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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 m², 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 m², 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% H₂O₂ at 40°C). The samples were then treated with sodium hexametaphosphate
156 ((NaPO₃)₆) 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 (CaCl₂,
164 0.5 mol.L⁻¹) and then washed to remove the salt excess.

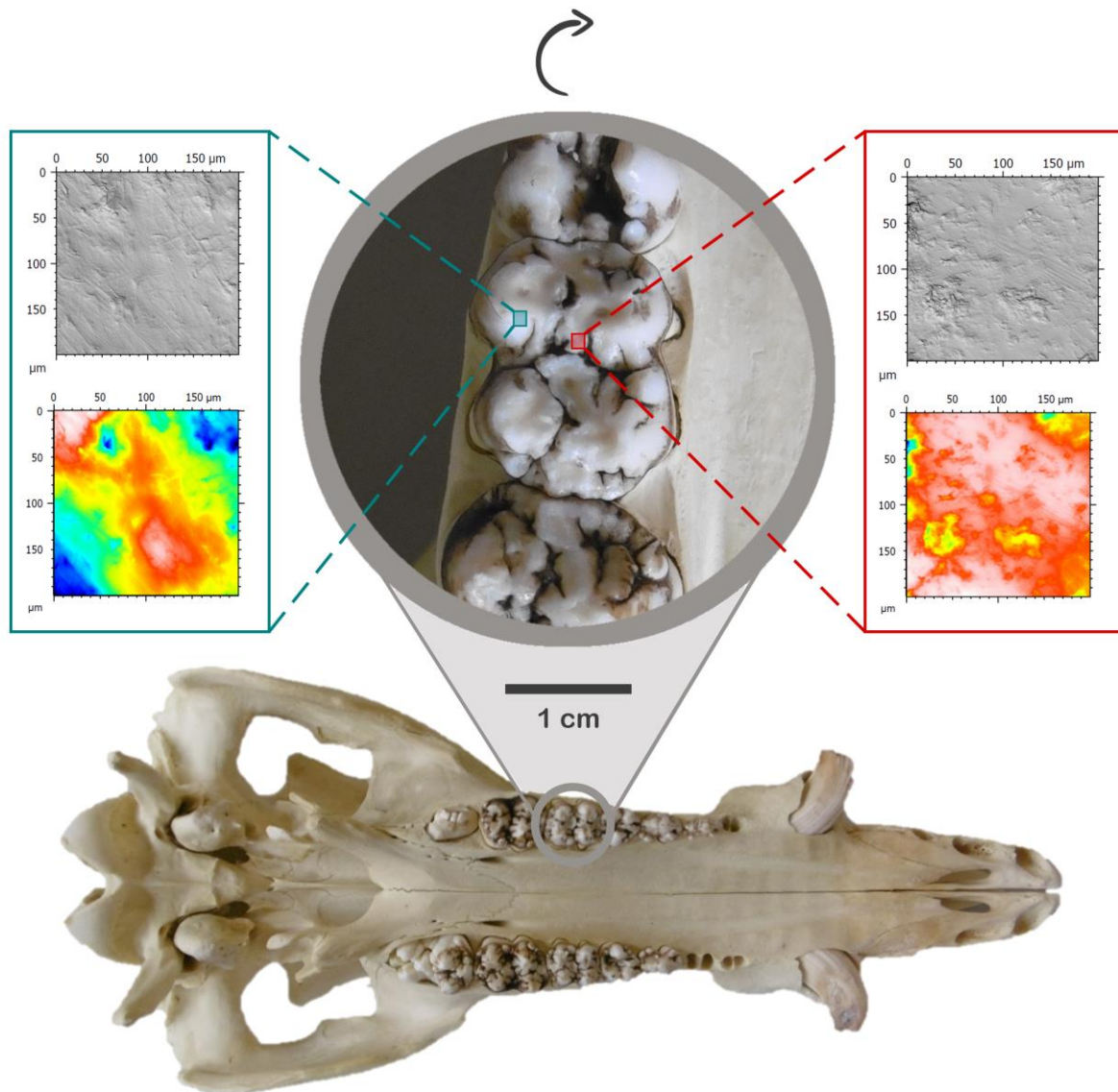
165 **2.2.2. Mineralogical analyses by X-ray diffraction**

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 $2\text{--}65^\circ$
169 2θ with steps of 0.025° 2θ 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 $2\text{--}35^\circ$ 2θ with steps of 0.016°
175 2θ 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 $200 \times 200 \mu\text{m}$ (1551×1551
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 (3×3 , 6×6 and 9×9 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).

