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About inter- and intra-specific variability of dental microwear texture in rodents: Study of two sympatric *Proechimys* (Echimyidae) species from the Cacao locality, French Guiana

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3

4 **About inter- and intra-specific variability of dental microwear texture in**
5 **rodents: study of two sympatric *Proechimys* (Echimyidae) species from the**
6 **Cacao locality, French Guiana**

7

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20 **Abstract.**

21 Material properties of the diet of extant species is reflected by the microwear texture recorded
22 on the enamel tooth surface, a signal that can be useful for estimating the diets of extinct
23 species. Intra-specific dietary variations can occur between sexes or depend on seasonal
24 vegetation cover changes in their habitat. However, these factors cannot, or very rarely, be
25 incorporated within a paleontological context, especially if the fossil record of an extinct
26 species is mainly composed of isolated teeth. In order to assess the impact of these factors on
27 microwear texture features, we studied 42 wild-caught specimens of two sympatric extant
28 species of caviomorph rodents, *Proechimys cuvieri* and *P. guyannensis* (Echimyidae,
29 Octodontoidea) from the Cacao area located in French Guiana. Animals were captured
30 between 2007 and 2012, in July and October, along a 1.5 kilometer transect ranging from an
31 old secondary forest to a disturbed forest. We applied a Scale Sensitive Fractal Analysis
32 (SSFA) to the first upper molars of these specimens. Differences of dental microwear textures
33 were found between sexes, between months, and between habitat, leading to one species
34 overlapping in microwear texture parameter space with the other in some cases. The results
35 obtained help identifying which factors might drive intra-population variations in dental
36 microwear texture. Its understanding is indeed a key-step to better interpret the dispersion
37 observed within a given fossil sample set to obtain refined dietary reconstructions.

38

39 **Keywords:** DMTA; SSFA; diet; Rodentia; Caviomorpha; South America

40 **1. Introduction**

41

42 Among placental mammals, rodents are the most diverse and speciose group (e.g., Wilson and
43 Reeder, 2005). The hystricognathous rodents from South America, or caviomorphs
44 (Caviomorpha Wood, 1955), display great taxonomical diversity with four superfamilies and
45 ten families (e.g., Lacher et al., 2016). Caviomorphs occupy a wide array of ecological niches,
46 and the diversity of ecological conditions they face is associated with an equally wide array of
47 morphological adaptations. Indeed, they show a large range of body-sizes, from about 100 g
48 to 65 kg (e.g., Alvarez et al., 2017), display different life modes (terrestrial, arboreal, semi-
49 aquatic, fossorial, etc.; e.g., Mares and Ojeda, 1982; Patton et al., 2015; Wilson et al., 2016),
50 different activity patterns (diurnal, nocturnal, cathemeral; e.g., Wilson et al., 2016), and
51 exhibit distinct locomotor behaviors (cursorial, scansorial, swimmers, etc.; Wilson and
52 Geiger, 2015). This diversity of life history traits reflects a differential exploitation of the
53 ecological resources (see Townsend and Croft, 2008; Robinet et al., 2020, and references
54 therein).

55 The fossil record of the group so far extends back to the end of the Eocene (Antoine et
56 al., 2012; Boivin et al., 2017, 2019a, 2022). Caviomorphs would thus testify to an at least 35
57 million year-long endemic evolutionary history on the South American continent, marked by
58 several adaptive radiation events. However, any role of ecological factors in those phases of
59 diversification remains poorly known (e.g., Boivin et al., 2019a). The Paleogene fossil record
60 of caviomorphs consists mainly of isolated teeth, but very few well-preserved skulls or
61 associated post-cranial remains allow for functional morphology approaches (Verzi, 2002;
62 Candela and Picasso, 2008, Boivin et al., 2019b). Among the ecological factors that may have
63 driven the radiations of caviomorphs, food preference is a factor that is known to be very

64 important in modern niche partitioning (Bowers, 1982; Castro-Arellano and Lacher, 2009;
65 Shiels et al., 2013).

