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1 **IDENTIFYING THE IMPACT OF SOIL INGESTION ON DENTAL MICROWEAR**  
2 **TEXTURES USING A WILD BOAR EXPERIMENTAL MODEL**

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23 **ABSTRACT**

24 Dental microwear has been widely used to reconstruct mammals' past diet and to understand  
25 their dental evolution. In archaeology, it can help reconstruct anthropogenic herd-feeding  
26 systems. However, deciphering the impact of exogenous mineral particles on dental wear is an  
27 ongoing challenge since studies have shown that soil ingestion can generate microwear traces  
28 that interfere with the dietary signals. To bridge this gap, this study relies on the first large-scale  
29 controlled-food experiment on wild boars (*Sus scrofa*) to test how soil ingestion can affect the  
30 dietary signal recorded in dental microwear. It provides the opportunity to investigate the  
31 impact of natural soil ingestion over microwear traces by comparing penned boars that were  
32 able to root with stalled boars that were not. We performed 3D Dental microwear texture  
33 analysis (DMTA) on 22 controlled-fed boars kept captive either in an indoor stall with no soil  
34 ingestion, or in a wooded pen with natural soil ingestion. We analysed shearing and crushing  
35 facets on upper and lower first and second molars using standard texture parameters. We also  
36 conducted particle size distribution analyses of the ingested soil. In line with previous works,  
37 the consumption of exogenous abrasives in rooting boars leads to less rough, less complex and  
38 more anisotropic wear surfaces than in stall-fed boars, even though they received the same diet.  
39 Thus, we highly recommend studying DMT when investigating ancient pig husbandry systems,  
40 particularly local changes in food management. Overall, this study contributes to a better  
41 comprehension of how exogenous abrasives impact DMT among mammals.

42

43 **Keywords:** Grit, Dust, Tooth wear, Feeding experiments, Rooting

44

## 45 1. INTRODUCTION

46 Mammals exhibit teeth that are generally adapted to their diet, optimizing not only tooth  
47 efficiency for food processing but also durability against wear (Hiemae, 2000). Although both  
48 intrinsic food material properties and exogenous mineral abrasives contribute to dental wear,  
49 their respective impacts remain unclear. This is a crucial issue for evolutionary biologists that  
50 focus on the selective pressures driving dental innovations among mammals during the  
51 Cenozoic, such as high crowned molars in ruminants (e.g. Madden, 2014), molar lengthening  
52 in African suids (e.g. Harris & Cerling, 2002) or enamel thickening in hominins (e.g. Lucas et  
53 al., 2008). Besides palaeontological or evolutionary perspectives, understanding how the  
54 consumption of exogenous mineral particles impacts dental wear is also of interest for  
55 archaeological contexts. Indeed, various husbandry practices and landscape uses may influence  
56 the frequency and the intensity of soil consumption among domesticated mammals.  
57 Particularly, boars/pigs are known to root under natural conditions (Keuling et al., 2017) while  
58 human intervention in their feeding behaviour such as food supply or penning would have  
59 reduced, if not prevented, rooting behaviours (Beattie & O'Connell, 2002). Although extensive  
60 pig domestication systems seem to have persisted in most part of Eurasia for several millennia  
61 since early domestication stages (Price & Hongo, 2020), it is not known in any regions when  
62 pigs began to be fed on stalls (Wilkie et al., 2007; Rowley-Conwy et al., 2012). Considering  
63 the huge diversity of pig management strategies through time and space, studying dental  
64 microwear (i.e. microscopic marks on the surface of tooth enamel) of archaeological specimens  
65 of *Sus* would contribute to better understand the evolution of pigs' herding practices over time  
66 (Rowley-Conwy et al., 2012). Despite the relevance of dental microwear to reconstruct past  
67 herding practices, such approach have rarely been applied on *Sus* dental remains (Wilkie et al.,  
68 2007; Vanpoucke et al., 2009; Yamada et al., 2021).

69 Dental microwear is highly dependent on the physical properties and biosilica content  
70 of the masticated food items, and records the diet over a short timescale, few weeks or months  
71 before death (e.g. Teaford & Oyen, 1989; Lucas, 2004; Lucas et al., 2013, 2014; Daegling et  
72 al., 2016; Merceron et al., 2016; Teaford et al., 2017, 2021 ; Winkler et al., 2020). The  
73 pertinence of Dental Microwear Texture Analysis (DMTA) for dietary reconstructions has  
74 largely been demonstrated, and notably when different ecological proxies are combined (e.g.  
75 R. S. Scott et al., 2006; Ungar et al., 2008; Merceron et al., 2009; R. S. Scott et al., 2012; Berlioz  
76 et al., 2018; Blondel et al., 2018; F. Martin et al., 2018; Lazagabaster, 2019; Merceron et al.,  
77 2021; Thiery et al., 2021). Both SSFA (Scale-Sensitive Fractal Analysis; Scott et al. 2006) and  
78 STA (Surface Texture Analysis; Schulz et al., 2010) approaches have shown their efficiency in  
79 detecting dietary differences between species (e.g. J. R. Scott, 2012; R. S. Scott et al., 2012;  
80 Schulz et al., 2013), and even small variations in dietary habits within the same species or  
81 populations (Merceron et al., 2010, 2014; Berlioz et al., 2017; Percher et al., 2017). However,  
82 despite a growing number of studies applying DMTA, notably on controlled-fed mammals (e.g.  
83 Merceron et al., 2017; Schulz et al., 2013; Winkler et al., 2019, 2020; Louail et al., 2021), the  
84 causes of microwear traces remain unclear. Particularly, there is an ongoing debate about how  
85 the consumption of exogenous abrasives impacts dental microwear textures (DMT), and  
86 whether its impact prevails over the one of diet (e.g. Mainland, 2003; Lucas et al., 2013, 2014;  
87 Hoffman et al., 2015; Xia et al., 2015; Merceron et al., 2016; van Casteren et al., 2018;  
88 Ackermans et al., 2020; Hua et al., 2020; Schulz-Kornas et al., 2020; Winkler et al., 2020;  
89 Fannin et al., 2021; Teaford et al., 2021).

90 Few experimental studies (whether *in-vitro* or on controlled-fed mammals) have  
91 investigated the impact of exogenous mineral particles on dental microwear (Hoffman et al.,  
92 2015; Merceron et al., 2016; Ackermans et al., 2020; Hua et al., 2020; Schulz-Kornas et al.,  
93 2020; Teaford et al., 2021; Winkler et al., 2020). Such studies enable targeting and quantifying

94 the effects of specific items (i.e. dietary resources, exogenous particles or the combination of  
95 the two) on DMT. Nevertheless, they yielded dissimilar results and only one study simulated  
96 soil ingestion under natural conditions (Merceron et al., 2016). Differences in composition,  
97 type, size, shape or concentration of exogenous particles may explain these contrasting results.  
98 Moreover, the digestive tractus of sheep used in Merceron et al. (2016) include, as all species  
99 of ruminants, a set of prestomach chambers in which grit particles are sorted out from the dietary  
100 bolus by gravity before rumination starts. Such adaptations had undoubtedly reduced the  
101 abrasive effects of grit-bearing food on teeth in the course of the evolution of ruminants (Hatt  
102 et al., 2020). More studies are needed with precise descriptions of the mineral composition,  
103 material properties and geometry of exogenous particles ingested in order to better understand  
104 their impact on DMT.

105         Here, we propose the first large-scale controlled-food experiment on captive wild boars  
106 with natural soil ingestion to investigate whether the consumption of exogenous mineral  
107 particles generates different DMT in a population fed on the same diet. We used the automated  
108 and replicable 3D-DMTA (Souron et al., 2015; Yamada et al., 2018, 2021; Louail et al., 2021)  
109 to measure DMT variations in 22 controlled-fed boars from the same wild population and fed  
110 the same food (porcine pellets). While one half of the boars is kept in an outdoor pen where  
111 rooting behaviours and soil consumption occur, the other half is kept in an indoor stall without  
112 possible rooting behaviour. We also performed particle size distribution analyses of the ingested  
113 soil and mineralogical analyses by X-ray diffraction. To our knowledge, this is the first study  
114 focusing on DMT of rooting vs stalled boars/pigs that precisely documents the diet and the  
115 composition of the ingested soil. Following previous works on rooting and stalled pigs (Ward  
116 & Mainland, 1999; Yamada et al., 2018), we expect that stall-fed boars would show high overall  
117 roughness and complexity due to their hard diet. Rooting boars, that ingested abrasive

118 exogenous particles, would tend to show more anisotropic and less complex surfaces than  
119 stalled ones.

120

## 121 **2. MATERIALS AND METHODS**

### 122 **2.1. Specimens, diet and habitats**

123 This study focused on 22 captive boars from the DOMEXP project: a multidisciplinary  
124 experiment aiming to assess the effect of captivity on the musculoskeletal system and obtain  
125 new phenotypic markers of early process of animal domestication in archaeology (Harbers et  
126 al., 2020a, 2020b; Neaux et al., 2021a, 2021b). All individuals were sampled as piglets from  
127 the same population of free-ranging wild boars (Urciers, Indre, France). They were raised from  
128 6 to 24 months at the Zoological Reserve of La Haute Touche (Indre, France). One group  
129 consisted of boars fed in an indoor stall (n = 10, “stall group”) of 100 m<sup>2</sup>, which had no  
130 possibility of foraging and rooting. The second group consisted of boars in a wooded pen (n =  
131 12, “enclosure group”) of 3000 m<sup>2</sup>, where they were able to engage in rooting behaviour,  
132 implying the consumption of exogenous mineral particles (see Online Resource 1). Each group  
133 had a similar number of females and males (see ESM 1). Both groups received a diet composed  
134 of dry pellets (~ 65 %) and corn kernels (~ 35 %). We considered that barley seeds, representing  
135 less than 1 % of the diet, would have no effect on DMT. This daily food supply was distributed  
136 on the ground and provided *ad libitum*. Only the enclosure group could have had access to few  
137 other resources from the wild (such as few grasses, acorns, roots, earthworms, insects), notably  
138 by rooting the ground. However, boars in enclosure were fed the same amount of food as the  
139 stall group, which reduced foraging behaviours. All the boars were slaughtered in June, months  
140 after the seasonal access to acorns and seeds. Thus, we expect differences in tooth wear driven  
141 by between-group differences in soil ingestion, not in seed consumption.

