, might reflect the intra-specific dietary variations among *Sus scrofa*, as well as seasonal variations in the diet (e.g., Keuling *et al.* 2017). Moreover, highly dispersed values most likely reflect the fact that our sample includes specimens from two different geographic areas in Poland and France, with different climates (continental and oceanic, respectively) and slaughtering periods (spring and winter, respectively), as well as differences in the access to agricultural crops or other anthropogenic food supplies. The Białowieża Forest in Poland is one of the best-preserved forest in Europe with limited human impact, and the Polish specimens contrast with the few individuals from France. Notably, the latter tend to show more complex surfaces compared to specimens from Poland (Fig. 3). This

could be explained by a higher consumption of acorns, nuts, roots and tubers in winter than in spring (Keuling *et al.* 2017). A greater consumption of agricultural crops or other by-products of human activities (notably due to hunter-provided supplemental foods in autumn and winter; Keuling *et al.* 2017) might also explain this pattern, as previously observed in wild/free-ranging and stall-fed populations of *Sus* (Yamada *et al.* 2018; Louail *et al.* 2021, 2022). However, we cannot further test this due to the lack of precise data on feeding habits and habitat.

The other omnivorous taxon *Potamochoerus* is similar to *Sus* in terms of anisotropy, but intermediate between *Phacochoerus* and *Sus* when looking at complexity and heterogeneity of complexity. Although a previous study observed more similar DMT patterns between *Potamochoerus* and *Sus scrofa* (Souron *et al.* 2015b; ESM1: Table S13), our results are not directly comparable because these authors used an interferometry-based microscope with a 50× objective whereas we used a confocal profilometer with a 100× objective. Moreover, some of the specimens of *Potamochoerus* and *Sus scrofa* that we studied were not included in Souron *et al.* (2015b). In the present study, some specimens of *Po. larvatus* come from a more open environment (specimens from MZUF, ESM1: Table S1) than the various ones characterizing this genus. Some of them show low complexity values, which might contribute to the differences between Souron *et al.* (2015b) and the present study at the generic level. Moreover, the use of different modules for extracting SSFA parameters might also contribute to differences between the two previous DMTA studies on extant suids (Souron *et al.* 2015b; Lazagabaster 2019; ESM1: Table S13) and the present one (i.e. use of Toothfrax module and, here, use of MountainsMap module; see Calandra *et al.* 2022). In his study, Lazagabaster (2019) observed different DMT patterns between *Po. larvatus* and *Po. porcus*, the former showing more anisotropic, less complex and less heterogeneous wear surfaces than the latter (ESM1: Table S13). The author suggested this could relate to differences in habitats, *Po. larvatus* inhabiting in general more open areas than *Po. porcus* (see also the compilation of isotopic data in Lazagabaster *et al.* 2021 suggesting higher intake of C₄ foods in *Po. larvatus*). Here, we observe that *Po. larvatus* tend to show more anisotropic but more complex and more heterogeneous wear surfaces than *Po. porcus*. These disparities between Lazagabaster's study (2019) and the present one could also be due to differences in geographic provenance or slaughtering periods of specimens sampled. In addition, two specimens identified as *Po. porcus* in Lazagabaster's study come from localities where only *Po. larvatus* is known and one specimen is impossible to identify to specific level without further study of its morphology as it comes from a region where both species occur. This implies a reduction of the sample size of *Po. porcus* in Lazagabaster (2019) from six to three specimens (and an increase of the sample

size of *Po. larvatus* from 23 to 25 specimens), which makes robust statistical comparisons between the two species difficult. More studies are needed to further investigate variations in dietary habits within and between the two species. Overall, our results show that the DMT patterns of *Potamochoerus* reflect the distinct dietary habits between them and herbivorous *Phacochoerus*. Dissimilarities with wild boars could reflect a less versatile diet in terms of physical and mechanical properties than in wild boars, which might face greater seasonal variation in food availability in mid-latitudes than *Potamochoerus* (see also differences in dental topographies documented by Rannikko *et al.* 2020). Observed similarities with *Hylochoerus* (notably in anisotropy and heterogeneity of complexity) could partly relate to their common preference for forested or ecotone areas (Reyna-Hurtado *et al.* 2017), although *Potamochoerus* probably have a more diversified diet than *Hylochoerus* in terms of physical and mechanical properties.

Our results on DMT patterns of *Hylochoerus* are quite surprising because they do not reflect the strong herbivory component in their diet, as observed in previous dental microwear studies (Souron *et al.* 2015b; Lazagabaster 2019; ESM1: Table S13). Nonetheless, in addition to differences in methodological approaches (see above and ESM1: Table S13) that could explain these incongruities, it is worth noting that Souron *et al.* (2015b) and Lazagabaster (2019) only included 5 and 3 specimens (respectively) of *Hylochoerus*, whereas 21 specimens were included in the present study. Here, specimens of *Hylochoerus* exhibit low complexity surfaces similarly to herbivorous *Phacochoerus*, but they show in average less anisotropic surfaces. They also exhibit more heterogeneous surfaces than *Phacochoerus*, but the difference between them is reduced compared to previous observations in Souron *et al.* (2015b) and Lazagabaster (2019) (HAsfc9 and HAsfc81; ESM1: Table S13). Our results on a larger sample of *Hylochoerus* are congruent with a lower amount of abrasive grasses in its diet than *Phacochoerus*, as documented by field studies. Less anisotropic surfaces could also be partly explained by differences in mastication biomechanics between the two species, with less extensive transverse movements in *Hylochoerus* (Ewer 1970; Herring 1980). As suggested by Souron *et al.* (2015b), the more heterogeneous surfaces could also be related to less frequent rooting behaviors (see also Louail *et al.* 2022) than in *Phacochoerus*. Even though the feeding ecology of *Hylochoerus* remains largely unknown, several studies have highlighted that this taxon does not feed predominantly on grasses and should rather be considered as an herbivorous mixed feeder (Harris & Cerling 2002; d'Huart & Kingdon 2013; Souron *et al.* 2015b). Notably, a previous work on stable carbon isotope composition of forest hog hair has shown that they consume very little C₄ grasses during the year, reaching only up to 20 % grass in the diet at the

beginning of the rainy season (Cerling & Viehl 2004). Although it is unclear why DMT patterns of *Hylochoerus* are that similar to those of the omnivorous *Potamochoerus*, it is likely that they reflect a diet consisting of various herbaceous vegetation in closed, forested habitats, probably including soft browse along with low-abrasive herbaceous plants (grasses and forbs), as reflected by low complexity and low anisotropy. Overall, this microwear pattern is coherent with much less abrasive foods in *Hylochoerus* diet than in *Phacochoerus*.

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

DENTAL MICROWEAR TEXTURES OF *KOLPOCHOERUS* FROM SHUNGURA: DIETARY PERSPECTIVES

We investigated dental microwear texture variations on extinct *Kolpochoerus* from the Shungura Formation. The total sample of *Kolpochoerus* shows DMT characterized by relatively low values of complexity, anisotropy and heterogeneity of complexity compared to most extant taxa. Thus, they tend to differ from all extant taxa. Although they resemble to *Phacochoerus* in Asfc and HAsfc, more specimens have lower Asfc and higher HAsfc values than in the warthog sample. More particularly, they strongly differ from *Phacochoerus* having the lowest anisotropy values. These differences between *Phacochoerus* and *Kolpochoerus* are expected considering that the former is highly specialized. Still, our results appear to contrast with previous studies on dental morphology and stable carbon isotopic compositions of *Kolpochoerus*, which have related dental morphological changes, mainly molar enlargement, to increasing consumption of abrasive grasses. The following paragraphs will discuss 1) the unlikeness that our dental microwear results on *Kolpochoerus* reflect a taphonomic alteration, and 2) the likelihood that DMT preserved a dietary signal reflecting a significant proportion of low-abrasive herbaceous plants (grasses and forbs).