66 Here we apply Dental Microwear Texture Analysis (DMTA), and more specifically
67 Scale Sensitive Fractal Analysis (SSFA), to assess niche partitioning among different species
68 of rodents as dental microwear has proven to be efficient for detecting intra- and inter-specific
69 variations of diet for both extant (Scott, 2012; Scott et al., 2012; Kaiser et al., 2016) and
70 extinct toothed mammals (e.g., Gill et al., 2014; Ungar et al., 2017; Merceron et al., 2018) as
71 well as among non-mammalian vertebrates (Purnell et al., 2007, 2012; Winkler et al., 2019b).
72 Because microwear texture reflects short-term ingesta-related wear features (Teaford and
73 Oyen, 1989; Teaford et al., 2018; Winkler et al., this issue), it can be used to detect seasonal
74 variations of diet (Merceron et al., 2010; Berlioz et al., 2018; Percher et al., 2018). However,
75 very few DMTA studies have so far been conducted on rodents (murids: Burgman et al.,
76 2016; Winkler et al., 2016; voles: Calandra et al., 2016; guinea pigs, Winkler et al., 2019a,
77 2020, 2021; wild caviomorphs: Robinet et al., 2020).

78 If DMTA is a state-of-the-art approach of surface metrological characterization (Ungar
79 and Evans, 2016; Arman et al., 2019), two factors challenge the robustness of dietary
80 reconstructions based on microwear texture: the inherently low sample sizes of
81 paleontological datasets and a tendency to overlook potential sources of intra-specific
82 variation (Calandra and Merceron, 2016; Arman et al., 2019). Indeed, fossil data are often
83 fragmentary and can suffer from post-mortem surface alterations during the fossilization
84 process (Weber et al., this issue). They suffer also from a lack of information regarding many
85 factors that can be a source of biological variations, such as sex, season of death, or
86 characteristics of the habitat in which the individuals lived. Thus, paleoecological inferences
87 are often made by analogy with extant taxa, at the specific or generic level, under the
88 assumption that the chosen sample of extant specimens is sufficiently representative. As such,

89 a majority of DMTA studies focus on inter-specific differences, accepting a presumably
90 minor intra-specific variability without exploring it.

91 Here, we explore the impact of inter- and intra-specific dietary differences linked to sex,
92 seasonality, and/or vegetation cover variations within the same forested environment through
93 dental microwear texture. For the purpose of this study, we analyze sympatric populations of
94 two species of spiny rats (*Proechimys*, Echimyidae, Octodontoidea, Caviomorpha) from
95 French Guiana. We aim to (1) test if DMTA can detect the differences of diet between the two
96 studied species, (2) analyze if sex, seasonality and vegetation cover have detectable and
97 significant effects on dental microwear texture, (3) assess if intra-specific variability has an
98 impact on the inter-specific differentiation, and finally (4) discuss the implications for
99 paleoecological interpretations.

100

101 **2. Materials and Methods**

102

103 *2.1. Locality*

104 The locality of Cacao is situated in the north-eastern part of French Guiana, along the
105 Comté River, 45 kilometers south of Cayenne. Specimens were sampled in five loci (LI-1,
106 LI-2, LI-4, LI-5, and LI-8; Table 1, Fig. 1) following a clear gradient of anthropization and
107 considering the known home range of the targeted species (see below). The vegetation
108 cover across the loci varies from nearby cultivated areas (various fruits and vegetables) and
109 highly disturbed areas around those fields (LI-4 and LI-5) to old secondary well-drained
110 forests (LI-1, LI-2, and LI-8) with relatively middle-height closed canopy (around 28 m)
111 and openings from small windfalls (Guitet et al., 2015). French Guiana is dominated by a
112 warm and wet tropical rainforest climate. Precipitation at Cacao can range from 3,500 to
113 4,000 mm yearly, with more than 250 rainy days per year (Météo France). Two rainy and

114 two dry seasons can be distinguished: a short rainy season from December to February, a
115 short dry season from March to mid April, a long rainy season from April to July, and
116 finally a long dry season between August and November (Catzefflis et al., 2018). The
117 lowest monthly rainfall values are recorded in September and October (Catzefflis et al.,
118 2018).