## 142 **2.2. Soil sample analyses**

143 The zoological Reserve is located in a temperate deciduous forest type landscape in the Brenne  
144 valley (temperate central France, GPS coordinates: 46°52'37''N 1°05'37.8''E). Soils are  
145 derived from complex and heterogeneous continental sandy-to silty clay deposits from  
146 Paleocene to Miocene overlying Cretaceous chalk (Service du Patrimoine naturel, 2017).  
147 Rooting boars were kept, alternately, in two side-by-side enclosures. We collected one bulk soil  
148 sample (about 30 cm depth) in each of the two enclosures (LHT 1 and LHT 2) in May (similar  
149 period when boars were slaughtered). We conducted particle size distribution analyses and  
150 mineralogical analyses by X-ray diffraction (XRD) on both soil samples, and expected strongly  
151 similar results between the two.

### 152 **2.2.1. Particle size distribution analyses**

153 The samples were first air-dried and sieved through a Ø 2-mm mesh to remove coarse  
154 fragments. A mass of 10g of each of these < 2 mm fractions was treated to remove organic  
155 matter (5% H<sub>2</sub>O<sub>2</sub> at 40°C). The samples were then treated with sodium hexametaphosphate  
156 ((NaPO<sub>3</sub>)<sub>6</sub>) to disperse soil particles with agitation for 4 hours. The coarse (2000-200 µm) and  
157 fine sands (200-50 µm) were separated by wet sieving, dried and weighed. The clay (< 2 µm)  
158 then the fine silt (20-2 µm) fractions were collected using a sedimentation technique (Stokes'  
159 law) with repeated siphoning. Each fraction was dried in an oven at 65°C, weighted, and  
160 expressed as percentage of the total sample < 2 mm. The coarse silt (20-50 µm) corresponds to  
161 the fraction that accumulated in the sedimentation cylinders. The percentages of each fraction  
162 are used to assess the soil texture using the United State Department of Agriculture (USDA)  
163 Soil Texture Triangle (USDA, 1987). Aliquots of the clay fractions were Ca-saturated (CaCl<sub>2</sub>,  
164 0.5 mol.L<sup>-1</sup>) and then washed to remove the salt excess.

### 165 **2.2.2. Mineralogical analyses by X-ray diffraction**

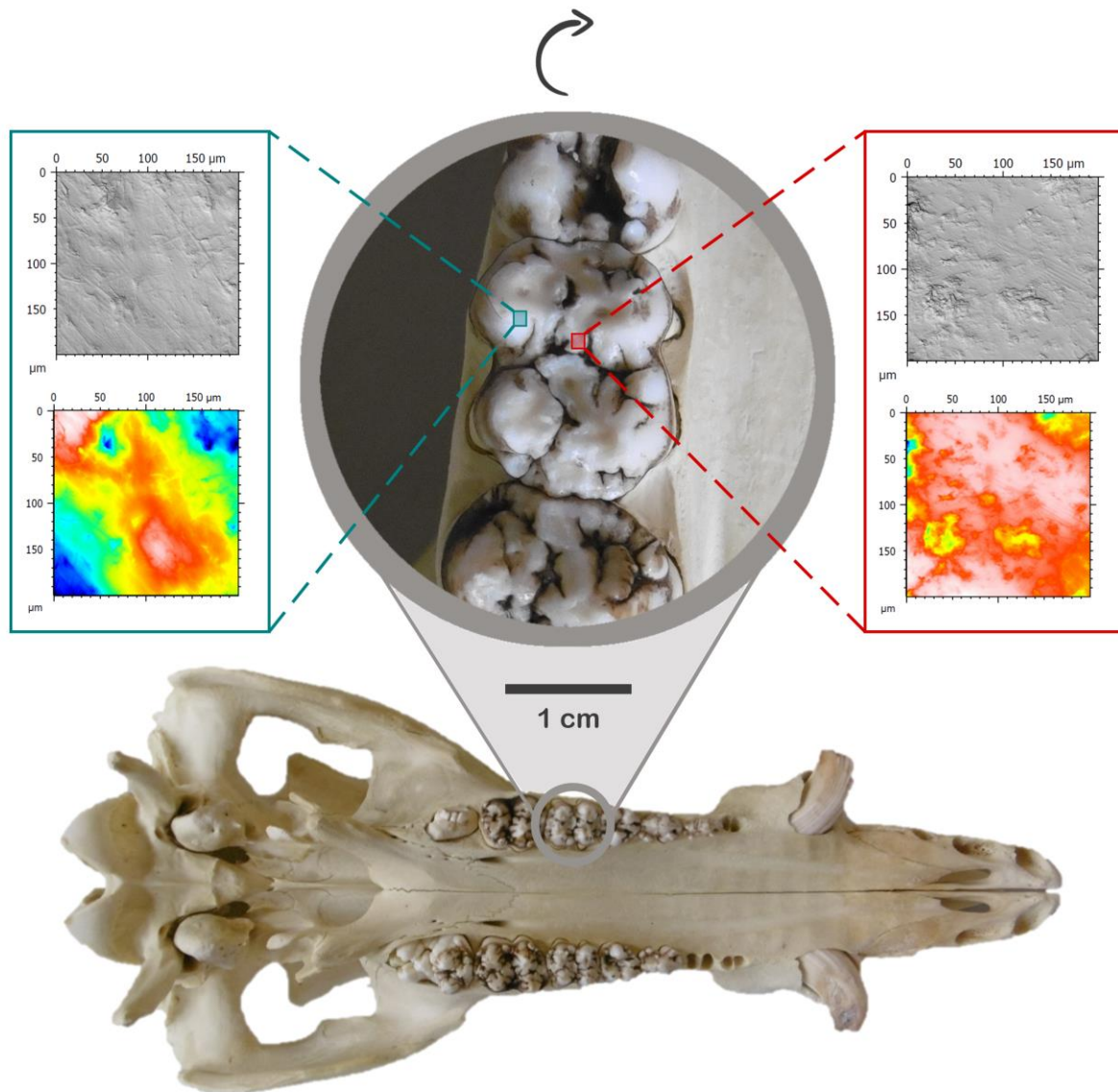


166 Mineralogical analyses were performed on the samples used for the particle size distribution  
167 analyses. The sand and silt fractions were ground using a McCrone Micronising Mill. X-ray  
168 diffraction (XRD) analyses were performed on randomly oriented powders in the range 2–65°  
169 2 $\theta$  with steps of 0.025° 2 $\theta$  and a counting time of 192 s per step using a Bruker D8 Advance  
170 diffractometer (Cu K $\alpha$  radiation, 40 kV and 40 mA) equipped with a Lynx eye detector. The  
171 clay fractions were analysed from oriented mounts obtained by depositing a small amount of  
172 suspensions onto glass slides and drying them at room temperature. Ca-saturated samples were  
173 analysed by XRD both in an air-dried (AD) state and after ethylene glycol solvation (EG,  
174 vapour at 50°C overnight) using the same equipment in the range 2–35° 2 $\theta$  with steps of 0.016°  
175 2 $\theta$  and a counting time of 229 s. The minerals were identified according to the position of the  
176 diffraction peaks (Brindley & Brown, 1980; Dixon & Weed, 1989; Moore & Reynolds Jr.,  
177 1989).

### 178 **2.3. Molding, scanning and processing of wear surfaces**

179 We analyzed wear facets on lower and upper first and second molars because molars  
180 are the teeth involved in the comminution of the food, meaning the teeth acting either as a blade  
181 or as a grinding pillar or both. All shearing and crushing facets were visible on first molars  
182 (stages d-e following Grant, 1982). Second molars corresponded to early stages of wear (stages  
183 b-c following Grant, 1982). Each tooth surface was cleaned with cotton swab soaked with  
184 acetone to remove organic matter, dust and dirt. Once dry, we moulded occlusal surfaces using  
185 polyvinylsiloxane (Regular Body President, ref. 6015 - ISO 4823, medium consistency,  
186 polyvinylsiloxane addition-type, Coltene Whaledent). We studied both one shearing facet  
187 (phase I) and one crushing facet (phase II) of the same tooth (Figure 1). On few molds, we could  
188 not locate any suitable wear facet. Thus, we only studied nine lower first molars of the boars in  
189 enclosure, and nine lower second and upper first molars in the stall-fed boars (see ESM 1). Each  
190 facet was carefully cut on the silicon impression and scanned as flat as possible using

191 “TRIDENT”, a white-light confocal profilometer Leica DCM8 with a 100× objective housed  
192 at the PALEVOPRIM lab, CNRS and University of Poitiers, France (Numerical aperture =  
193 0.90; Working distance = 0.9 mm; Leica Microsystems). Each scanned surface was pre-  
194 processed using LeicaMap v8.0 (Leica Microsystems; MountainsMap, Digital Surf). We  
195 inverted surfaces along the z-axis and filled non-measured points (< 3 %) with a smooth shape  
196 (Laplacian filter) calculated from neighbouring points. We applied a morphological filter to  
197 remove artefacts such as aberrant peaks (Merceron et al., 2016). A  $200 \times 200 \mu\text{m}$  ( $1551 \times 1551$   
198 pixels) levelled area was automatically generated at the center of each surface. In case of  
199 adhering dirt particles, the extracted area was shifted aside to get the particles out of the field  
200 of selection. For 3 out of 164 surfaces, we had to manually erase the particles using a user-  
201 defined contour and we replaced them with a smooth shape calculated from neighboring points.  
202 Photosimulations and false color elevation maps of dental wear facets are provided in Online  
203 Resource 2.



204  
 205 **Fig. 1** Exemplary ventral view of a mandible, and occlusal view of the right upper first molar,  
 206 topography (false color elevation map) and photo-simulation for each scanned shearing (blue,  
 207 buccal facet) and crushing (red, lingual facet) facet. The arrow indicates the mesio-lingual  
 208 direction. The scale bar refers to the zoom scale.