The question of potential taphonomic alterations in our sample of *Kolpochoerus* arises because their DMT patterns differ from all extant suid taxa in their very isotropic wear surfaces. Notably, samples from members E (n = 13) and L (n = 12) significantly differ from all other extant taxa in this parameter (Tables 1 and 2, Fig. 5). Unfortunately, the impact of taphonomic alterations (mechanical or chemical) on dental microwear remains largely unknown, as only few studies have investigated this issue (Gordon 1983, 1984; King *et al.* 1999; Böhm *et al.*

2019; Uzunidis *et al.* 2021; Weber *et al.* 2022). Only three of them have been conducted on non-human mammal teeth (Böhm *et al.* 2019; Uzunidis *et al.* 2021; Weber *et al.* 2022), and only two have considered standard and commonly used DMTA parameters (Böhm *et al.* 2019; Weber *et al.* 2022). Overall, all these studies observed slightly polished wear surfaces following tumbling experiments, but showed that the dietary signal is still preserved. One recent study pointed out that new abrasion marks following a tumbling experiment have a more isotropic distribution (Uzunidis *et al.* 2021). However, these authors used 2D low-magnification microwear analysis and not standard 3D textural parameters, and this trend is not confirmed by the other studies (Böhm *et al.* 2019; Weber *et al.* 2022). Further studies are needed to better understand how texture parameters, notably epLsar, might be influenced by post-mortem alterations, particularly fluvial transport in sediments. To date, none of these works can be used to validate or invalidate the hypothesis of potential taphonomic alterations in our sample. In contrast, although some specimens excluded from the analyses might have been altered by fluvial transport, several elements strengthen our assumption that wear surfaces used in this study have preserved their dietary signal. Indeed, we first conducted a meticulous selection of fossil surfaces and discarded all specimens with evident post-mortem alterations, as well as dubious ones (see Fig. 2 and Weber *et al.* 2021). We also calculated the mean values of several scanned microwear areas on the same (or similar) facet, which avoids including extreme values in our analysis. Overall, DMT parameters measured on *Kolpochoerus* specimens are still within the range of our extant suid baseline. At last, although Lazagabaster (2019) focused on Pliocene specimens, his published DMT data on *Kolpochoerus* from the Hadar Formation also show this trend towards lower anisotropy than in his extant sample, except for *Po. porcus*, a situation nearly similar to our observations. Knowing that fossil preservation and depositional conditions (predominantly lacustrine) are quite different between Shungura and the Hadar Formation, this parallel situation in DMT signals reinforces our assumption that these low anisotropy values in Shungura *Kolpochoerus* are not the results of a taphonomic process, but reflect dietary habits.

The DMT patterns of *Kolpochoerus* analyzed in this study suggest substantial differences in dietary habits from extant suid taxa. They do not reflect the consumption of fibrous, abrasive plants as in herbivorous *Phacochoerus*, neither the consumption of hard or brittle foods as among omnivorous taxa. Although we observe a notable increase in anisotropy from Member E to Member G (both differ significantly; Fig. 4, ESM1: Table S8), values are still much lower than among *Phacochoerus* through all the sequence (except in Lower G). As such, DMT patterns of *Kolpochoerus* do not reflect a major change in the physical and mechanical properties of the diet through time that would reflect an increasing consumption of grasses, as

suggested by dental morphological changes. Nonetheless, regarding the heterogeneity of complexity (which is the only texture parameter that strongly distinguish the highly specialized species from the other suids), *Kolpochoerus* appear similar to *Phacochoerus*, having on average low values (Fig. 3). Although *Kolpochoerus* display more heterogeneous surfaces in members F and G (and L to a lesser extent; Fig. 3, ESM1: Table S6), these similarities with extant *Phacochoerus* could reflect a rather monotypic diet. At the species level, *Kolpochoerus* spp. from Shungura appear more similar to some specimens of common warthogs (*Ph. africanus*) that show low anisotropy values (Fig. 3). Differences in dietary habits between the two warthogs species need to be further investigated, but these resemblances between *Kolpochoerus* and common warthogs might reflect a less abrasive and specialized diet than in desert warthogs. Thus, we suggest their overall DMT patterns likely reflect the consumption of herbaceous plants, but rather low-abrasive than fibrous ones. It could explain the overall isotropic wear surfaces in *Kolpochoerus*, conversely to the highly specialized *Phacochoerus*. Indeed, we have highlighted that the more isotropic wear surfaces in numerous specimens of common warthogs (Fig. 4) might reflect their dietary preference for fresh, short, low-abrasive grasses. Moreover, preliminary observations by M.L. on controlled-fed pigs suggest that increasing consumption of low-abrasive herbaceous plants leads to decreasing anisotropy. Thus, our results appear in line with the hypothesis of *Kolpochoerus* having feeding preferences for fresh grass shoots, probably in more mesic habitats compared to other extinct suid taxa (Harris & Cerling 2002; Rannikko *et al.* 2017, 2020; Yang *et al.* 2022). We propose that this dietary niche is reflected, at Shungura, in the combination of a progressive enlargement and complexity of third molars, a strong C₄ signal, together with DMT patterns reflecting low-abrasive foods (Fig. 4).

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 give an advantage, among herbivorous suids that do not have a specialized digestive physiology such as *Kolpochoerus*, for reducing as much as possible short, young grasses (Lucas 2004; Souron 2017). Thus, dental morphological changes are still in line with feeding preferences on short, young, low-abrasive grasses, as reflected by their DMT patterns. In addition, even if the strong C₄ signal observed in *Kolpochoerus* resemble that of extant warthogs (Fig. 4), it does not necessarily reflect the consumption of abrasive grasses. It is largely assumed that grasses possessing the C₄ photosynthetic pathway are high accumulators of silicon (Si), and consequently are more abrasive than C₃ grasses or browse. However, a recent

study has shown that Si concentrations in C₃ and C₄ grasses are also related to growth conditions (hot and dry conditions promoting higher Si accumulation), not only the photosynthetic pathway (Brightly *et al.* 2020). Other studies have investigated the factors of Si accumulation in grasses, and they all highlight a substantial role of growth conditions (e.g., Katz *et al.* 2014, 2018; Quigley *et al.* 2017). Thus, while a strong C₄ signal likely reflects the consumption of herbaceous plants (mostly graminoids), it does not indicate the abrasiveness of the diet, whereas DMT does. Past environmental conditions, such as humidity and insolation, might have more impacted the physical properties of the vegetation. Several studies have highlighted that while Pliocene and Pleistocene eastern African sites show a general trend toward more open landscapes dominated by C₄ resources, the Lower Omo Valley was composed of a mosaic of closed and wooded habitats, riverine forests and open grasslands (e.g., Levin *et al.* 2011; Barr 2015; Negash *et al.* 2015, 2020). This implies that the Lower Omo Valley would have provided a diversity of habitats to exploit, with the persistence of mesic conditions. All studies that analyzed stable oxygen isotopes in *Kolpochoerus* in eastern African sites have shown low $\delta^{18}\text{O}$ values compared to other extinct suid taxa, notably at Shungura (Harris & Cerling 2002; Bedaso *et al.* 2010, 2013; Bibi *et al.* 2013; Negash *et al.* 2020). Moreover, *Kolpochoerus* tend to show lower values than contemporaneous *Metridiochoerus* from the same sites (Harris & Cerling 2002; Patterson *et al.* 2019; see also Negash *et al.* 2020), which might indicate they were more water dependent. This is supported by other studies that focused on relative abundances and dental topography of Plio-Pleistocene suids in the Turkana basin (Rannikko *et al.* 2017, 2020). Altogether, the combination of these different paleoecological proxies tend to support the hypothesis that *Kolpochoerus* favored more mesic and/or woody habitats, such as at Shungura, with significant consumption of herbaceous plants but dietary preferences for short, soft and low-abrasive ones.