119

120 2.2. Materials

121 The species studied here are the Cuvier's spiny rat, *Proechimys cuvieri* Petter, 1978, and the
122 Cayenne spiny rat, *Proechimys guyannensis* Geoffroy, 1803. We analyzed a total of 42 wild
123 adult individuals (27 of *P. cuvieri* and 15 of *P. guyannensis*; detailed list in Supplementary
124 Data SD1) from the vicinity of Cacao (municipality of Roura), in French Guiana. All
125 specimens were collected by a team led by one of us (FC) during several fieldwork seasons
126 conducted between 2007 and 2012, following the ethical guidelines established by the
127 American Society of Mammalogists for the use of wild mammals in research (Gannon and
128 Sikes, 2007). Specimens were captured during the months of July (n = 20) and October (n =
129 22). All specimens were identified following Patton (1987), Malcom (1992), Catzefflis and
130 Steiner (2000) and Voss et al. (2001), and are housed in the collections of the Museum of
131 Natural History of Geneva, Switzerland (MHNG).

132 The number of studied specimens is the result of an extensive trapping effort made at a
133 very small scale during five different fieldwork campaigns. Although it may appear somewhat
134 limited, this sample is, nonetheless, equivalent in size to microwear studies on rodents
135 captured in the wild (see Burgman et al., 2016; Calandra et al., 2016; Winkler et al., 2016).
136 Furthermore, this is the first of its kind among wild caviomorph microwear studies, which
137 relied on specimens captured over broad geographical and temporal ranges (2D, Townsend
138 and Croft, 2008; 3D, Robinet et al., 2020).

139 Species of *Proechimys* are primarily frugivorous and granivorous (Table 2; Guillotin,
140 1982; Adler, 1995; Henry, 1997; Patton and Leite, 2015). In both species, hard exocarps of
141 fruit are not ingested, but gnawed away with incisors to extract the nutritive seed inside.
142 Feer et al. (2001) observed that *P. cuvieri* consumes pulp in higher proportion than seeds, and
143 Guillotin (1982) listed 48 species consumed by *P. cuvieri* in two French Guianan forests
144 (Annexe 1; Guillotin, 1982), with a preference for fruit of 1 to 3 cm of diameter. The diet of
145 *P. cuvieri* also includes a notable proportion of insects (Table 2; Guillotin, 1982; Feer et al.,
146 2001). However, no detail is available regarding the type of insects consumed. Males of *P.*
147 *cuvieri* are reported as more frugivorous than females, and consuming fewer insects (Henry,
148 1997). On the other hand, the primarily frugivorous diet of *P. guyannensis* is supplemented by
149 fungi (arbuscular mycorrhizal fungi, Janos et al., 1995; Mangan and Adler, 1999) and leaves.
150 No detailed diet data is available for *P. guyannensis*, however, in other mycophagous species
151 of *Proechimys*, it is recorded that the consumption varies along the year depending on
152 sporocarp availability (Janos et al., 1995). All diet data were obtained through the study of
153 stomach contents of several populations of *Proechimys* in French Guiana (Guillotin, 1982;
154 Henry, 1997; Feer et al., 2001). Ecological data, including diet, for each species are
155 summarized in Table 2.

156 The studied specimens were not radio-tracked because the objective of the fieldwork
157 was to collect (trap and kill) specimens. However, Guillotin (1982) studied in detail the home
158 range (3,145 m² for females and 8,431 m² for males, with a maximum diameter of
159 approximately 85 m for females and 131 m for males, Table 1; Guillotin, 1982), and the
160 cumulated distance traveled per night (297 m for females and 586 m for males) of *P. cuvieri*
161 in French Guiana. Everard and Tikasingh (1973) described the home range of *P. guyannensis*
162 (14,000 m² for males and 1,500 m² for females). Those values indicate that both species stay
163 in a relatively small area and do not tend to move over large distances.