#### 209 **2.4. Acquisition of textural parameters**

210 We calculated two sets of data on each processed surface using LeicaMap v.8.0: 1)  
 211 Scale-Sensitive Fractal Analysis parameters (SSFA; R. S. Scott et al., 2006) and 2) ISO 25178  
 212 parameters (including the ones that are being mostly employed, e.g. Lazagabaster, 2019; Schulz

213 et al., 2013; Schulz-Kornas et al., 2020; Yamada et al., 2018). Prior to the calculation of SSFA  
214 parameters, we subtracted a second-order least square polynomial surface to better visualize the  
215 relief due to wear. According to Francisco et al.'s study (2018), we calculated ISO 25178  
216 parameters on surfaces subtracted from an eight-order least square polynomial surface because  
217 it enhances roughness clarity.

218 1) We considered five SSFA parameters in this study: Area-scale fractal complexity  
219 (Asfc), exact proportion of Length-scale anisotropy of relief (epLsar) and Heterogeneity of Asfc  
220 calculated through 9 (HAsfc9), 36 (HAsfc) and 81 (HAsfc81) cells. Complexity (Asfc)  
221 measures the surface roughness at a given scale. Anisotropy (epLsar) quantifies the orientation  
222 concentration of surface roughness. HAsfc measures the variation of complexity of subsampled  
223 parts of the surface ( $3 \times 3$ ,  $6 \times 6$  and  $9 \times 9$  cells). See detailed descriptions of these parameters  
224 in R.S. Scott et al. (2006).

225 2) We then calculated 14 parameters from the international standard ISO 25178:  
226 skewness and kurtosis of the height distribution (Ssk and Sku, respectively), maximum peak  
227 height (Sp), maximum pit height (Sv), maximum height (Sz), arithmetical mean height (Sa),  
228 dale and core void volume (Vvv and Vvc, respectively), peak and core material volume (Vmp  
229 and Vmc, respectively), mean dale area (Sda), mean hill area (Sha), developed interfacial area  
230 ratio (Sdr) and texture aspect ratio (Str). This ISO 25178 dataset includes six measures of  
231 feature height (Ssk, Sku, Sp, Sv, Sz, Sa), four measures of feature volume (Vmp, Vmc, Vvv,  
232 Vvc), two measures of feature area (Sda, Sha), one measure of complexity (Sdr) and one  
233 measure of anisotropy (Str).

## 234 **2.5. Data analysis**

235 All statistical analyses were conducted in the R environment (R Core Team, 2020,  
236 v.4.0.3). According to Ramdarshan et al. (2017) who showed that upper and lower teeth have

237 different functions, we conducted the statistical analyses by treating separately upper and lower  
 238 first and second molars shearing and crushing facets. Data were Box-Cox transformed to meet  
 239 the assumptions of normal distributions and homogeneity of variances. Two-sample t-tests were  
 240 performed on each texture variable included in this study to assess whether the two groups  
 241 significantly differ. In case of violation of the assumptions, an alternative Mann-Whitney U test  
 242 was performed.

### 243 3. RESULTS

#### 244 3.1. Particle size distribution and mineralogical composition of the ingested soil

245 The results (Table 1, Figure 2) indicate that the two soil samples have similar particle  
 246 size distribution. The soil in the enclosures is mainly composed of silt (43 %,  $50 < \text{particle}$   
 247  $\text{diameter } \varnothing < 2 \mu\text{m}$ ) and sand (38 %,  $2000 < \varnothing < 50 \mu\text{m}$ ), and less granulometric clays (19 %,  $\varnothing < 2 \mu\text{m}$ ). Coarse sand and fine silt are the most abundant fractions (24 % and 26 %, respectively). Accordingly, soil texture can be classified as a loam (Table 1, Figure 2).

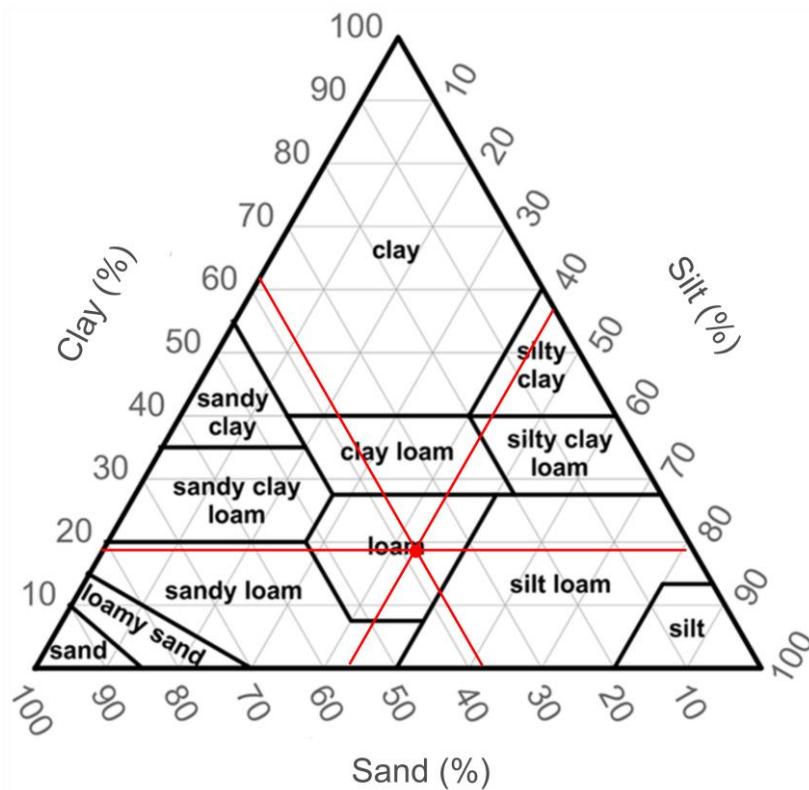
250

251 **Table 1** Particle size distribution (mean and standard deviation SD) and texture of the soil  
 252 samples (LHT 1 and LHT 2).

Sample	Particle size distribution (%)					Texture
	Coarse sand (2000-200 $\mu\text{m}$ )	Fine sand (200-50 $\mu\text{m}$ )	Coarse silt (50-20 $\mu\text{m}$ )	Fine silt (20-2 $\mu\text{m}$ )	Clay ( $< 2 \mu\text{m}$ )	
LHT 1	22.70	14.74	18.06	25.43	19.07	Loam
LHT 2	25.25	12.94	17.17	25.86	18.78	Loam
Mean ( $\pm$ SD)	23.98 ( $\pm 1.80$ )	13.84 ( $\pm 1.27$ )	17.62 ( $\pm 0.63$ )	25.65 ( $\pm 0.30$ )	18.93 ( $\pm 0.21$ )	Loam

253

254



255 **Fig. 2** Mean soil texture as averaged from the two soil samples (red circle) and classified  
 256 following the USDA Soil Texture Triangle (USDA, 1987). Soil texture can be classified as a  
 257 loam.

258 Mineralogical analyses by XRD reveal that the two samples are strongly similar (Table  
 259 2). Quartz is the most dominant mineral identified in coarse and fine sands, as well as in coarse  
 260 and fine silts, at 80 % or more. Other minerals are identified in low proportions (less than 15  
 261 %): potassium feldspars (microcline and orthoclase), plagioclases (albite and anorthite),  
 262 rutile/anatase (titanium oxides), augite and illite/mica. In the clay fractions, phyllosilicates  
 263 (mostly kaolinite, but also smectite, chlorite and interstratified illite/smectite) are the most  
 264 abundant minerals at about 60 to 70 %. Other minerals identified, but in small quantity or traces,  
 265 are mica/illite (10-15 %) and quartz (10-15 %). Detailed results of the mineralogical analyses  
 266 are presented in Figures S1 and S2 (Online Resource 3).

267

268 **Table 2** Mineralogical analyses (XRD) of the soil samples (LHT 1 and LHT 2) for each particle  
 269 size fractions. Particle size fractions: CSa (coarse sand), FSa (fine sand), CSi (coarse silt), FSi  
 270 (fine silt) and Clay. “+++”: dominant ( $\geq 60$  %); “+”: small amount to traces ( $\leq 15$  %); “tr”:  
 271 traces ( $\leq 1$  %). Here, potassium feldspars include microcline and orthoclase, plagioclases  
 272 include albite and anorthite, and phyllosilicates include mostly kaolinite, as well as chlorite,  
 273 smectite and interstratified illite/smectite.

	LHT 1					LHT 2				
	CSa	FSa	CSi	FSi	Clay	CSa	FSa	CSi	FSi	Clay
Quartz	+++	+++	+++	+++	tr	+++	+++	+++	+++	tr
Potassium feldspars	+	+	+	+		+	+	+	+	
Plagioclases	tr	tr	+	+		tr	tr	+	+	
Rutile/anatase	tr	tr				tr			tr	
Augite			tr	tr				tr	tr	
Illite/Mica				tr	+++				tr	+++
Phyllosilicates					+++					+++

274

### 275 3.2. DMTA differences between boars from indoor stall and rooting boars in an enclosure

276 Our results show that both crushing and shearing wear facets among boars kept in  
 277 enclosure are more anisotropic (epLsar) and less complex (Asfc) than those observed on stall-  
 278 fed boars, showing wear scratches that are more preferentially oriented and more homogeneous  
 279 in terms of size (Figure 3 on upper molars, see also ESM 3 for box-plots on lower molars:  
 280 Figures S3 and S4). The heterogeneity of complexity is higher among stall-fed boars than  
 281 rooting ones. Independent sample t-tests on crushing facets indicate significant differences  
 282 between rooting and stall-fed boars in epLsar on upper M1 only ( $p = 0.03$ , Tables 3 and S3,  
 283 Online Resource 3), Asfc on upper M2 only ( $p = 0.03$ , Tables 3 and S4, Online Resource 3)  
 284 and HASfc on both upper M1 and M2 ( $p < 0.03$ , Tables 3, S3 and S4, Online Resource 3). On  
 285 shearing facets, the groups show similar trends (Figure 3) but significantly differ only in terms  
 286 of complexity on upper M2 ( $p = 9.7e-4$ , Tables 3 and S8, Online Resource 3), and HASfc81 on

287 lower M2 ( $p = 0.04$ , Table S6, Online Resource 3). Our observations on lower molars are less  
288 conclusive than on upper molars, but they show overall a similar trend toward wear facets with  
289 higher epLsar and lower Asfc among rooting boars than among stall-fed ones (Figures S3 and  
290 S4, Tables 3 and S1-S8, Online Resource 3).