This study focused on specimens of the *K. limnetes/K. aff. paiceae* lineage from the Shungura Formation. As stated in the introduction, *Kolpochoerus* was ubiquitous in the Plio-Pleistocene Africa (Broom 1931; Harris & White 1979; Hendeby & Cooke 1985; White 1995; Brunet & White 2001; Suwa *et al.* 2003; Bishop 2011; Haile-Selassie & Simpson 2013; Souron *et al.* 2015a), and was highly diversified notably in terms of dental morphologies (Harris & White 1979; Brunet & White 2001; Bishop *et al.* 2006; Souron 2012, 2017; Haile-Selassie & Simpson 2013). It most likely exploited a variety of habitats and had various feeding habits depending on the species considered and on local environmental and ecological conditions. As such, we do not pretend here to reconstruct the diet on the generic scale, nor on the Plio-Pleistocene Africa as a whole. Rather, we provide new insights on the paleoecology of this

specific lineage and at a local scale. It is possible that specimens attributed to other species, such as *Kolpochoerus majus* that overall retained a more conservative dental morphology (Souron *et al.* 2015a), had different dietary habits despite similarly displaying high $\delta^{13}\text{C}$ values. In addition, given the apparent ecological flexibility of *Kolpochoerus*, one might expect that specimens from other sites than the Shungura Formation had different feeding habits, reflecting different local environmental dynamics. This underlines the potential of this taxon to contribute to the reconstruction of past environments throughout Plio-Pleistocene Africa, as well as for understanding the relationships between environmental, dietary, and morphological changes in omnivorous-to-herbivorous taxa.

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Conflict of interest

The authors declare no competing interests.

Author contributions

ML, AS, GM and JRB designed the study. GM, AS and JRB provided supervision. AS and ML were responsible for data curation. JRB supervised fieldwork, curated collections, and managed specimen database. ML was responsible for formal analysis and visualization. ML wrote the article with contributions from all the co-authors.

Data availability

Supplementary information accompanies this paper at <https://osf.io/ept6r/>.

REFERENCES

ALEMSEGED Z., BOBE R. & GERAADS D. 2007. — Comparability of fossil data and its significance for the interpretation of hominin environments, in BOBE R., ALEMSEGED Z. & BEHRENSMEYER A. K. (eds.), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer Netherlands, Dordrecht: 159-181. https://doi.org/10.1007/978-1-4020-3098-7_7

- ANDREWS P., LORD J. M. & EVANS E. M. N. 1979. — Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* 11(2): 177-205. <https://doi.org/10.1111/j.1095-8312.1979.tb00034.x>
- ARAMBOURG C. 1934. — Le *Dinotherium* des gisements de l'Omo (Abyssinie). *Bulletin de La Société Géologique de France* 5: 305-310.
- ARAMBOURG C. 1943. — Observations sur les Suidés fossiles du Pléistocène d'Afrique. *Bulletin Du Muséum National d'Histoire Naturelle* 15(6): 471-476.
- BARR W. A. 2015. — Paleoenvironments of the Shungura Formation (Plio-Pleistocene: Ethiopia) based on ecomorphology of the bovid astragalus. *Journal of Human Evolution* 88: 97-107. <https://doi.org/10.1016/j.jhevol.2015.05.002>
- BEDASO Z. K., WYNN J. G., ALEMSEGED Z. & GERAADS D. 2010. — Paleoenvironmental reconstruction of the Asbole fauna (Busidima Formation, Afar, Ethiopia) using stable isotopes. *Geobios* 43(2): 165-177. <https://doi.org/10.1016/j.geobios.2009.09.008>
- BEDASO Z. K., WYNN J. G., ALEMSEGED Z. & GERAADS D. 2013. — Dietary and paleoenvironmental reconstruction using stable isotopes of herbivore tooth enamel from middle Pliocene Dikika, Ethiopia: Implication for *Australopithecus afarensis* habitat and food resources. *Journal of Human Evolution* 64(1): 21-38. <https://doi.org/10.1016/j.jhevol.2012.05.015>
- BERLIOZ E., AZORIT C., BLONDEL C., RUIZ M. S. T. & MERCERON G. 2017. — Deer in an arid habitat: Dental microwear textures track feeding adaptability. *Hystrix, the Italian Journal of Mammalogy* 28: 222-230. <https://doi.org/10.4404/hystrix-28.2-12048>
- BERLIOZ E., KOSTOPOULOS D. S., BLONDEL C. & MERCERON G. 2018. — Feeding ecology of *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe during the early Pleistocene. *Comptes Rendus Palevol* 17(4): 320-332. <https://doi.org/10.1016/j.crpv.2017.07.002>
- BIBI F., PANTE M., SOURON A., STEWART K., VARELA S., WERDELIN L., BOISSERIE J.-R., FORTELIUS M., HLUSKO L., NJAU J. & DE LA TORRE I. 2018. — Paleoecology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania: The mammal and fish evidence. *Journal of Human Evolution* 120: 48-75. <https://doi.org/10.1016/j.jhevol.2017.10.009>
- BIBI F., SOURON A., BOCHERENS H., UNO K. & BOISSERIE J.-R. 2013. — Ecological change in the lower Omo Valley around 2.8 Ma. *Biology Letters* 9(1): 20120890-20120890. <https://doi.org/10.1098/rsbl.2012.0890>