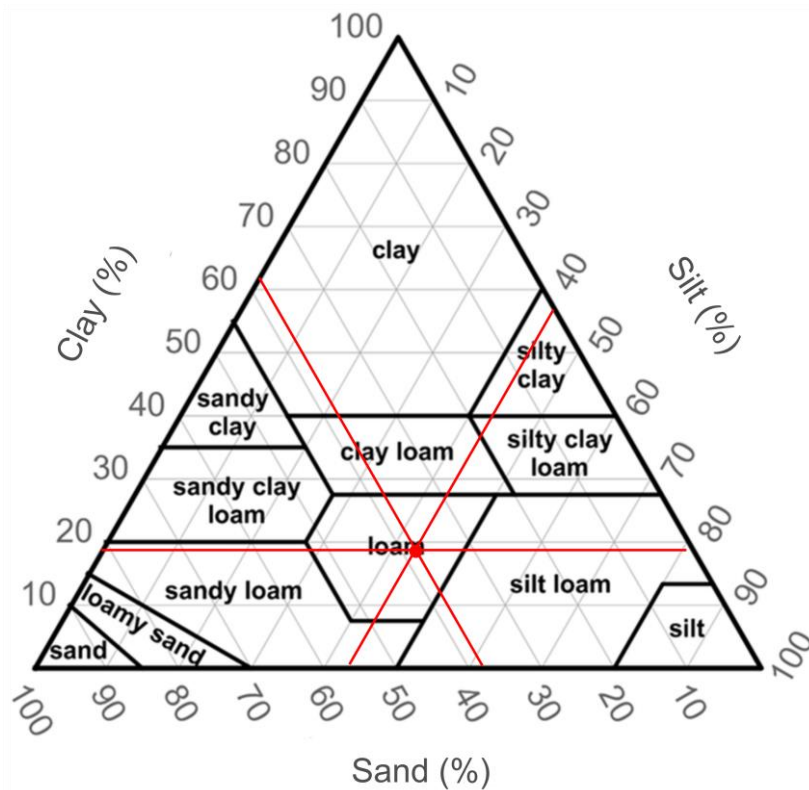
250

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 μm)	Fine sand (200-50 μm)	Coarse silt (50-20 μm)	Fine silt (20-2 μm)	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 (± 1.80)	13.84 (± 1.27)	17.62 (± 0.63)	25.65 (± 0.30)	18.93 (± 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 (≥ 60 %); “+”: small amount to traces (≤ 15 %); “tr”:
 271 traces (≤ 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

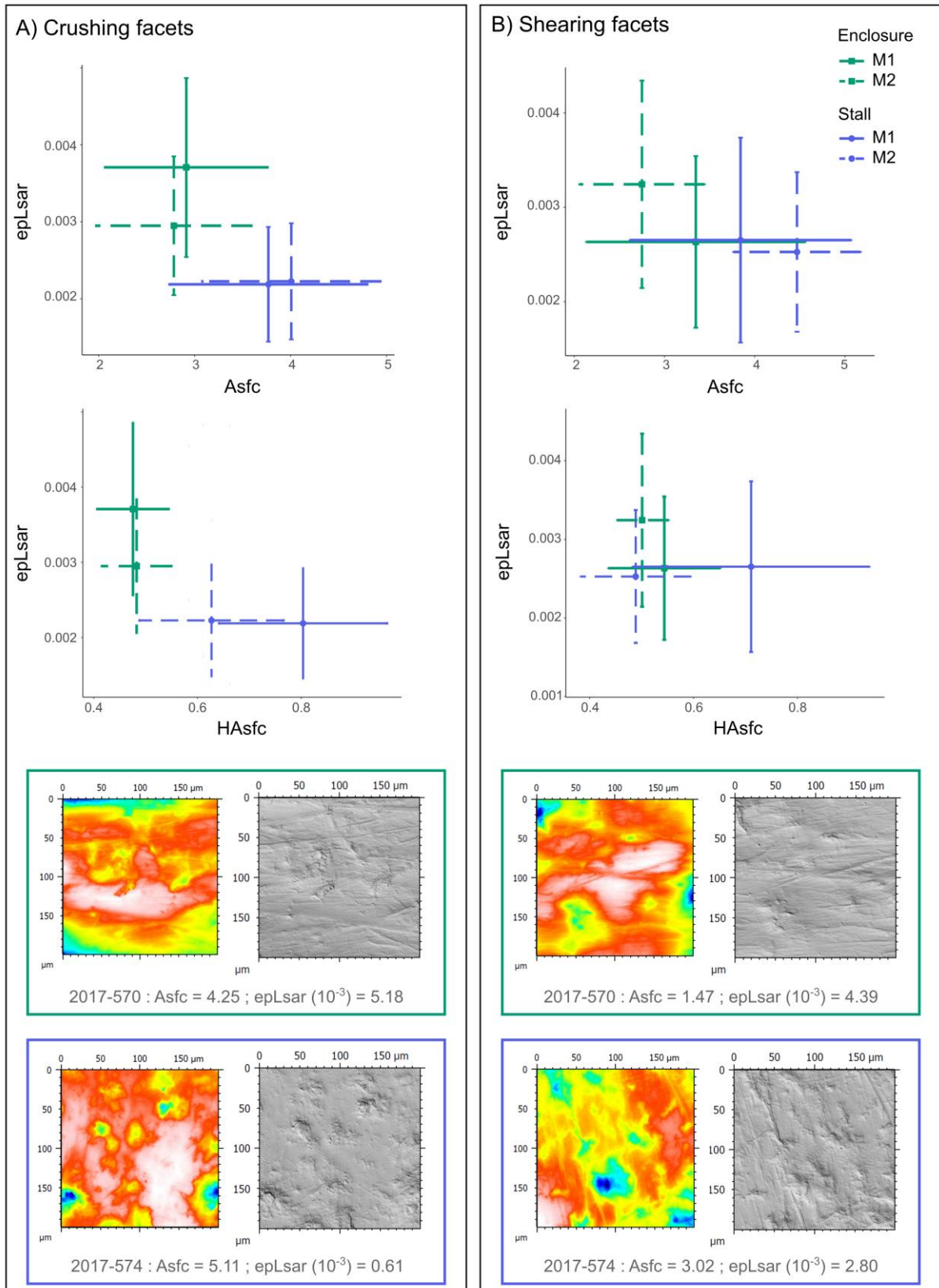
312 facets ($p = 0.02$, Table S11, Online Resource 3) and on upper M2 shearing facets ($p = 0.01$,
 313 Table S16, Online Resource 3). Thus, although ISO 25178 parameters reveal more significant
 314 differences on shearing facets and SSFA parameters reveal more on crushing ones, the results
 315 on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

	Discriminant parameters
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 μm) 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 μm 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 fodders 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 m² 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
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487

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501

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