291         When considering the ISO 25178 parameters (Figures S5-S10, Tables 3 and S9-S16,  
292 Online Resource 3), we observe that the stall-fed boars show on average higher values of  
293 parameters related to the height and roughness of surface textures (Sa, Sp, Sv, Sz) than the boars  
294 in enclosure (Figures S5 and S8, Online Resource 3). However, significant difference is only  
295 detected in Sa on lower M2 shearing facets ( $p = 0.04$ , Tables 3 and S14, Online Resource 3).  
296 Regarding parameters related to height distribution, we observe that rooting boars tend to show  
297 lower Sku and higher Ssk than stall-fed ones, but are only significantly different on upper M1  
298 crushing facets ( $p = 0.05$  and  $p = 0.02$ , respectively, Tables 3 and S11, Online Resource 3). This  
299 suggests surface texture with greater relief amplitude among stall-fed boars. Parameters related  
300 to the volume of surface texture (Vmp, Vmc, Vvv, Vvc) tend to be higher among stall-fed pigs  
301 (Figures S6 and S9, Online Resource 3) but only Vmc and Vvv significantly differ between the  
302 two groups on lower M2 shearing facets ( $p = 0.05$  and  $p = 0.02$ , respectively, Tables 3 and S14,  
303 Online Resource 3). Parameters quantifying mean dale (Sda) and hill (Sha) areas are highly  
304 variable and we do not observe consistent trends (Figures S7 and S10, Online Resource 3). The  
305 parameter related to the complexity of surface texture (Sdr) is, on average, higher among stall-  
306 fed boars than among boars in enclosure (Figures S7 and S10, Online Resource 3). They show  
307 significantly higher Sdr on lower and upper M2 shearing facets ( $p = 0.04$  and  $p = 0.01$ ,  
308 respectively, Tables S14 and S16, Online Resource 3). The parameter related to anisotropy (Str)  
309 also tends to be higher among stall-fed boars, suggesting more isotropic wear surfaces among  
310 this group than among the enclosure group (Figures S7 and S10, Online Resource 3).  
311 Specifically, stall-fed boars significantly differ from rooting ones in Str on upper M1 crushing



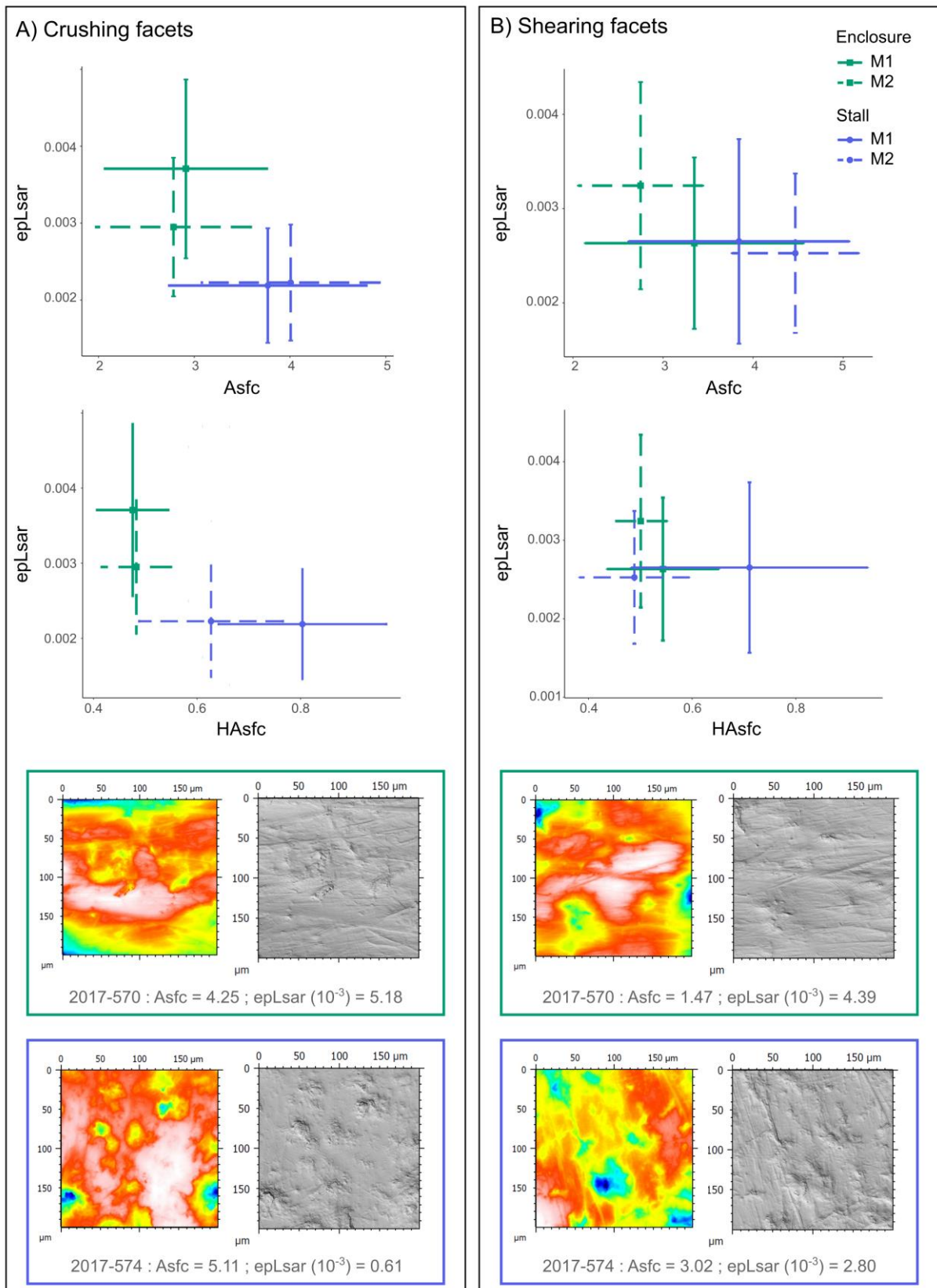
312 facets ( $p = 0.02$ , Table S11, Online Resource 3) and on upper M2 shearing facets ( $p = 0.01$ ,  
 313 Table S16, Online Resource 3). Thus, although ISO 25178 parameters reveal more significant  
 314 differences on shearing facets and SSFA parameters reveal more on crushing ones, the results  
 315 on both sets of texture parameters are congruent.

316

317 **Table 3** Summary of the significant differences observed on dental microwear texture  
 318 parameters between boars in enclosure and stall-fed boars following two-sample t-tests  
 319 conducted separately on upper and lower first and second molars' crushing and shearing facets.  
 320 Discriminant ( $p < 0.05$ ) parameters on shearing facets are indicated in italics, others are  
 321 discriminant on crushing facets.

	<b>Discriminant parameters</b>
Upper M1	epLsar, HAsfc9, HAsfc, HAsfc81, Ssk, Str
Upper M2	<i>Asfc, HAsfc, Asfc, Sda, Sdr, Str</i>
Lower M1	
Lower M2	<i>HAsfc81, Sa, Vvv, Sdr</i>

322



323

324 **Fig. 3** Dental microwear textures on upper molar wear facets (M1: solid lines; M2: dotted lines)

325 among stall-fed boars (blue circles) and rooting boars in enclosure (green squares). A) Biplots

326 of anisotropy (epLsar) and complexity (Asfc), and anisotropy and heterogeneity of complexity  
327 (HAsfc, calculated through 36 cells) on crushing facets. Colormap and photosimulation of one  
328 crushing facet are shown for each group. B) Biplots of anisotropy (epLsar) and complexity  
329 (Asfc), and anisotropy and heterogeneity of complexity (HAsfc) on shearing facets. Colormap  
330 and photosimulation of one shearing facet are shown for each group. Mean and mean  
331 confidence interval at 95% are indicated.

332

#### 333 **4. DISCUSSION**

334 In this study, we focused on two groups of captive wild boars that only differ in habitat  
335 and on the possibility to root the floor and ingest soil particles. We investigated whether, and  
336 how, DMT of rooting boars differ from those of stalled boars, even though they were fed with  
337 the same diet. Our results show that, although the groups overlap in most parameters, rooting  
338 boars exhibit more anisotropic wear surfaces (i.e. wear scratches with a preferential orientation)  
339 than stall-fed ones. The stall group show more rough and complex surfaces, which was expected  
340 as these boars only consumed a mixture of pellets and corn kernels i.e. relatively hard and not  
341 tough food items. A previous study on modern stalled vs. free-ranging *Sus* specimens using  
342 low-magnification dental microwear observed generally greater density of features among  
343 rooting boars, as well as more striations and less pits than among stalled boars (Ward &  
344 Mainland, 1999; see also Wilkie et al., 2007 and Vanpoucke et al., 2009). Comparing our results  
345 to theirs is challenging because we did not employ the same approach as in low-magnification  
346 studies. Notably, number of pits is not related to DMT parameters (DeSantis et al., 2013).  
347 Nonetheless, Ward & Mainland (1999) observed larger features among stalled boars than  
348 rooting ones, which could be related to the higher values of volume parameters, such as larger  
349 valleys, that Yamada et al. (2018) and we observed in stalled boars using 3D dental microwear,  
350 as well as to higher roughness. Overall, these studies suggest a more abrasive diet due to soil