- BISHOP L. C., KING T., HILL A. & WOOD B. 2006. — Palaeoecology of *Kolpochoerus heseloni* (= *K. limnetes*): A multiproxy approach. *Transactions of the Royal Society of South Africa* 61(2): 81-88. <https://doi.org/10.1080/00359190609519956>
- BISHOP L. C. 2011. — Suidae, in HARRISON T. (ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context: Volume 2: Fossil hominins and the associated fauna*. Springer Netherlands, Dordrecht: 327-337.
- BLONDEL C., MERCERON G., ROWAN J., SURAULT J. & BOISSERIE J.-R. 2022. — Dietary ecology of Reduncini (Bovidae) from the Shungura Formation, Lower Omo Valley, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 587: 110789. <https://doi.org/10.1016/j.palaeo.2021.110789>
- BLONDEL C., ROWAN J., MERCERON G., BIBI F., NEGASH E., BARR W. A. & BOISSERIE J.-R. 2018. — Feeding ecology of Tragelaphini (Bovidae) from the Shungura Formation, Omo Valley, Ethiopia: Contribution of dental wear analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 496: 103-120. <https://doi.org/10.1016/j.palaeo.2018.01.027>
- BÖHM K., WINKLER D. E., KAISER T. M. & TÜTKEN T. 2019. — Post-mortem alteration of diet-related enamel surface textures through artificial biostratinomy: A tumbling experiment using mammal teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 518: 215-231. <https://doi.org/10.1016/j.palaeo.2019.01.008>
- BOISSERIE J.-R., GUY F., DELAGNES A., HLUSKO L. J., BIBI F., BEYENE Y. & GUILLEMOT C. 2008. — New palaeoanthropological research in the Plio-Pleistocene Omo Group, Lower Omo Valley, SNNPR (Southern Nations, Nationalities and People Regions), Ethiopia. *Comptes Rendus Palevol* 7(7): 429-439. <https://doi.org/10.1016/j.crpv.2008.07.010>
- BOISSERIE J.-R., SOURON A., MACKAYE H. T., LIKIUS A., VIGNAUD P. & BRUNET M. 2014. — A new species of *Nyanzachoerus* (Cetartiodactyla: Suidae) from the late Miocene Toros-Ménalla, Chad, central Africa. *PLoS One* 9(8): e103221
- BREYTENBACH G. J. & SKINNER J. D. 1982. — Diet, feeding and habitat utilization by bushpigs *Potamochoerus porcus* Linnaeus. *South African Journal of Wildlife Research* 12: 1-7.
- BRIGHTLY W. H., HARTLEY S. E., OSBORNE C. P., SIMPSON K. J. & STRÖMBERG C. A. E. 2020. — High silicon concentrations in grasses are linked to environmental conditions and not associated with C₄ photosynthesis. *Global Change Biology* 26(12): 7128-7143. <https://doi.org/10.1111/gcb.15343>

- BRINK J. S., GOWLETT J. A. J., HERRIES A. I. R., HANCOX J., MOGGI-CECCHI J., CODRON D., ROSSOUW L., TROWER G., STONE O. M. L., BOUSMAN B., GRÜN R. & SOURON A. 2022 — Cornelia-Uitzoek: Paleoecology, Archeology, and Geochronology, *in* Bobe R., Reynolds S. C. (eds.), *African Paleoecology and Human Evolution*. Cambridge University Press, Cambridge: 120-134. <https://doi.org/10.1017/9781139696470.012>
- BROOM R. 1931 — A new extinct giant pig from the diamond gravels of Windsorton, South Africa. *Records of the Albany Museum Grahamstown*, 4: 167-168.
- BRUNET M. & WHITE T. D. 2001. — Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Éthiopie; Tchad). *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* 332(1): 51-57. [https://doi.org/10.1016/S1251-8050\(00\)01492-0](https://doi.org/10.1016/S1251-8050(00)01492-0)
- BUTYNSKI T. M. & DE JONG Y. A. 2017. — Common Warthog *Phacochoerus africanus* (Gmelin, 1788), *in* MELLETTI M. & MEJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 85-100. [HTTPS://DOI.ORG/10.1017/9781316941232.011](https://doi.org/10.1017/9781316941232.011)
- CALANDRA I., BOB K., MERCERON G., BLATEYRON F., HILDEBRANDT A., SCHULZ-KORNAS E., SOURON A., WINKLER D.E. 2022. — Surface texture analysis in Toothfrax and MountainsMap® SSFA module: Different software packages, different results? *Peer Community Journal* 2: e77. <https://doi.org/10.24072/pcjournal.204>
- CERLING T. E. & VIEHL K. 2004. — Seasonal diet changes of the forest hog (*Hylochoerus meinertzhageni* Thomas) based on the carbon isotopic composition of hair. *African Journal of Ecology* 42(2): 88-92. <https://doi.org/10.1111/j.1365-2028.2004.00500.x>
- CHAVASSEAU O. 2008. — *Les faunes miocènes de grands mammifères d'Asie du Sud-Est: biochronologie et biogéographie*. PhD thesis, University of Montpellier 2, Montpellier, 308 p.
- COOKE H. B. S. 1985. — Plio-Pleistocene Suidae in relation to African hominid deposits, *in* COOPENS Y. (ed.), *L'Environnement des Hominidés au Plio-Pléistocène*. Masson, Paris: 101-117.
- COOKE H. B. S. 2007. — Stratigraphic variation in Suidae from the Shungura Formation and some coeval deposits, *in* BOBE R., ALEMSEGED Z. & BEHRENSMEYER A. K. (eds.), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer Netherlands, Dordrecht : 107-127. https://doi.org/10.1007/978-1-4020-3098-7_5

- COPPENS Y. 1975. — Évolution des hominidés et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Éthiopie. *Comptes Rendus de l'Académie Des Sciences Paris* 281(22): 1693-1696.
- CUMMING D. H. M. 1975. — *Field study of the ecology and behaviour of warthog*. The Trustees of the National Museums and Monuments of Rhodesia, Salisbury, 179 p.
- CUMMING D. H. M. 2013. — *Phacochoerus africanus*, in Kingdon J. & Hoffmann M. (eds.), *Mammals of Africa. Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*. Bloomsbury Publishing, London: 54-60.
- D'HUART J. P. 1978. — *Ecologie de l'hylochère (Hylochoerus meinertzhageni Thomas) au Parc national des Virunga. Exploration du Parc National des Virunga. Deuxième Série, Fascicule 25*. Fondation pour Favoriser les Recherches scientifiques en Afrique, Brussels, 156 p.
- D'HUART J. P. & GRUBB P. 2005. — A photographic guide to the differences between the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*). *Suiform Soundings* 5: 4-8.
- D'HUART J. P. & KINGDON J. 2013. — *Hylochoerus meinertzhageni*, in KINGDON J. & HOFFMANN M. (eds.), *Mammals of Africa. Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*. Bloomsbury Publishing, London: 42-49.
- DAEGLING D. J., HUA L.-C. & UNGAR P. S. 2016. — The role of food stiffness in dental microwear feature formation. *Archives of Oral Biology* 71: 16-23. <https://doi.org/10.1016/j.archoralbio.2016.06.018>
- DAVIS M. & PINEDA-MUNOZ S. 2016. — The temporal scale of diet and dietary proxies. *Ecology and Evolution* 6(6): 1883-1897. <https://doi.org/10.1002/ece3.2054>
- DE JONG Y. A. & BUTYNSKI T. M. 2017. — Desert Warthog *Phacochoerus aethiopicus* (Pallas, 1766), in MELLETTI M. & MEIJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 101-113. <https://doi.org/10.1017/9781316941232.012>
- DE JONG Y. A., D'HUART J. P. & BUTYNSKI T. M. 2023. — Biogeography and conservation of desert warthog *Phacochoerus aethiopicus* and common warthog *Phacochoerus africanus* (Artiodactyla: Suidae) in the Horn of Africa. *Mammalia* 87(1): 1-19.
- EDOSSA A., BEKELE A. & DEBELLA H. J. 2021. — Diet preferences of common warthogs (*Phacochoerus africanus*) in Gassi and Haro Aba Diko controlled hunting areas, Western Ethiopia. *Global Ecology and Conservation* 29: e01722. <https://doi.org/10.1016/j.gecco.2021.e01722>