164

165 *2.3. Dental Microwear Textural Analysis (DMTA)*

166 We considered the first upper molar because it is diagnostic in rodents (e.g., Gomes
167 Rodrigues et al., 2009; Firmat et al., 2010, 2011; Oliver et al., 2014) and followed the
168 protocol of cleaning and molding (using polyvinyl siloxane ISO 4823, President Regular
169 Body, Coltène-Whaledent Corporation) developed by Robinet et al. (2020). Similar to
170 several rodent microwear studies (e.g., Townsend and Croft, 2008; Burgman et al., 2016;
171 Calandra et al., 2016; Winkler et al., 2019; Robinet et al., 2020), the mesiolingual aspect of
172 the protocone was analyzed (Fig. 2).

173 Scans were performed directly on the silicon molds with the "TRIDENT" Leica
174 DCM8 white-light scanning confocal microscope (Leica Microsystems) with a 100× long-
175 distance lens (Numerical Aperture = 0.90; working distance = 0.9 mm), housed at the
176 PALEVOPRIM laboratory (CNRS and *Université de Poitiers*, France). One scan was
177 retained by specimen. The scanning process generated 1360×1024 point clouds with a
178 vertical sampling resolution lower than $0.002 \mu\text{m}$ and a lateral sampling (x, y) of $0.129 \mu\text{m}$
179 ($175 \times 132 \mu\text{m}$) that were saved as ".plu" files by the LeicaScan software (Leica
180 Microsystems). After applying a pre-treatment using LeicaMap software (Leica
181 Microsystems; Mountain technology) and including notably the extraction of aberrant
182 peaks (see supplementary data in Merceron et al. 2016) and a vertical inversion, a 50×50
183 μm area was extracted, from which the 2nd order polynomial surface was subtracted
184 (Francisco et al., 2018). Finally, the surface was leveled and saved as a Digital Elevation
185 Model (".sur") for Scale Sensitive Fractal Analysis (SSFA; Fig. 2).

186 The SSFA (Scott et al., 2006) on the selected enamel surface was conducted with the
187 Toothfrax and Sfrax software programs (Surfract Corporation, Norwich, Vermont, USA).
188 We obtained the complexity (area scale of fractal complexity: Asfc), the anisotropy (exact

189 proportion of length scale anisotropy of relief: epLsar), the heterogeneity of complexity
190 (heterogeneity of the area scale of fractal complexity between sub-surfaces from a given
191 surface: HAsfc), and the textural fill volume (Tfv; textural fill volume at 0.2 μm) of the
192 studied surface. In this study, we calculated heterogeneity of complexity from four
193 (HAsfc4), nine (HAsfc9) and 16 (HAsfc16) cells, respectively (Supplementary Data S1).
194 Scott et al. (2006) have described each of these variables in detail.

195 The most important food properties controlling the formation of microwear texture
196 are hardness, toughness, and abrasiveness (Calandra and Merceron, 2016). When
197 considering primates or ungulates, complex microwear texture is seen among species
198 eating hard food items, while high anisotropy generally relates to food items requiring
199 more shearing motion, be they tough and/or abrasive (for a review see Ungar, 2015).
200 Heterogeneity of complexity was interpreted to be related to the diversity of food items
201 that an individual consumes on a daily basis (Souron et al., 2015). Thus, species with a
202 narrow spectrum of feeding resources are expected to have a lower heterogeneity than
203 opportunistic species (see Ramdarshan et al., 2016 and Merceron et al., 2018b).

204

205 *2.4. Statistics*

206 All statistical analyses were performed with R (R Development Core Team, 2018).

207 As the data were not normally distributed, we used a Box–Cox transformation (Box
208 and Cox, 1964) from the ‘Car’ package (Fox and Weisberg, 2011) for the data to meet the
209 parametric test requirements.