351 ingestion when rooting, leading notably to more anisotropic, less complex and less rough wear  
352 surfaces among boars. Thus, if also supported by other proxies, this wear pattern among past  
353 populations would suggest substantial access to wild environment. Besides, a recent study  
354 investigated human-suid relationships during medieval periods through dental microwear  
355 textures by specifically focusing on ISO 25178 Sq parameter, a roughness parameter (Yamada  
356 et al., 2021). Although we do not present here the results on this specific parameter, we explored  
357 six others related to surface roughness that, indeed, all show higher values among stalled boars.  
358 Yet, in this study, SSFA parameters appear to better distinguish stall-fed boars from boars in  
359 enclosure than ISO parameters. We thus recommend considering both approaches (ISO 25178  
360 as well as SSFA) for future studies. Particularly, we observed in the present study that the  
361 heterogeneity of complexity (HASfc) reveals even stronger differences between the two groups  
362 than the complexity. Though more studies are needed to better understand how HASfc relates  
363 to feeding habits, it would be relevant to consider this parameter when investigating past  
364 husbandry practices since it has no ISO 25178 equivalent, unlike Asfc and epLsar. A previous  
365 work conducted on extant suid species, including two populations of wild boars, has suggested  
366 that HASfc could be partly related to soil ingestion, proposing that “the more frequent the  
367 ingestion of underground resources, the more grit ingested, potentially causing a more  
368 homogeneous abrasion of the surfaces” (Souron et al., 2015). Here, rooting boars exhibit more  
369 homogeneous surfaces than stall-fed pigs, supporting the idea that grit consumption leads to  
370 more homogeneous abrasion. However, we only focused on captive boars from the same  
371 population and with the same diet, so we cannot test their primary hypothesis that HASfc could  
372 be related to dietary diversity. Moreover, as suggested before, we may expect that dust/grit  
373 consumption would have different impact on DMT depending on the physical properties of the  
374 food item on which it is deposited (Hua et al., 2020; Teaford et al., 2021). In this study, the  
375 food items given to the boars lead to isotropic, complex and heterogeneous surfaces. It would

376 be interesting to further test whether similar trends are observed among boars fed with tough  
377 (i.e. abrasive) food items, with the addition or no of exogenous mineral particles. In addition,  
378 as pointed out by (Vanpoucke et al., 2009), different substrates and geological backgrounds  
379 may have different impacts on dental microwear and more studies are needed to explore this  
380 question.

381 In recent years, several *in-vivo* experimental studies have investigated the effect of  
382 exogenous abrasives on DMT of controlled-fed mammals, sometimes yielding contrasting  
383 results (Hoffman et al., 2015; Merceron et al., 2016; Ackermans et al., 2020; L. F. Martin et al.,  
384 2020; Schulz-Kornas et al., 2020; Winkler, Tütken, et al., 2020). In their experimental study,  
385 Merceron and colleagues (2016) highlighted a predominant impact of the diet on dental  
386 abrasion. Still, their study also showed that the addition of dust – simulating natural conditions  
387 (~ 1 %,  $\text{Ø} < 100 \mu\text{m}$ ) – leads to a slight trend toward decreased complexity and heterogeneity  
388 of complexity, and increased anisotropy among controlled-fed sheep with browse diet. DMT  
389 patterns are more similar among sheep fed with dust-free and dust-laden grass. Other studies  
390 aimed at disentangling the effects of more specific factors (size, shape, concentration of  
391 particles and type of mineral) on DMT. Winkler and colleagues (2020) observed in controlled-  
392 fed guinea pigs an increase in anisotropy associated with either an increased concentration of  
393 abrasives or angular-shaped abrasives, and complexity to be positively correlated with particle  
394 size. Overall, they concluded that DMT patterns, within the same mineral abrasive, are particle  
395 size dependent (see also Ackermans et al., 2020 on controlled-fed sheep). Nevertheless, as they  
396 pointed out, mammals under natural conditions encounter a mixture of abrasives of different  
397 size, shape and type, and in varying quantities. In the present study, the ingested soil is naturally  
398 composed of particles of various size, with coarse sand ( $> 200 \mu\text{m}$ ) and fine silt (20-2  $\mu\text{m}$ ) being  
399 the most represented particle size fractions (on average 24 % and 26 %, respectively). In terms  
400 of mineralogy, quartz is the most abundant mineral in the soil ingested (about 80 % in sand and

401 silt fractions, which represent around 80 % of the soil), making our results comparable to  
402 previous studies. We assume that other minerals, such as potassium feldspars, kaolinite or  
403 mica/illite, had negligible impact on DMT considering their lower proportion in the soil than  
404 quartz. Moreover, following Mohs scratch resistance scale, quartz is harder (7.0-6.0 GPa) than  
405 enamel (5.0 GPa) whereas kaolinite and mica/illite are much softer (1.0-2.0 GPa) ie. less  
406 abrasive (Broz et al., 2006; Lucas et al., 2013; Mineralogy Database WebMineral, 2021). In our  
407 study, while an important amount of particles is above 100  $\mu\text{m}$  diameter, more than half is  
408 below and we show a trend toward increased anisotropy and decreased complexity and  
409 heterogeneity among mammals fed on exogenous abrasives. Our results thus appear more in  
410 line with those observed in Merceron et al.'s study (2016, exogenous particles  $\text{\O} < 100 \mu\text{m}$ ),  
411 although it is worth noting that they fed sheep with clover/grass and not pellets as in the present  
412 study. On the contrary, we do not observe increased complexity, as previously shown following  
413 the ingestion of medium (silt-size) or large (sand-size) abrasives (Hoffman et al., 2015;  
414 Ackermans et al., 2020; L. F. Martin et al., 2020; Schulz-Kornas et al., 2020; Winkler, Tütken,  
415 et al., 2020). Incongruities between these studies and ours could also be related to different  
416 amounts of ingested soil but we were unable to measure it.

417 Overall, this study provides new insights for a better comprehension of past feeding  
418 habits among mammals. In line with previous works, this study suggests that dental microwear  
419 analysis is relevant to investigate past pig feeding systems, and more generally husbandry  
420 practices (e.g. Ward & Mainland, 1999; Wilkie et al., 2007; Vanpoucke et al., 2009; Rivals et  
421 al., 2011; Yamada et al., 2018, 2021; Gallego-Valle et al., 2020; Sierra et al., 2020, 2021). To  
422 our knowledge, very few studies have focused on dental microwear of extant pigs/boars in a  
423 domestication context, and with few individuals or information about diets and habitats (Ward  
424 & Mainland, 1999; Yamada et al., 2018). Here, we provide details of the diet and the ingested  
425 soil, and our results are congruent with previous observations using standard DMTA

426 parameters. Moreover, we show that even though the two groups of captive boars were fed with  
427 the same diet and in the same proportion, DMT patterns of rooting and unrooting boars are  
428 different. We thus highly recommend considering DMTA when investigating pig husbandry  
429 systems used by ancient societies, notably local changes in food management. Above all, it is  
430 not known in any region when pigs started to be stall-fed (Wilkie et al., 2007; Rowley-Conwy  
431 et al., 2012), and our study strongly suggests that DMTA can discriminate between stall-fed  
432 pigs that are not allowed to root and pigs that were able to root. To apply such approach to  
433 Neolithic domesticated pigs at Eurasian sites where several lines of evidence suggest  
434 intensification of domestication and greater confinement of pig populations, such as in late  
435 Neolithic China, would be benefic (Cucchi et al., 2016; Balasse et al., 2018). It would also be  
436 interesting to conduct further experimental studies with diets more similar to those potentially  
437 given to pigs in ancient feeding systems (such as foddors or other by-products of human  
438 activities; see Gallego-Valle et al., 2020 for controlled-food trials on domestic ewes). Moreover,  
439 we would like to emphasize that DMTA can complement other indicators that do not reflect the  
440 same timescale and that are influenced by other factors. Here, we show that DMTA reflects the  
441 distinction between rooting and stalled boars. On the contrary, a previous study that included  
442 the exact same specimens have shown that mandibular morphology and muscle force do not  
443 differ between these two groups (Neaux et al., 2021a, 2021b). These differences are expected  
444 as mandibular morphology and DMTA record different timescales (Davis & Pineda Munoz,  
445 2016) and have different relationships with diet (Ross et al., 2012). This highlight the need for  
446 more comprehensive studies combining different proxies (mandibular shape and dental  
447 microwear textures, but also gross tooth wear and enamel biogeochemical compositions) to  
448 better understand the links between these different indicators. It will allow a better assessment  
449 of the dietary habits of palaeontological and zooarchaeological populations. Nonetheless,  
450 although we focused here on boars with natural soil ingestion, they were restricted to an

451 enclosure of 3000 m<sup>2</sup> so we did not study individuals that had access to wild environment.  
452 Moreover, both groups received a mixture of pellets and corn kernels. Such a diet is very  
453 different from a diet composed of wild resources, and probably also differs strongly from the  
454 foods given to/eaten by pigs in the early phases of domestication, especially considering that  
455 extensive pig management seems to have persisted for several millennia (Price & Hongo, 2020).  
456 Thus, while this study provides new insights to help explore pig management systems,  
457 particularly local changes in food management, further research is needed to investigate the  
458 impact of different agricultural crops and human by-products on dental microwear textures, as  
459 well as the impact of different soil particles. Despite these limitations, we think the present  
460 study that integrates detailed information on the diet and soil ingested by boars represent an  
461 important step in addressing these questions.

462 Overall, we show here that exogenous particles have a substantial effect on dental  
463 abrasion. Yet, more studies are needed to better track the consumption of exogenous particles  
464 in the palaeontological or archaeological record, and for a better understanding of its impact on  
465 dental abrasion. These issues require further investigation for a better assessment of the  
466 potential key factors that have driven the selection of some dental phenotypes.

467

## 468 **5. CONCLUSIONS**

469 This study is the first focusing on DMT of rooting vs. non-rooting controlled-fed boars  
470 that also precisely documents the composition of the soil ingested. Our results show that dental  
471 microwear textures of rooting boars differ from those observed on stalled boars that cannot  
472 engage in rooting behaviour, even though they were fed with the same diet. Overall, they are in  
473 line with more anisotropic wear surfaces (i.e. wear scratches with a preferential orientation)  
474 among boars that frequently ingest exogenous mineral particles when rooting on the floor. They



475 are also consistent with more complex surfaces among stalled boars than rooting ones (Ward &  
476 Mainland, 1999; Yamada et al., 2018). To our knowledge, this is the first work on stall-fed vs.  
477 rooting boars that focuses on standard SSFA parameters, which are widely employed among  
478 researchers aiming at investigating past dietary habits. As a complement to other proxies, this  
479 study suggests that DMTA is relevant to investigate pig husbandry practices used by ancient  
480 societies. It also brings new insights for the comprehension of how the consumption of  
481 exogenous mineral particles impacts dental microwear textures of bunodont omnivorous  
482 mammals.