- EWER R. F. 1970. — The head of the forest hog, *Hylochoerus meinertzhageni*. *African Journal of Ecology* 8: 43–52. <https://doi.org/10.1111/j.1365-2028.1970.tb00829.x>
- FEIBEL C. S., BROWN F. H. & MCDUGALL I. 1989. — Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* 78(4): 595-622. <https://doi.org/10.1002/ajpa.1330780412>
- FORTELIUS M., ERONEN J., JERNVALL J., LIU L., PUSHKINA D., RINNE J., TESAKOV A., VISLOBOKOVA I., ZHANG Z. & ZHOU L. 2002. — Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research* 4: 1005-1016.
- FRANCISCO A., BRUNETIÈRE N. & MERCERON G. 2018. — Gathering and Analyzing Surface Parameters for Diet Identification Purposes. *Technologies* 6(3): 75. <https://doi.org/10.3390/technologies6030075>
- GERAADS D., GUÉRIN C. & FAURE M. 1986. — Les suidés du Pléistocène ancien d'Oubeidiyeh (Israël). *Mémoires et Travaux du Centre de Recherche Français de Jérusalem*, 5: 93105.
- GERAADS D., ALEMSEGED Z., REED D., WYNN J. & ROMAN D. C. 2004 — The Pleistocene fauna (other than Primates) from Asbole, lower Awash Valley, Ethiopia, and its environmental and biochronological implications. *Geobios*, 37(6): 697-718. <https://doi.org/10.1016/j.geobios.2003.05.011>
- GIMÉNEZ-ANAYA A., HERRERO J., ROSELL C., COUTO S. & GARCÍA-SERRANO A. 2008. — Food habits of wild boars (*Sus scrofa*) in a mediterranean coastal wetland. *Wetlands* 28(1): 197-203. <https://doi.org/10.1672/07-18.1>
- GORDON K. D. 1983. — Taphonomy of dental microwear: Can fossil microwear be studied productively? *American Journal of Physical Anthropology* 60(2): 169-273.
- GORDON K. D. 1984. — Hominoid Dental Microwear: Complications in the Use of Microwear Analysis to Detect Diet. *Journal of Dental Research* 63(8): 1043-1046. <https://doi.org/10.1177/00220345840630080601>
- GROVES C. & GRUBB P. 2011. — *Ungulate taxonomy*. Johns Hopkins University Press, Baltimore, 317 p.
- GRUBB P. & D'HUART J. P. 2010. — Rediscovery of the Cape warthog *Phacochoerus aethiopicus*: a review. *Journal of East African Natural History* 99(2): 77-102. <https://doi.org/10.2982/028.099.0204>

- GRUBB P. & D'HUART J. P. 2013. — *Phacochoerus aethiopicus*, in KINGDON J. & HOFFMANN M. (eds.), *Mammals of Africa. Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*. Bloomsbury Publishing, London: 51-53.
- HAILE-SELASSIE Y. & SIMPSON S. W. 2013. — A new species of *Kolpochoerus* (Mammalia: Suidae) from the Pliocene of Central Afar, Ethiopia: Its Taxonomy and Phylogenetic Relationships. *Journal of Mammalian Evolution* 20(2): 115-127. <https://doi.org/10.1007/s10914-012-9207-0>
- HARRIS J. M. & CERLING T. E. 2002. — Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256(1): 45-54. <https://doi.org/10.1017/S0952836902000067>
- HARRIS J. M. & WHITE T. D. 1979. — Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society* 69(2): 1-128. <https://doi.org/10.2307/1006288>
- HEINZELIN J. DE 1983. — *The Omo Group. Archives of the International Omo Research Expedition*. Volume 85. Annales du Musée Royal de l'Afrique Centrale, série 8, Sciences géologiques, Tervuren, 388 p.
- HENDEY Q. B. & COOKE H. B. S. 1985. — *Kolpochoerus paiceae* (Mammalia, Suidae) from Skurwerug, near Saldanha, South Africa, and its palaeoenvironmental implications. *Annals of the South African Museum*, 97(2): 9-56.
- HERRING S. W. 1980. — Functional Design of Cranial Muscles Comparative and Physiological Studies in Pigs. *American Zoologist* 20(1): 283-293. <https://doi.org/10.1093/icb/20.1.283>
- HIEMAE K. M. 2000. — Feeding in Mammals, in SCHWENK K. (ed.), *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. Academic Press, San Diego: 411-448. <https://doi.org/10.1016/B978-012632590-4/50014-9>
- HOWELL C. 1968. — Omo Research Expedition. *Nature* 219(5154): 5154. <https://doi.org/10.1038/219567a0>
- HULLOT M., LAURENT Y., MERCERON G. & ANTOINE P.-O. 2021. — Paleoecology of the Rhinocerotidae (Mammalia, Perissodactyla) from Béon 1, Montréal-du-Gers (late early Miocene, SW France): Insights from dental microwear texture analysis, mesowear, and enamel hypoplasia. *Palaeontologia Electronica* 24(2): a27. <https://doi.org/10.26879/1163>
- JANIS C. M. 2008. — An Evolutionary History of Browsing and Grazing Ungulates, in GORDON I. J. & PRINS H. H. T. (eds.), *The Ecology of Browsing and Grazing*. Springer Berlin Heidelberg, Berlin: 21-45. https://doi.org/10.1007/978-3-540-72422-3_2

- JANIS C. M. & FORTELIUS M. 1988. — On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews* 63(2): 197-230. <https://doi.org/10.1111/j.1469-185X.1988.tb00630.x>
- KATZ O., LEV-YADUN S. & BAR P. 2014. — Do phytoliths play an antiherbivory role in southwest Asian Asteraceae species and to what extent? *Flora - Morphology, Distribution, Functional Ecology of Plants* 209(7): 349-358. <https://doi.org/10.1016/j.flora.2014.03.010>
- KATZ O., LEV-YADUN S. & BAR P. 2018. — Plant Silicon and Phytolith Contents as Affected by Water Availability and Herbivory: Integrating Laboratory Experimentation and Natural Habitat Studies. *Silicon* 10(5): 2387-2389. <https://doi.org/10.1007/s12633-015-9310-y>
- KEULING O., PODGÓRSKI T., MONACO A., MELLETTI M., MERTA D., ALBRYCHT M., GENOV P. V., GETHÖFFER F., VETTER S. G., JORI F., SCALERA R. & GONGORA J. 2017. — Eurasian Wild Boar *Sus scrofa* (Linnaeus, 1758), in MELLETTI M. & MEJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 202-233. <https://doi.org/10.1017/9781316941232.023>
- KIDANE T., BROWN F. H. & KIDNEY C. 2014. — Magnetostratigraphy of the Fossil-Rich Shungura Formation, southwest Ethiopia. *Journal of African Earth Sciences* 97: 207-223. <https://doi.org/10.1016/j.jafrearsci.2014.05.005>
- KING T., ANDREWS P. & BOZ B. 1999. — Effect of taphonomic processes on dental microwear. *American Journal of Physical Anthropology* 108(3): 359-373. [https://doi.org/10.1002/\(SICI\)1096-8644\(199903\)108:3<359::AID-AJPA10>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1096-8644(199903)108:3<359::AID-AJPA10>3.0.CO;2-9)
- KULLMER O. 1999. — Evolution of African Plio-Pleistocene Suids (Artiodactyla: Suidae) Based on Tooth Pattern Analysis. *Kaupia Darmstädter Beiträge Zur Naturgeschichte* 9: 1-34.
- LAZAGABASTER I. A. 2019. — Dental microwear texture analysis of Pliocene Suidae from Hadar and Kanapoi in the context of early hominin dietary breadth expansion. *Journal of Human Evolution* 132: 80-100. <https://doi.org/10.1016/j.jhevol.2019.04.010>
- LAZAGABASTER I. A., CERLING T. E. & FAITH J. T. 2021. — A Late Pleistocene third molar of *Hylochoerus* (Suidae, Mammalia) from Rusinga Island, Kenya: Paleoenvironmental implications and a note on the hypsodonty of African forest hogs. *Historical Biology* 33(12): 3673-3685. <https://doi.org/10.1080/08912963.2021.1887861>
- LAZAGABASTER I. A., SOURON A., ROWAN J., ROBINSON J. R., CAMPISANO C. J. & REED K. E. 2018. — Fossil Suidae (Mammalia, Artiodactyla) from Lee Adoyta, Ledi-Geraru, lower Awash Valley, Ethiopia: Implications for late Pliocene turnover and paleoecology.