210 For each parameter, in order to consider all the factors and their interactions, we
211 started with a model that can be described as: DMT parameter \sim Species x Sex x
212 Vegetation cover x Month of capture, where the factor "species" has the modalities
213 *Proechimys cuvieri* and *P. guyannensis*, the factor "sex" has the modalities males and

214 females, the factor "vegetation cover" has the modalities old secondary forest
215 (corresponding to loci 1, 2 and 8) and disturbed forest (corresponding to loci 4 and 5), and
216 the factor "month of capture" has the modalities July and October. We then conducted a
217 stepwise model selection based on Akaike's Information Criterion (AIC) values using the
218 stepAIC function incorporated in the MASS package (detailed in Supplementary Data
219 SD2) and retained the best model (lowest AIC's values).

220 Specimens were captured during five different years: 2007, 2008, 2009, 2010, and
221 2012. The factor "year" was not included in the studied model because of its overlap with
222 other factors in our dataset. However, it seems to not have a significative effect by itself.
223 All information and details about the factor "year" are available in Supplementary Data
224 SD3.

225 Analyses of variance ANOVA (Anova; "Car" package) were undertaken to assess if
226 there was a significant difference between groups for a given texture parameter. Posthoc
227 pairwise tests combining the Tukey's honestly significant difference test (HSD) and
228 Fisher's least significant difference (LSD) pairwise tests were performed in order to detect
229 whether a significant difference between the groups existed. The LSD test is incorporated
230 in the R package agricolae (de Mendiburu, 2019). Both tests were used to balance risks of
231 type I and type II errors (Cook and Farewell, 1996). When only Fisher's LSD test detected
232 significant variation, we considered results of marginal significance (Burgman et al., 2016;
233 Hullot et al., 2019; Robinet et al., 2020).

234

235 **3. Results**

236

237 Mean, median and standard deviation of the mean for all parameters are given per group in
238 Table 3. All final models retained for each parameter are available in Supplementary Data

239 SD2, and include the factors species, vegetation cover, sex (except final model for HAsfc16),
240 and month of capture (except final model for HAsfc9), as well as combination of the factor
241 species x vegetation cover, species x sex (except final model for HAsfc16) and species x
242 month of capture (except final models for HAsfc4 and HAsfc9). The complete ANOVA
243 results for the best selected model for each microwear textural parameters are available in
244 Supplementary Data SD4. The ANOVAs detected that complexity (Asfc) and textural fill
245 volume (Tfv) are significantly different across taxa, sexes, and months of capture (Table 4).
246 Textural fill volume (Tfv) values are significantly different across types of vegetation cover
247 (Table 4). Complexity (Asfc), textural fill volume (Tfv), and anisotropy (epLsar) display
248 differences across the combination of several factors (Table 4; Figs. 3 and 4). None of the
249 three variables of heterogeneity of complexity display significant difference.

250 Microwear textures of *P. cuvieri* are more complex (Asfc) and have higher values of
251 textural fill volume (Tfv) than *P. guyannensis* (Fig. 3). Males display more complex (Asfc)
252 microwear textures and higher values of textural fill volume (Tfv) than females (Tables 3 and
253 4). Posthoc tests reveal significant differences in complexity (Asfc) and textural fill volume
254 (Tfv) between females of *P. guyannensis* and both females and males of *P. cuvieri* (Table 5;
255 Fig. 3). Males of *P. guyannensis* also have lower values of complexity (Asfc) and textural fill
256 volume (Tfv) than males of *P. cuvieri*, but do not show significant differences with females of
257 *P. cuvieri*. For *P. cuvieri*, the dental microwear texture of females shows marginally lower
258 textural fill volume (Tfv) and complexity (Asfc) than those of males (Table 5; Fig. 3). The
259 dental microwear textures of the individuals captured during October are significantly less
260 complex (Asfc) and are characterized by lower values of textural fill volume (Tfv) than the
261 individuals captured in July (Tables 3 and 4). In particular, the individuals of *P. guyannensis*
262 captured during October display significantly less complex (Asfc) dental microwear textures
263 and are characterized by lower values of textural fill volume (Tfv) than individuals of *P.*