483

#### 484 **Competing Interest**

485 The authors declare that they have no known competing financial interests or personal  
486 relationships that could have influenced the work reported in this paper.

487

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501

## 502 **References**

503 Ackermans, N. L., Winkler, D. E., Martin, L. F., Kaiser, T. M., Clauss, M., & Hatt, J.-M. (2020).

504 Dust and grit matter: Abrasives of different size lead to opposing dental microwear  
505 textures in experimentally fed sheep (*Ovis aries*). *The Journal of Experimental Biology*,  
506 223(3), jeb220442. <https://doi.org/10.1242/jeb.220442>

507 Balasse, M., Cucchi, T., Evin, A., Bălăşescu, A., Frémondeau, D., & Horard-Herbin, M.-P.

508 (2018). Wild game or farm animal? Tracking human-pig relationships in ancient times  
509 through stable isotope analysis. In C. Stépanoff & J.-D. Vigne (Eds.), *Hybrid*  
510 *Communities. Biosocial Approaches to Domestication and Other Trans-species*  
511 *Relationships* (pp. 81–96). Routledge.

512 <https://www.taylorfrancis.com/books/9781351717984>

513 Beattie, V. E., & O'Connell, N. E. (2002). Relationship Between Rooting Behaviour and  
514 Foraging in Growing Pigs. *Animal Welfare*, 11(3), 295–303.

515 Berlioz, E., Azorit, C., Blondel, C., Ruiz, M. S. T., & Merceron, G. (2017). Deer in an arid  
516 habitat: Dental microwear textures track feeding adaptability. *Hystrix, the Italian*  
517 *Journal of Mammalogy*, 28, 222–230. <https://doi.org/10.4404/hystrix-28.2-12048>

518 Berlioz, É., Kostopoulos, D. S., Blondel, C., & Merceron, G. (2018). Feeding ecology of  
519 *Eucladoceros ctenoides* as a proxy to track regional environmental variations in Europe  
520 during the early Pleistocene. *Comptes Rendus Palevol*, 17(4), 320–332.  
521 <https://doi.org/10.1016/j.crpv.2017.07.002>

522 Billet, G., Blondel, C., & de Muizon, C. (2009). Dental microwear analysis of notoungulates  
523 (Mammalia) from Salla (Late Oligocene, Bolivia) and discussion on their precocious

524 hypsodonty. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274(1), 114–124.  
525 <https://doi.org/10.1016/j.palaeo.2009.01.004>

526 Blondel, C., Rowan, J., Merceron, G., Bibi, F., Negash, E., Barr, W. A., & Boisserie, J.-R.  
527 (2018). Feeding ecology of Tragelaphini (Bovidae) from the Shungura Formation, Omo  
528 Valley, Ethiopia: Contribution of dental wear analyses. *Palaeogeography,*  
529 *Palaeoclimatology,* *Palaeoecology,* 496, 103–120.  
530 <https://doi.org/10.1016/j.palaeo.2018.01.027>

531 Brindley, G. W., & Brown, G. (1980). *Crystal Structures of Clay Minerals and their X-Ray*  
532 *Identification*. <https://doi.org/10.1180/mono-5>

533 Broz, M. E., Cook, R. F., & Whitney, D. L. (2006). Microhardness, toughness, and modulus of  
534 Mohs scale minerals. *American Mineralogist*, 91(1), 135–142.  
535 <https://doi.org/10.2138/am.2006.1844>

536 Cucchi, T., Dai, L., Balasse, M., Zhao, C., Gao, J., Hu, Y., Yuan, J., & Vigne, J.-D. (2016).  
537 Social Complexification and Pig (*Sus scrofa*) Husbandry in Ancient China: A Combined  
538 Geometric Morphometric and Isotopic Approach. *PLOS ONE*, 11(7), e0158523.  
539 <https://doi.org/10.1371/journal.pone.0158523>

540 Daegling, D. J., Hua, L.-C., & Ungar, P. S. (2016). The role of food stiffness in dental  
541 microwear feature formation. *Archives of Oral Biology*, 71, 16–23.  
542 <https://doi.org/10.1016/j.archoralbio.2016.06.018>

543 Damuth, J., & Janis, C. M. (2011). On the relationship between hypsodonty and feeding ecology  
544 in ungulate mammals, and its utility in palaeoecology. *Biological Reviews*, 86(3), 733–  
545 758. <https://doi.org/10.1111/j.1469-185X.2011.00176.x>

546 Davis, M., & Pineda Munoz, S. (2016). The temporal scale of diet and dietary proxies. *Ecology*  
547 *and Evolution*, 6(6), 1883–1897. <https://doi.org/10.1002/ece3.2054>

548 DeSantis, L. R. G., Scott, J. R., Schubert, B. W., Donohue, S. L., McCray, B. M., Stolk, C. A.  
549 V., Winburn, A. A., Greshko, M. A., & O’Hara, M. C. (2013). Direct Comparisons of  
550 2D and 3D Dental Microwear Proxies in Extant Herbivorous and Carnivorous  
551 Mammals. *PLOS ONE*, 8(8), e71428. <https://doi.org/10.1371/journal.pone.0071428>

552 Dixon, J. B., & Weed, S. B. (Eds.). (1989). *Minerals in Soil Environments*. Soil Science Society  
553 of America. <https://doi.org/10.2136/sssabookser1.2ed>

554 Fannin, L. D., Singels, E., Esler, K. J., & Dominy, N. J. (2021). Grit and consequence.  
555 *Evolutionary Anthropology: Issues, News, and Reviews*, evan.21927.  
556 <https://doi.org/10.1002/evan.21927>

557 Gallego-Valle, A., Colominas, L., Burguet-Coca, A., Aguilera, M., Palet, J.-M., & Tornero, C.  
558 (2020). What is on the menu today? Creating a microwear reference collection through  
559 a controlled-food trial to study feeding management systems of ancient agropastoral  
560 societies. *Quaternary International*, 557, 3–11.  
561 <https://doi.org/10.1016/j.quaint.2020.02.020>

562 Grant, A. (1982). The use of tooth wear as a guide to the age of domestic animals. In B. Wilson,  
563 S. Grigson, & S. Payne (Eds.), *Ageing and Sexing Animal Bones from Archaeological*  
564 *Sites* (pp. 91–108). British Archaeological Reports, British series.

565 Guy, F., Lazzari, V., Gilissen, E., & Thiery, G. (2015). To What Extent is Primate Second  
566 Molar Enamel Occlusal Morphology Shaped by the Enamel-Dentine Junction? *PLOS*  
567 *ONE*, 10(9), e0138802. <https://doi.org/10.1371/journal.pone.0138802>

568 Harbers, H., Neaux, D., Ortiz, K., Blanc, B., Laurens, F., Baly, I., Callou, C., Schafberg, R.,  
569 Haruda, A., Lecompte, F., Casabianca, F., Studer, J., Renaud, S., Cornette, R., Locatelli,  
570 Y., Vigne, J.-D., Herrel, A., & Cucchi, T. (2020a). The mark of captivity: Plastic  
571 responses in the ankle bone of a wild ungulate (*Sus scrofa*). *Royal Society Open Science*,  
572 7(3), 192039. <https://doi.org/10.1098/rsos.192039>

573 Harbers, H., Zanolli, C., Cazenave, M., Theil, J.-C., Ortiz, K., Blanc, B., Locatelli, Y.,  
574 Schafberg, R., Lecompte, F., Baly, I., Laurens, F., Callou, C., Herrel, A., Puymeraul, L.,  
575 & Cucchi, T. (2020b). Investigating the impact of captivity and domestication on limb  
576 bone cortical morphology: An experimental approach using a wild boar model.  
577 *Scientific Reports*, 10(1), 19070. <https://doi.org/10.1038/s41598-020-75496-6>

578 Harris, J. M., & Cerling, T. E. (2002). Dietary adaptations of extant and Neogene African suids.  
579 *Journal of Zoology*, 256(1), 45–54. <https://doi.org/10.1017/S0952836902000067>

580 Hatt, J.-M., Codron, D., Ackermans, N. L., Martin, L. F., Richter, H., Kircher, P. R., Gerspach,  
581 C., Hummel, J., & Clauss, M. (2020). The effect of the rumen washing mechanism in  
582 sheep differs with concentration and size of abrasive particles. *Palaeogeography,*  
583 *Palaeoclimatology, Palaeoecology*, 550, 109728.  
584 <https://doi.org/10.1016/j.palaeo.2020.109728>

585 Hiiemae, K. M. (2000). CHAPTER 13—Feeding in Mammals. In K. Schwenk (Ed.), *Feeding*  
586 (pp. 411–448). Academic Press. <https://doi.org/10.1016/B978-012632590-4/50014-9>

587 Hoffman, J. M., Fraser, D., & Clementz, M. T. (2015). Controlled feeding trials with ungulates:  
588 A new application of in vivo dental molding to assess the abrasive factors of microwear.  
589 *Journal of Experimental Biology*, 218(10), 1538–1547.  
590 <https://doi.org/10.1242/jeb.118406>

591 Hua, L., Chen, J., & Ungar, P. S. (2020). Diet reduces the effect of exogenous grit on tooth  
592 microwear. *Biosurface and Biotribology*, 6(2), 48–52.  
593 <https://doi.org/10.1049/bsbt.2019.0041>

594 Keuling, O., Podgórski, T., Monaco, A., Melletti, M., Merta, D., Albrycht, M., Genov, P. V.,  
595 Gethöffer, F., Vetter, S. G., Jori, F., Scalera, R., & Gongora, J. (2017). Eurasian Wild  
596 Boar *Sus scrofa* (Linnaeus, 1758). In M. Melletti & E. Meijaard (Eds.), *Ecology,*

597           *Conservation and Management of Wild Pigs and Peccaries* (1st ed., pp. 202–233).  
598           Cambridge University Press. <https://doi.org/10.1017/9781316941232.023>