- Palaeogeography, Palaeoclimatology, Palaeoecology* 504: 186-200.
<https://doi.org/10.1016/j.palaeo.2018.05.029>
- LESLIE JR D. M. & HUFFMAN B. A. 2015. — *Potamochoerus porcus* (Artiodactyla: Suidae). *Mammalian species* 47(919): 15-31. <https://doi.org/10.1093/mspecies/sev002>
- LEVIN N. E., BROWN F. H., BEHRENSMEYER A. K., BOBE R. & CERLING T. E. 2011. — Paleosol carbonates from the Omo Group: Isotopic records of local and regional environmental change in East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307(1-4): 75-89. <https://doi.org/10.1016/j.palaeo.2011.04.026>
- LOUAIL M., CANER L., NEAUX D., ORTIZ K., LOCATELLI Y. & CUCCHI T. 2022. — Identifying the Impact of Soil Ingestion on Dental Microwear Textures Using a Wild Boar Experimental Model. *Journal of Archaeological Method and Theory* 30(3): 855-875. <https://doi.org/10.1007/s10816-022-09574-6>
- LOUAIL M., FERCHAUD S., SOURON A., WALKER A. E. C. & MERCERON G. 2021. Dental microwear textures differ in pigs with overall similar diets but fed with different seeds. *Palaeogeography, Palaeoclimatology, Palaeoecology* 572: 110415. <https://doi.org/10.1016/j.palaeo.2021.110415>
- LUCAS P. W. 2004. — *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge, 355 p. <https://doi.org/10.1017/CBO9780511735011>
- LUCAS P. W., VAN CASTEREN A., AL-FADHALAH K., ALMUSALLAM A. S., HENRY A. G., MICHAEL S., WATZKE J., REED D. A., DIEKWISCH T. G. H., STRAIT D. S. & ATKINS A. G. 2014. — The Role of Dust, Grit and Phytoliths in Tooth Wear. *Annales Zoologici Fennici* 51(1-2): 143-152. <https://doi.org/10.5735/086.051.0215>
- LUCAS P. W., OMAR R., AL-FADHALAH K., ALMUSALLAM A. S., HENRY A. G., MICHAEL S., THAI L. A., WATZKE J., STRAIT D. S. & ATKINS A. G. 2013. — Mechanisms and causes of wear in tooth enamel: Implications for hominin diets. *Journal of The Royal Society Interface* 10(80): 20120923. <https://doi.org/10.1098/rsif.2012.0923>
- MADDEN R. H. 2014. — *Hypsodonty in Mammals: Evolution, Geomorphology and the Role of Earth Surface Processes*. Cambridge University Press, Cambridge, 443 p. <https://doi.org/10.1017/CBO9781139003384>
- MARTIN F., PLASTIRAS C.-A., MERCERON G., SOURON A. & BOISSERIE J.-R. 2018. — Dietary niches of terrestrial cercopithecines from the Plio-Pleistocene Shungura Formation, Ethiopia: Evidence from Dental Microwear Texture Analysis. *Scientific Reports* 8(1): 14052. <https://doi.org/10.1038/s41598-018-32092-z>

- MCDUGALL I. & BROWN F. H. 2006. — Precise $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *Journal of the Geological Society* 163(1): 205-220. <https://doi.org/10.1144/0016-764904-166>
- MCDUGALL I. & BROWN F. H. 2008. Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. *Journal of the Geological Society* 165(2): 549-562. <https://doi.org/10.1144/0016-76492006-170>
- MCDUGALL I., BROWN F. H., VASCONCELOS P. M., COHEN B. E., THIEDE D. S. & BUCHANAN M. J. 2012. — New single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ ages improve time scale for deposition of the Omo Group, Omo–Turkana Basin, East Africa. *Journal of the Geological Society* 169(2): 213-226. <https://doi.org/10.1144/0016-76492010-188>
- MEKONNEN A., BEKELE A., BALAKRISHNAN M. 2018. — Population ecology of the giant forest hog, *Hylochoerus meinertzhageni* in Chebera Churchura National Park, Ethiopia. *African Journal of Ecology* 56: 272-278. <https://doi.org/10.1111/aje.12446>
- MELLETTI M., BREUER T., HUFFMAN B. A., TURKALO A. K., MIRABILE M. & MAISELS F. 2017. — Red River Hog *Potamochoerus porcus* (Linnaeus, 1758), in MELLETTI M. & MEIJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 134-149. <https://doi.org/10.1017/9781316941232.015>
- MERCERON G., BERLIOZ E., VONHOF H., GREEN D. R., GAREL M. & TÜTKEN T. 2021. — Tooth tales told by dental diet proxies: An alpine community of sympatric ruminants as a model to decipher the ecology of fossil fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 562: 110077. <https://doi.org/10.1016/j.palaeo.2020.110077>
- MERCERON G., COLYN M. & GERAADS D. 2018. — Browsing and non-browsing extant and extinct giraffids: Evidence from dental microwear textural analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 505: 128-139. <https://doi.org/10.1016/j.palaeo.2018.05.036>
- MERCERON G., ESCARGUEL G., ANGIBAUT J.-M. & VERHEYDEN-TIXIER H. 2010. — Can Dental Microwear Textures Record Inter-Individual Dietary Variations? *PLoS ONE* 5(3): e9542. <https://doi.org/10.1371/journal.pone.0009542>
- MERCERON G., HOFMAN-KAMIŃSKA E. & KOWALCZYK R. 2014. — 3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland. *Forest Ecology and Management* 328: 262-269. <https://doi.org/10.1016/j.foreco.2014.05.041>