264 *cuvieri* captured during both periods, and the individuals of *P. guyannensis* captured during
265 July. However, they display only marginally higher values of anisotropy (epLsar) compared
266 to individuals of *P. cuvieri* captured during October and individuals of *P. guyannensis*
267 captured during July (Table 5; Fig. 4). Specimens captured in July in the disturbed forest
268 display significantly more complex (Asfc) microwear textures than specimens captured
269 during October in both disturbed and old secondary forests (Tables 3 and 4). The microwear
270 textures of individuals captured in the old secondary forest (loci 8, 1, and 2) are characterized
271 by lower values of textural fill volume (Tfv) than individuals captured in the disturbed forest
272 (loci 4 and 5; Tables 3 and 4; Fig. 4).

273 Marginal anisotropy differences were detected through the combination of the factors
274 species, sex, and vegetation cover (Table 4), with female specimens of *P. guyannensis*
275 captured in old secondary forest having slightly more anisotropic microwear textures than any
276 other group, except for male specimens of *P. guyannensis* captured in disturbed forest with
277 which no difference was detected (Table 3).

278

279 **4. Discussion**

280

281 *4.1. Ecological interpretations*

282 Applied to these two sympatric species of *Proechimys*, DMTA detects inter-specific
283 differences consistent with their respective known ecology. The analysis also indicates intra-
284 specific differences, in particular between sexes and months of capture, as well as differences
285 between types of vegetation cover.

286 Although fruit pulp is the primary component of the diet of both species of
287 *Proechimys*, our results show that this "soft" (Vogel et al. 2014) item is most likely not the
288 diet component having the largest impact on the enamel surfaces, as differences in dental

289 microwear textures are noticed between the two species (Table 4; Fig. 3). On one hand, the
290 inclusion of seeds and insects (Guillotin, 1982; Feer et al., 2001), many of them being hard
291 and brittle, in the diet of *P. cuvieri* may generate more variable and more complex (Asfc)
292 microwear textures, associated with more deeply scarred textures as highlighted by the higher
293 textural fill volume (Tfv) values (Table 2; Fig. 3A). On the other hand, the diet of *P.*
294 *guyannensis* is supplemented by leaves but also AMF (Arbuscular Mycorrhizal Fungi, Janos
295 et al., 1995; Mangan and Adler, 1999). These AMF contain chitin-bearing spores protected by
296 compact aggregations of spores called sporocarps (Giovannetti and Gianinazzi-Pearson,
297 1994). One may guess that those micrometric (between 30 to 160 μm ; Janos et al., 1995)
298 spores might lead to less complex (Asfc) microwear textures and lower values of textural fill
299 volume (Tfv) (Tables 3 and 4; Fig. 3), having a similar effect as siliceous phytoliths and other
300 small abrasives in grazer species (Scott, 2012).

301 Overall, textural fill volume (Tfv) and complexity (Asfc) of females are lower than
302 those of males (Tables 3 and 5), which may reflect differences in diet between sexes in
303 *Proechimys*. Dietary differences between males and females are known among different
304 species of mammals reflecting differences in energetic requirements and physiology (e.g.,
305 Cransac et al., 2001; Kamilar and Pokemper, 2008). Such differences in diet being reflected in
306 dental microwear patterns has previously been recorded in other species (see Merceron et al.,
307 2010; Percher et al., 2018). The ecology of *P. guyannensis* is not known in details, but males
308 of *P. cuvieri* seem to be more frugivorous than females, and consume fewer insects (Henry,
309 1997). As males have a home range twice larger than females (Guillotin, 1982), they might
310 resort to secondary components of their diet less often than females. Furthermore, insects
311 might fulfill the increased protein requirements of gestation and lactation periods in female
312 rodents (Zambrano et al., 2005). Thus, the slight differences in textural fill volume (Tfv) and
313 complexity (Asfc) observed between males and females of *P. cuvieri* might reflect a slightly

314 higher proportion of seeds in the diet of males compared to females. Lower values of textural
315 fill volume (Tfv) indicate a less deeply scarred texture. Insects (preferentially consumed by
316 females) and seeds (preferentially consumed by males) are both hard items, but the former are
317 more diverse mechanically speaking (e.g., beetles vs. caterpillars) and might offer less
318 resistance to mastication than dense seeds (Strait, 1993).