599   Lazagabaster, I. A. (2019). Dental microwear texture analysis of Pliocene Suidae from Hadar  
600           and Kanapoi in the context of early hominin dietary breadth expansion. *Journal of*  
601           *Human Evolution*, 132, 80–100. <https://doi.org/10.1016/j.jhevol.2019.04.010>

602   Louail, M., Ferchaud, S., Souron, A., Walker, A. E. C., & Merceron, G. (2021). Dental  
603           microwear textures differ in pigs with overall similar diets but fed with different seeds.  
604           *Palaeogeography, Palaeoclimatology, Palaeoecology*, 572, 110415.  
605           <https://doi.org/10.1016/j.palaeo.2021.110415>

606   Lucas, P. W. (2004). *Dental Functional Morphology: How Teeth Work* (1st ed.). Cambridge  
607           University Press. <https://doi.org/10.1017/CBO9780511735011>

608   Lucas, P. W., Casteren, A. van, Al-Fadhalah, K., Almusallam, A. S., Henry, A. G., Michael, S.,  
609           Watzke, J., Reed, D. A., Diekwisch, T. G. H., Strait, D. S., & Atkins, A. G. (2014). The  
610           Role of Dust, Grit and Phytoliths in Tooth Wear. *Annales Zoologici Fennici*, 51(1–2),  
611           143–152. <https://doi.org/10.5735/086.051.0215>

612   Lucas, P. W., Constantino, P., Wood, B., & Lawn, B. (2008). Dental enamel as a dietary  
613           indicator in mammals. *BioEssays*, 30(4), 374–385. <https://doi.org/10.1002/bies.20729>

614   Lucas, P. W., Omar, R., Al-Fadhalah, K., Almusallam, A. S., Henry, A. G., Michael, S., Thai,  
615           L. A., Watzke, J., Strait, D. S., & Atkins, A. G. (2013). Mechanisms and causes of wear  
616           in tooth enamel: Implications for hominin diets. *Journal of The Royal Society Interface*,  
617           10(80), 20120923. <https://doi.org/10.1098/rsif.2012.0923>

618   Madden, R. H. (2014). *Hypsodonty in Mammals: Evolution, Geomorphology and the Role of*  
619           *Earth Surface Processes*. Cambridge University Press.  
620           <https://doi.org/10.1017/CBO9781139003384>

621 Mainland, I. L. (2003). Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*)  
622 and its implications for dietary reconstruction. *Journal of Archaeological Science*,  
623 30(11), 1513–1527. [https://doi.org/10.1016/S0305-4403\(03\)00055-4](https://doi.org/10.1016/S0305-4403(03)00055-4)

624 Martin, F., Plastiras, C.-A., Merceron, G., Souron, A., & Boisserie, J.-R. (2018). Dietary niches  
625 of terrestrial cercopithecines from the Plio-Pleistocene Shungura Formation, Ethiopia:  
626 Evidence from Dental Microwear Texture Analysis. *Scientific Reports*, 8(1), 14052.  
627 <https://doi.org/10.1038/s41598-018-32092-z>

628 Martin, L. F., Krause, L., Ulbricht, A., Winkler, D. E., Codron, D., Kaiser, T. M., Müller, J.,  
629 Hummel, J., Clauss, M., Hatt, J.-M., & Schulz-Kornas, E. (2020). Dental wear at macro-  
630 and microscopic scale in rabbits fed diets of different abrasiveness: A pilot  
631 investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 556, 109886.  
632 <https://doi.org/10.1016/j.palaeo.2020.109886>

633 Merceron, G., Blondel, C., Brunetiere, N., Francisco, A., Gautier, D., & Ramdarshan, A.  
634 (2017). Dental microwear and controlled food testing on sheep: The TRIDENT project.  
635 *Biosurface and Biotribology*, 3(4), 174–183. <https://doi.org/10.1016/j.bsbt.2017.12.005>

636 Merceron, G., Escarguel, G., Angibault, J.-M., & Verheyden-Tixier, H. (2010). Can Dental  
637 Microwear Textures Record Inter-Individual Dietary Variations? *PLoS ONE*, 5(3),  
638 e9542. <https://doi.org/10.1371/journal.pone.0009542>

639 Merceron, G., Hofman-Kamińska, E., & Kowalczyk, R. (2014). 3D dental microwear texture  
640 analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest,  
641 Poland. *Forest Ecology and Management*, 328, 262–269.  
642 <https://doi.org/10.1016/j.foreco.2014.05.041>

643 Merceron, G., Kallend, A., Francisco, A., Louail, M., Martin, F., Plastiras, C.-A., Thiery, G.,  
644 & Boisserie, J.-R. (2021). Further away with dental microwear analysis: Food resource  
645 partitioning among Plio-Pleistocene monkeys from the Shungura Formation, Ethiopia.

646 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 572, 110414.  
647 <https://doi.org/10.1016/j.palaeo.2021.110414>

648 Merceron, G., Ramdarshan, A., Blondel, C., Boisserie, J.-R., Brunetiere, N., Francisco, A.,  
649 Gautier, D., Milhet, X., Novello, A., & Pret, D. (2016). Untangling the environmental  
650 from the dietary: Dust does not matter. *Proceedings of the Royal Society B: Biological*  
651 *Sciences*, 283(1838), 20161032. <https://doi.org/10.1098/rspb.2016.1032>

652 Merceron, G., Scott, J., Scott, R. S., Geraads, D., Spassov, N., & Ungar, P. S. (2009). Folivory  
653 or fruit/seed predation for Mesopithecus, an earliest colobine from the late Miocene of  
654 Eurasia? *Journal of Human Evolution*, 57(6), 732–738.  
655 <https://doi.org/10.1016/j.jhevol.2009.06.009>

656 Merceron, G., Taylor, S., Scott, R., Chaimanee, Y., & Jaeger, J.-J. (2006). Dietary  
657 characterization of the hominoid Khoratpithecus (Miocene of Thailand): Evidence from  
658 dental topographic and microwear texture analyses. *Naturwissenschaften*, 93(7), 329–  
659 333. <https://doi.org/10.1007/s00114-006-0107-0>

660 Moore, D. M., & Reynolds Jr., R. C. (1989). *X-ray diffraction and the identification and*  
661 *analysis of clay minerals*. Oxford University Press.

662 Neaux, D., Blanc, B., Ortiz, K., Locatelli, Y., Schafberg, R., Herrel, A., Debat, V., & Cucchi,  
663 T. (2021a). Constraints associated with captivity alter craniomandibular integration in  
664 wild boar. *Journal of Anatomy*, 239(2), 489–497. <https://doi.org/10.1111/joa.13425>

665 Neaux, D., Blanc, B., Ortiz, K., Locatelli, Y., Laurens, F., Baly, I., Callou, C., Lecompte, F.,  
666 Cornette, R., Sansalone, G., Haruda, A., Schafberg, R., Vigne, J.-D., Debat, V., Herrel,  
667 A., & Cucchi, T. (2021b). How Changes in Functional Demands Associated with  
668 Captivity Affect the Skull Shape of a Wild Boar (*Sus scrofa*). *Evolutionary Biology*.  
669 <https://doi.org/10.1007/s11692-020-09521-x>



- 670 Percher, A. M., Merceron, G., Nsi Akoue, G., Galbany, J., Romero, A., & Charpentier, M. J.  
671 (2017). Dental microwear textural analysis as an analytical tool to depict individual  
672 traits and reconstruct the diet of a primate. *American Journal of Physical Anthropology*,  
673 *165*(1), 123–138. <https://doi.org/10.1002/ajpa.23337>
- 674 Peterson, A., Abella, E. F., Grine, F. E., Teaford, M. F., & Ungar, P. S. (2018). Microwear  
675 textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to  
676 paleoenvironment and diet. *Journal of Human Evolution*, *119*, 42–63.  
677 <https://doi.org/10.1016/j.jhevol.2018.02.004>
- 678 Price, M., & Hongo, H. (2020). The Archaeology of Pig Domestication in Eurasia. *Journal of*  
679 *Archaeological Research*, *28*(4), 557–615. [https://doi.org/10.1007/s10814-019-09142-](https://doi.org/10.1007/s10814-019-09142-9)  
680 [9](https://doi.org/10.1007/s10814-019-09142-9)
- 681 Rabenold, D., & Pearson, O. M. (2011). Abrasive, Silica Phytoliths and the Evolution of Thick  
682 Molar Enamel in Primates, with Implications for the Diet of *Paranthropus boisei*. *PLoS*  
683 *ONE*, *6*(12), e28379. <https://doi.org/10.1371/journal.pone.0028379>
- 684 Rivals, F., Gardeisen, A., & Cantuel, J. (2011). Domestic and wild ungulate dietary traits at  
685 Kouphovouno (Sparta, Greece): Implications for livestock management and  
686 paleoenvironment in the Neolithic. *Journal of Archaeological Science*, *38*(3), 528–537.  
687 <https://doi.org/10.1016/j.jas.2010.10.007>
- 688 Ross, C. F., Iriarte-Diaz, J., & Nunn, C. L. (2012). Innovative Approaches to the Relationship  
689 Between Diet and Mandibular Morphology in Primates. *International Journal of*  
690 *Primatology*, *33*(3), 632–660. <https://doi.org/10.1007/s10764-012-9599-y>
- 691 Rowley-Conwy, P., Albarella, U., & Dobney, K. (2012). Distinguishing Wild Boar from  
692 Domestic Pigs in Prehistory: A Review of Approaches and Recent Results. *Journal of*  
693 *World Prehistory*, *25*(1), 1–44. <https://doi.org/10.1007/s10963-012-9055-0>

694 Schulz, E., Calandra, I., & Kaiser, T. M. (2010). Applying tribology to teeth of hoofed  
695 mammals. *Scanning*, 32(4), 162–182. <https://doi.org/10.1002/sca.20181>

696 Schulz, E., Calandra, I., & Kaiser, T. M. (2013). Feeding ecology and chewing mechanics in  
697 hoofed mammals: 3D tribology of enamel wear. *Wear*, 300(1), 169–179.  
698 <https://doi.org/10.1016/j.wear.2013.01.115>

699 Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., & Kaiser, T. M. (2013). Dietary  
700 Abrasiveness Is Associated with Variability of Microwear and Dental Surface Texture  
701 in Rabbits. *PLoS ONE*, 8(2), e56167. <https://doi.org/10.1371/journal.pone.0056167>