- MERCERON G., KALLEND A., FRANCISCO A., LOUAIL M., MARTIN F., PLASTIRAS C.-A., THIERY G. & BOISSERIE J.-R. 2021. — Further away with dental microwear analysis: Food resource partitioning among Plio-Pleistocene monkeys from the Shungura Formation, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 572: 110414. <https://doi.org/10.1016/j.palaeo.2021.110414>
- MERCERON G., RAMDARSHAN A., BLONDEL C., BOISSERIE J.-R., BRUNETIÈRE N., FRANCISCO A., GAUTIER D., MILHET X., NOVELLO A. & PRET D. 2016. — Untangling the environmental from the dietary: Dust does not matter. *Proceedings of the Royal Society B: Biological Sciences* 283(1838): 20161032. <https://doi.org/10.1098/rspb.2016.1032>
- MIYAMOTO K., KUBO M. O. & YOKOHATA Y. 2022. — The dental microwear texture of wild boars from Japan reflects inter- and intra-populational feeding preferences. *Frontiers in Ecology and Evolution* 10: 875. <https://doi.org/10.3389/fevo.2022.957646>
- NEGASH E. W., ALEMSEGED Z., BOBE R., GRINE F., SPONHEIMER M. & WYNN J. G. 2020. — Dietary trends in herbivores from the Shungura Formation, southwestern Ethiopia. *Proceedings of the National Academy of Sciences* 117(36): 21921-21927. <https://doi.org/10.1073/pnas.2006982117>
- NEGASH E. W., ALEMSEGED Z., WYNN J. G. & BEDASO Z. K. 2015. — Paleodietary reconstruction using stable isotopes and abundance analysis of bovids from the Shungura Formation of South Omo, Ethiopia. *Journal of Human Evolution* 88: 127-136. <https://doi.org/10.1016/j.jhevol.2015.07.009>
- OLIVER W. L. (ed.). 1993. — *Pigs, peccaries, and hippos: status survey and conservation action plan*. Volume 19. IUCN, Switzerland, 219 p.
- OWEN, R. 1850. — On the development and homologies of the molar teeth of the wart-hogs (*Phacochoerus*), with illustrations of a system of notation for the teeth in the Class Mammalia. *Philosophical Transactions of the Royal Society of London* 140: 481-498. <https://doi.org/10.1098/rstl.1850.0025>
- PATTERSON D. B., BRAUN D. R., ALLEN K., BARR W. A., BEHRENSMEYER A. K., BIERNAT M., LEHMANN S. B., MADDOX T., MANTHI F. K., MERRITT S. R., MORRIS S. E., O'BRIEN K., REEVES J. S., WOOD B. A. & BOBE R. 2019. — Comparative isotopic evidence from East Turkana supports a dietary shift within the genus *Homo*. *Nature Ecology & Evolution* 3(7): 1048-1056. <https://doi.org/10.1038/s41559-019-0916-0>
- PERCHER A. M., MERCERON G., NSI AKOUE G., GALBANY J., ROMERO A. & CHARPENTIER M. J. 2017. — Dental microwear textural analysis as an analytical tool to depict individual traits

- and reconstruct the diet of a primate. *American Journal of Physical Anthropology* 165(1): 123-138. <https://doi.org/10.1002/ajpa.23337>
- PICKFORD M. 2012. — Ancestors of Broom's pigs. *Transactions of the Royal Society of South Africa*, 67(1): 17-35. <https://doi.org/10.1080/0035919X.2012.689265>
- QUIGLEY K. M., DONATI G. L. & ANDERSON T. M. 2017. Variation in the soil 'silicon landscape' explains plant silica accumulation across environmental gradients in Serengeti. *Plant and Soil* 410(1-2): 217-229. <https://doi.org/10.1007/s11104-016-3000-4>
- RAMDARSHAN A., BLONDEL C., BRUNETIÈRE N., FRANCISCO A., GAUTIER D., SURAULT J. & MERCERON G. 2016. — Seeds, browse, and tooth wear: A sheep perspective. *Ecology and Evolution* 6(16): 5559-5569. <https://doi.org/10.1002/ece3.2241>
- RANNIKKO J., ADHIKARI H., KARME A., ŽLIOBAITĖ I. & FORTELIUS M. 2020. — The case of the grass-eating suids in the Plio-Pleistocene Turkana Basin: 3D dental topography in relation to diet in extant and fossil pigs. *Journal of Morphology* 281(3): 348-364. <https://doi.org/10.1002/jmor.21103>
- RANNIKKO J., ŽLIOBAITĖ I. & FORTELIUS M. 2017. — Relative abundances and palaeoecology of four suid genera in the Turkana Basin, Kenya, during the late Miocene to Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487: 187-193. <https://doi.org/10.1016/j.palaeo.2017.08.033>
- REYNA-HURTADO R., D'HUART J. P. & TURKALO A. K. 2017. — Forest Hog *Hylochoerus meinertzhageni* (Thomas 1904), in MELLETTI M. & MEIJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 114-121. <https://doi.org/10.1017/9781316941232.013>
- SCHULZ E., CALANDRA I. & KAISER T. M. 2010. — Applying tribology to teeth of hoofed mammals. *Scanning* 32(4): 162-182. <https://doi.org/10.1002/sca.20181>
- SCHULZ E., CALANDRA I. & KAISER T. M. 2013. — Feeding ecology and chewing mechanics in hoofed mammals: 3D tribology of enamel wear. *Wear* 300(1): 169-179. <https://doi.org/10.1016/j.wear.2013.01.115>
- SCOTT J. R. 2012. — Dental microwear texture analysis of extant African Bovidae. *Mammalia* 76(2): 157-174. <https://doi.org/10.1515/mammalia-2011-0083>
- SCOTT R. S., TEAFORD M. F. & UNGAR P. S. 2012. — Dental microwear texture and anthropoid diets. *American Journal of Physical Anthropology* 147(4): 551-579. <https://doi.org/10.1002/ajpa.22007>

- SCOTT R. S., UNGAR P. S., BERGSTROM T. S., BROWN C. A., CHILDS B. E., TEAFORD M. F. & WALKER A. 2006. — Dental microwear texture analysis: Technical considerations. *Journal of Human Evolution* 51(4): 339-349. <https://doi.org/10.1016/j.jhevol.2006.04.006>
- SEYDACK A. H. W. 1990. — *Ecology of the bushpig Potamochoerus porcus Linn. 1758 in the Cape Province, South Africa*. PhD thesis, Stellenbosch University, Stellenbosch, 728 p. <https://scholar.sun.ac.za:443/handle/10019.1/19406>
- SEYDACK A. H. W. 2017. — Bushpig *Potamochoerus larvatus* (F. Cuvier, 1822), in MELLETTI M. & MEIJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 122-133. <https://doi.org/10.1017/9781316941232.014>
- SKINNER J. D., BREYTENBACH G. J. & MABERLY C. 1976. — Observations on the ecology and biology on the bushpig *Potamochoerus porcus* in the northern Transvaal. *South African Journal of Wildlife Research* 6(2): 123-128. https://journals.co.za/doi/pdf/10.10520/AJA03794369_3217
- SOURON A. 2012. — *Histoire évolutive du genre Kolpochoerus (Cetartiodactyla : Suidae) au Plio-Pléistocène en Afrique orientale*. PhD thesis, University of Poitiers, Poitiers, 517 p.
- SOURON A. 2015. — Are we ready for meta-analyses of mammalian faunas based on faunal lists? A case-study using the Plio-Pleistocene African Suidae. *Suiform Soundings* 14: 35-43.
- SOURON, A. 2016. — On specimens of extant warthogs (*Phacochoerus*) from the Horn of Africa with unusual basicranial morphology: rare variants of *Ph. africanus* or hybrids between *Ph. africanus* and *Ph. aethiopicus*?. *Suiform Soundings* 15(1): 86-92.
- SOURON A. 2017. — Diet and Ecology of Extant and Fossil Wild Pigs, in MELLETTI M. & MEIJAARD E. (eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge University Press, Cambridge: 29-38. <https://doi.org/10.1017/9781316941232.005>
- SOURON A., BOISSERIE J.-R. & WHITE T. D. 2015a. — A new species of the suid genus *Kolpochoerus* from Ethiopia. *Acta Palaeontologica Polonica* 60(1): 79-96. <https://doi.org/10.4202/app.2012.0083>
- SOURON A., MERCERON G., BLONDEL C., BRUNETIÈRE N., COLYN M., HOFMAN-KAMIŃSKA E. & BOISSERIE J.-R. 2015b. — Three-dimensional dental microwear texture analysis and diet in extant Suidae (Mammalia: Cetartiodactyla). *Mammalia* 79(3): 279-291. <https://doi.org/10.1515/mammalia-2014-0023>