319 Specimens captured in October have less complex (Asfc) microwear textures
320 associated with lower values of textural fill volume (Tfv) than specimens captured in July
321 (Tables 3-5; Fig. 4). These differences are mainly apparent in individuals of *P. guyannensis*
322 captured in October, which also have lower values in complexity (Asfc) and textural fill
323 volumes (Tfv) as well as slightly higher values of anisotropy than those of *P. cuvieri* captured
324 the very same month (Table 5, Fig. 4). Besides, *P. guyannensis* individuals captured in
325 October also have slightly higher values of anisotropy than individuals of the same species
326 captured in July (Table 5). It is known that fruit availability is highly seasonal even in tropical
327 rainforests (Leigh, 1999; Forget et al., 2002; Jansen et al., 2002), even if the amplitude of
328 fructification seasonality is lessened in secondary forests compared to primary forests in
329 French Guiana (Sabatier, 1985). The peak of fructification generally coincides with the start
330 of the wet season, between March and May. Neither July nor October can be considered as
331 high fructification seasons, however, overall availability of fruit seems higher in July than in
332 October (Charles-Dominique et al., 1981; Guillotin, 1982). It then seems that a drop-in food
333 availability occurring during the dry season (October) has a significant impact on the diet,
334 particularly that of *P. guyannensis*. As observed for other mycophageous species of
335 *Proechimys*, AMF may become especially critical when competition for primary resources
336 (fruit) is elevated due to scarcity of fruit (Mangan and Adler, 1999). No difference of
337 microwear texture is detected between individuals of *P. cuvieri* captured in both months,
338 which could indicate either that *P. cuvieri* does not modify its diet much across the months or

339 that their potential fallback food –mostly consumed in October– either have similar material
340 properties as their preferred food resources, or have few effects on enamel surface. On the
341 contrary, the seasonal differences in dental microwear texture in *P. guyannensis* support that
342 in October when fruit are less abundant, the new component in diet, mostly leaves and fungi
343 (AMF), have different properties than the primary dietary components (fruit and seeds). Our
344 results also confirm that when fruit are abundant, during the wet season in July, both species
345 seem to have more similar diets.

346 With regards to the vegetation cover, individuals from the disturbed forest display
347 higher values of textural fill volume (Tfv) than their counterparts from the old secondary
348 forest (Table 4; Fig. 4). These results reflect differences in material properties of available
349 food in the disturbed forest. Disturbed forests are generally less diverse from a vegetation
350 cover and faunal diversity point of view (Weibull et al., 2003; de Thoisy et al., 2010; Mitchell
351 et al., 2014). Arbuscular mycorrhizal fungi (AMF) are particularly sensible to disturbance of
352 the soil, which would be the case around cultivated areas, which can reduce or even eliminate
353 their presence (Mangan and Adler, 1999). Both species of *Proechimys* studied here are known
354 to maintain their presence when they are constrained by anthropogenic disturbances.
355 However, it is worth mentioning that only three specimens of *P. guyannensis* were captured in
356 the disturbed forest (Table 3). Winkler et al. (2016) obtained similar results on *Rattus rattus*,
357 comparing populations from disturbed and natural habitats. They found that specimens in
358 disturbed environment were showing rougher microwear textures, to the extent that it could
359 belong to different species, indicating higher diet abrasiveness (Winkler et al., 2016).
360 Furthermore, the specimens captured in July in the disturbed forest have more complex (Asfc)
361 microwear textures than those captured in October in both type of vegetation cover (Tables 3
362 and 4). This could show that, even if July is not the high period of fructification (Catzefflis et
363 al., 2018), fruit and seeds are consumed in the disturbed forest.