702 Schulz-Kornas, E., Winkler, D. E., Clauss, M., Carlsson, J., Ackermans, N. L., Martin, L. F.,  
703 Hummel, J., Müller, D. W. H., Hatt, J.-M., & Kaiser, T. M. (2020). Everything matters:  
704 Molar microwear texture in goats (*Capra aegagrus hircus*) fed diets of different  
705 abrasiveness. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 552, 109783.  
706 <https://doi.org/10.1016/j.palaeo.2020.109783>

707 Scott, J. R. (2012). Dental microwear texture analysis of extant African Bovidae. *Mammalia*,  
708 76(2). <https://doi.org/10.1515/mammalia-2011-0083>

709 Scott, R. S., Teaford, M. F., & Ungar, P. S. (2012). Dental microwear texture and anthropoid  
710 diets. *American Journal of Physical Anthropology*, 147(4), 551–579.  
711 <https://doi.org/10.1002/ajpa.22007>

712 Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Childs, B. E., Teaford, M. F., &  
713 Walker, A. (2006). Dental microwear texture analysis: Technical considerations.  
714 *Journal of Human Evolution*, 51(4), 339–349.  
715 <https://doi.org/10.1016/j.jhevol.2006.04.006>

716 Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Grine, F. E., Teaford, M. F., &  
717 Walker, A. (2005). Dental microwear texture analysis shows within-species diet

718 variability in fossil hominins. *Nature*, 436(7051), 693–695.  
719 <https://doi.org/10.1038/nature03822>

720 Service du Patrimoine naturel (collectif) (2017). *Inventaire naturaliste de la Réserve*  
721 *zoologique de la Haute-Touche (Indre) du 1er au 3 juin 2016*. Service du  
722 patrimoine naturel, Muséum national d'Histoire naturelle, Paris.

723 Sierra, A., Balasse, M., Rivals, F., Fiorillo, D., Utrilla, P., & Saña, M. (2021). Sheep husbandry  
724 in the early Neolithic of the Pyrenees: New data on feeding and reproduction in the cave  
725 of Chaves. *Journal of Archaeological Science: Reports*, 37, 102935.  
726 <https://doi.org/10.1016/j.jasrep.2021.102935>

727 Sierra, A., Merino, G. O., Rivals, F., & Saña, M. (2020). Feeding practices and management of  
728 domestic mammals during the Neolithic in the Iberian Peninsula through dental  
729 microwear. *Historical Biology*, 1–13. <https://doi.org/10.1080/08912963.2020.1860957>

730 Souron, A. (2017). Diet and Ecology of Extant and Fossil Wild Pigs. In M. Melletti & E.  
731 Meijaard (Eds.), *Ecology, Conservation and Management of Wild Pigs and Peccaries*  
732 (1st ed., pp. 29–38). Cambridge University Press.  
733 <https://doi.org/10.1017/9781316941232.005>

734 Souron, A., Merceron, G., Blondel, C., Brunetière, N., Colyn, M., Hofman-Kamińska, E., &  
735 Boisserie, J.-R. (2015). Three-dimensional dental microwear texture analysis and diet  
736 in extant Suidae (Mammalia: Cetartiodactyla). *Mammalia*, 79(3).  
737 <https://doi.org/10.1515/mammalia-2014-0023>

738 Teaford, M. F., & Oyen, O. J. (1989). In vivo and in vitro turnover in dental microwear.  
739 *American Journal of Physical Anthropology*, 80(4), 447–460.  
740 <https://doi.org/10.1002/ajpa.1330800405>

741 Teaford, M. F., Ross, C. F., Ungar, P. S., Vinyard, C. J., & Laird, M. F. (2021). Grit your teeth  
742 and chew your food: Implications of food material properties and abrasives for rates of

743 dental microwear formation in laboratory *Sapajus apella* (Primates). *Palaeogeography,*  
744 *Palaeoclimatology,* *Palaeoecology,* 110644.  
745 <https://doi.org/10.1016/j.palaeo.2021.110644>

746 Teaford, M. F., Ungar, P. S., Taylor, A. B., Ross, C. F., & Vinyard, C. J. (2017). In vivo rates  
747 of dental microwear formation in laboratory primates fed different food items.  
748 *Biosurface and Biotribology*, 3(4), 166–173. <https://doi.org/10.1016/j.bsbt.2017.11.005>

749 Thiery, G., Gibert, C., Guy, F., Lazzari, V., Geraads, D., Spassov, N., & Merceron, G. (2021).  
750 From leaves to seeds? The dietary shift in late Miocene colobine monkeys of  
751 southeastern Europe. *Evolution*, 75(8), 1983–1997. <https://doi.org/10.1111/evo.14283>

752 Tütken, T., Kaiser, T. M., Vennemann, T., & Merceron, G. (2013). Opportunistic Feeding  
753 Strategy for the Earliest Old World Hypsodont Equids: Evidence from Stable Isotope  
754 and Dental Wear Proxies. *PLOS ONE*, 8(9), e74463.  
755 <https://doi.org/10.1371/journal.pone.0074463>

756 Ungar, P. S. (2009). Tooth Form and Function: Insights into Adaptation through the Analysis  
757 of Dental Microwear. In T. Koppe, G. Meyer, K. W. Alt, A. Brook, M. C. Dean, I. Kjaer,  
758 J. R. Lukacs, B. H. Smith, & M. F. Teaford (Eds.), *Frontiers of Oral Biology* (Vol. 13,  
759 pp. 38–43). KARGER. <https://doi.org/10.1159/000242388>

760 Ungar, P. S., Grine, F. E., & Teaford, M. F. (2008). Dental Microwear and Diet of the Plio-  
761 Pleistocene Hominin *Paranthropus boisei*. *PLoS ONE*, 3(4), e2044.  
762 <https://doi.org/10.1371/journal.pone.0002044>

763 USDA, United States Department of Agriculture (1987). *Soil Mechanics Level 1 Module 3*  
764 *USDA Soil Textural Classification Study Guide*. USDA Soil Conservation Service,  
765 Washington DC.

766 van Casteren, A., Lucas, P. W., Strait, D. S., Michael, S., Bierwisch, N., Schwarzer, N., Al-  
767 Fadhlah, K. J., Almusallam, A. S., Thai, L. A., Saji, S., Shekeban, A., & Swain, M. V.

768 (2018). Evidence that metallic proxies are unsuitable for assessing the mechanics of  
769 microwear formation and a new theory of the meaning of microwear. *Royal Society*  
770 *Open Science*, 5(5), 171699. <https://doi.org/10.1098/rsos.171699>

771 Vanpoucke, S., Mainland, I., De Cupere, B., & Waelkens, M. (2009). Dental microwear study  
772 of pigs from the classical site of Sagalassos (SW Turkey) as an aid for the reconstruction  
773 of husbandry practices in ancient times. *Environmental Archaeology*, 14(2), 137–154.  
774 <https://doi.org/10.1179/146141009X12481709928328>

775 Ward, J., & Mainland, I. L. (1999). Microwear in Modern Rooting and Stall-fed Pigs: The  
776 Potential of Dental Microwear Analysis for Exploring Pig Diet and Management in the  
777 Past. *Environmental Archaeology*, 4(1), 25–32. <https://doi.org/10.1179/env.1999.4.1.25>

778 Wilkie, T., Mainland, I., Albarella, U., Dobney, K., & Rowley-Conwy, P. (2007). A dental  
779 microwear study of pig diet and management in Iron Age, Romano-British, Anglo-  
780 Scandinavian, and medieval contexts in England. In U. Albarella, K. Dobney, A.  
781 Ervynck, & P. Rowley-Conwy (Eds.), *Pigs and Humans: 10,000 Years of Interaction*  
782 (pp. 241–254). Oxford University Press.

783 Winkler, D. E., Schulz-Kornas, E., Kaiser, T. M., Codron, D., Leichliter, J., Hummel, J., Martin,  
784 L. F., Clauss, M., & Tütken, T. (2020). The turnover of dental microwear texture:  
785 Testing the” last supper” effect in small mammals in a controlled feeding experiment.  
786 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 557, 109930.  
787 <https://doi.org/10.1016/j.palaeo.2020.109930>

788 Winkler, D. E., Schulz-Kornas, E., Kaiser, T. M., De Cuyper, A., Clauss, M., & Tütken, T.  
789 (2019). Forage silica and water content control dental surface texture in guinea pigs and  
790 provide implications for dietary reconstruction. *Proceedings of the National Academy*  
791 *of Sciences*, 116(4), 1325–1330. <https://doi.org/10.1073/pnas.1814081116>

- 792 Winkler, D. E., Tütken, T., Schulz-Kornas, E., Kaiser, T. M., Müller, J., Leichliter, J., Weber,  
793 K., Hatt, J.-M., & Clauss, M. (2020). Shape, size, and quantity of ingested external  
794 abrasives influence dental microwear texture formation in guinea pigs. *Proceedings of*  
795 *the National Academy of Sciences*, 202008149.  
796 <https://doi.org/10.1073/pnas.2008149117>
- 797 Xia, J., Zheng, J., Huang, D., Tian, Z. R., Chen, L., Zhou, Z., Ungar, P. S., & Qian, L. (2015).  
798 New model to explain tooth wear with implications for microwear formation and diet  
799 reconstruction. *Proceedings of the National Academy of Sciences*, 112(34), 10669–  
800 10672. <https://doi.org/10.1073/pnas.1509491112>
- 801 Yamada, E., Hongo, H., & Endo, H. (2021). Analyzing historic human-suid relationships  
802 through dental microwear texture and geometric morphometric analyses of  
803 archaeological suid teeth in the Ryukyu Islands. *Journal of Archaeological Science*,  
804 132, 105419. <https://doi.org/10.1016/j.jas.2021.105419>
- 805 Yamada, E., Kubo, M. O., Kubo, T., & Kohno, N. (2018). Three-dimensional tooth surface  
806 texture analysis on stall-fed and wild boars (*Sus scrofa*). *PLOS ONE*, 13(10), e0204719.  
807 <https://doi.org/10.1371/journal.pone.0204719>