- SUWA G., NAKAYA H., ASFAW B., SAEGUSA H., AMZAYE A., KONO R. T., BEYENE Y. & KATOH S. 2003. — Plio-Pleistocene terrestrial mammal assemblage from Konso, Southern Ethiopia. *Journal of Vertebrate Paleontology*, 23(4): 901-916. <https://doi.org/10.1671/2469-15>
- SUWA G., SOURON A. & ASFAW B. 2014. — Fossil Suidae of the Konso Formation, in SUWA G., BEYENE Y. & ASFAW B. (eds.), *Konso-Gardula Research Project. Volume 1. Paleontological Collections: Background and Fossil Aves, Cercopithecidae, and Suidae*. The University Museum, The University of Tokyo, Tokyo, Bulletin No. 47: 73-88.
- TAUSCH J., KULLMER O. & BROMAGE T.G. 2015. — A new method for determining the 3D spatial orientation of molar microwear. *Scanning* 37(6): 446–457. <https://doi.org/10.1002/sca.21234>
- TEAFORD M. F. & OYEN O. J. 1989. — In vivo and in vitro turnover in dental microwear. *American Journal of Physical Anthropology* 80(4): 447-460. <https://doi.org/10.1002/ajpa.1330800405>
- TEAFORD M. F., ROSS C. F., UNGAR P. S., VINYARD C. J. & LAIRD M. F. 2021. — Grit your teeth and chew your food: Implications of food material properties and abrasives for rates of dental microwear formation in laboratory *Sapajus apella* (Primates). *Palaeogeography, Palaeoclimatology, Palaeoecology* 583: 110644. <https://doi.org/10.1016/j.palaeo.2021.110644>
- TEAFORD M. F., UNGAR P. S., TAYLOR A. B., ROSS C. F. & VINYARD C. J. 2017. — In vivo rates of dental microwear formation in laboratory primates fed different food items. *Biosurface and Biotribology* 3(4): 166-173. <https://doi.org/10.1016/j.bsbt.2017.11.005>
- TREYDTE A. C., BERNASCONI S. M., KREUZER M. & EDWARDS P. J. 2006. — Diet of the Common Warthog (*Phacochoerus africanus*) on Former Cattle Grounds in a Tanzanian Savanna. *Journal of Mammalogy* 87(5): 889-898. <https://doi.org/10.1644/05-MAMM-A-336R2.1>
- UNGAR P. S., ABELLA E. F., BURGMAN J. H. E., LAZAGABASTER I. A., SCOTT J. R., DELEZENE L. K., MANTHI F. K., PLAVCAN J. M. & WARD C. V. 2017. — Dental microwear and Pliocene paleocommunity ecology of bovids, primates, rodents, and suids at Kanapoi. *Journal of Human Evolution* 140: 102315. <https://doi.org/10.1016/j.jhevol.2017.03.005>
- UNGAR P. S., GRINE F. E. & TEAFORD M. F. 2008. — Dental Microwear and Diet of the Plio-Pleistocene Hominin *Paranthropus boisei*. *PLoS ONE* 3(4): e2044. <https://doi.org/10.1371/journal.pone.0002044>

- UNGAR P. S., MERCERON G. & SCOTT R. S. 2007. — Dental Microwear Texture Analysis of Varswater Bovids and Early Pliocene Paleoenvironments of Langebaanweg, Western Cape Province, South Africa. *Journal of Mammalian Evolution* 14(3): 163-181. <https://doi.org/10.1007/s10914-007-9050-x>
- UZUNIDIS A., PINEDA A., JIMÉNEZ-MANCHÓN S., XAFIS A., OLLIVIER V. & RIVALS F. 2021. — The impact of sediment abrasion on tooth microwear analysis: An experimental study. *Archaeological and Anthropological Sciences* 13(8): 134. <https://doi.org/10.1007/s12520-021-01382-5>
- WEBER K., WINKLER D. E., SCHULZ-KORNAS E., KAISER T. M. & TÜTKEN T. 2021. — The good, the bad and the ugly – A visual guide for common post-mortem wear patterns in vertebrate teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 578: 110577. <https://doi.org/10.1016/j.palaeo.2021.110577>
- WEBER K., WINKLER D. E., SCHULZ-KORNAS E., KAISER T. M. & TÜTKEN T. 2022. — Post-mortem enamel surface texture alteration during taphonomic processes—Do experimental approaches reflect natural phenomena? *PeerJ* 10: e12635. <https://doi.org/10.7717/peerj.12635>
- WHITE T. D. & HARRIS J. M. 1977. — Suid Evolution and Correlation of African Hominid Localities. *Science* 198(4312): 13-21. <https://doi.org/10.1126/science.331477>
- WHITE T. D. 1995 — African omnivores: global climatic change and Plio-Pleistocene hominids and suids, in VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds.), *Paleoclimate and evolution with emphasis on human origins*. Yale University Press, New Haven: 369-384.
- WINKLER D. E., SCHULZ-KORNAS E., KAISER T. M., CODRON D., LEICHLITER J., HUMMEL J., MARTIN L. F., CLAUSS M. & TÜTKEN T. 2020. — The turnover of dental microwear texture: Testing the “last supper” effect in small mammals in a controlled feeding experiment. *Palaeogeography, Palaeoclimatology, Palaeoecology* 557: 109930. <https://doi.org/10.1016/j.palaeo.2020.109930>
- YAMADA E., HONGO H. & ENDO H. 2021. — Analyzing historic human-suid relationships through dental microwear texture and geometric morphometric analyses of archaeological suid teeth in the Ryukyu Islands. *Journal of Archaeological Science* 132: 105419. <https://doi.org/10.1016/j.jas.2021.105419>

- YAMADA E., KUBO M. O., KUBO T. & KOHNO N. 2018. — Three-dimensional tooth surface texture analysis on stall-fed and wild boars (*Sus scrofa*). *PLOS ONE* 13(10): e0204719. <https://doi.org/10.1371/journal.pone.0204719>
- YANG D. 2020. — *Investigating abiotic and biotic factors that influenced Plio-Pleistocene African suid evolution: implications for hominins*. PhD thesis, Stony Brook University, Stony Brook, 390 p.
- YANG D., PISANO A., KOLASA J., JASHASHVILI T., KIBII J., GOMEZ CANO A. R., VIRIOT L., GRINE F. E. & SOURON A. 2022. — Why the long teeth? Morphometric analysis suggests different selective pressures on functional occlusal traits in Plio-Pleistocene African suids. *Paleobiology* 48(4): 655-676. <https://doi.org/10.1017/pab.2022.11>