364

365 *4.2. Intra-specific variation versus inter-specific variation*

366 Here, we do not only detect differences between two sympatric species from the same genus,
367 but we also observed differences in dental microwear textures between seasons, types of
368 vegetation cover, even at the small 1.5-km-transect scale of our study, and sexes (Table 4;
369 Figs 3 and 4). These are related to seasonal variations in fruit and seed availability, as well as
370 differences in feeding requirements between males and females. Such intra-specific
371 differences were highlighted in other groups of mammals (e.g., Merceron et al., 2010;
372 Bignon-Lau et al., 2017). In some cases, the intra-specific variability of both species overlaps,
373 thereby partially obscuring inter-specific differences. For example, if inter-specific
374 differences are obvious when all specimens of *P. cuvieri* and *P. guyannensis* are compared,
375 no significant difference is found when the microwear texture of only *P. cuvieri* females and
376 *P. guyannensis* males are compared (Table 5; Fig. 3).

377 However, other sources can contribute to increased inter-individual differences. The
378 scanned surface was set to 50 $\mu\text{m} \times 50 \mu\text{m}$ to make sure it would fit with the dental facet for
379 these small species. Such dimensions might seem small as the effects of a small hard or
380 abrasive element impact a larger portion of the scanned area compared to larger surfaces
381 usually considered for studies on other larger-bodied species of mammals (200 $\mu\text{m} \times 200 \mu\text{m}$;
382 Martin et al., 2018; Merceron et al., 2018a). This means that analyses on small surfaces (here
383 for rodents but still true for any other mammals) would increase intra-specific variability (see
384 Ramdarshan et al., 2017). Anisotropy (epLsar) is known to be particularly sensible to the
385 effect of scanned surface area size (Ramdarshan et al., 2017). The intra-specific variations
386 being high, it would partly explain why few inter-specific differences were found to be
387 significant, especially on this very texture parameter

388

389 *4.3. Implications for paleoecology*

390 Although composed of wild individuals belonging to present-day species, the characteristics
391 of the present dataset (wild specimens, moderate sample size, multi-year and multi-season
392 trapping, and variations in habitat) reflect what could be the properties of a fossil sample.
393 Indeed, by nature, a fossil sample might be rather homogenous in its dental wear properties if
394 it records a single catastrophic depositional event (i.e. mortality due to flooding or a volcanic
395 eruption), or rather heterogeneous if it records successive embedding or reworking events,
396 distinct in duration (from a few years to a few thousands of years). Comparing the intra-
397 sample variability of a fossil sample with the ones of different wild extant samples with
398 different mortality curves allows the estimation of modality and timing of deposition for the
399 fossil samples (Rivals et al., 2015).

400 An important point to keep in mind, when estimating the diet of extinct species, is that
401 similar dental microwear textures can be the result of different ingested dietary items sharing
402 similar material properties (Calandra and Merceron, 2016). Conversely, significant
403 differences in dental microwear textures on homologous dental facets of different species are
404 indeed evidence for difference in dietary habits. The primary component of diet does not
405 always have the strongest impact on dental microwear texture. Marshall and Wrangham
406 (2007) suggested that dental adaptations might reflect fallback foods (such as fungi, leaves,
407 and insects) rather than preferred foods (such as fruit). For many species, preferred foods
408 require little specialization and can be processed relatively easily, whereas fallback foods are
409 less easily processed, and require more specialization (Robinson and Wilson, 1998).
410 Experimental settings (Merceron et al., 2016b; Ramdarshan et al., 2016; Teaford et al., 2018;
411 Winkler et al., 2019a) and applied studies (Merceron et al., 2010; Berlioz et al., 2018) have
412 shown that fallback foods and secondary components of the diet may considerably affect
413 dental microwear textures. Our results on a wild population of caviomorph rodents confirm

414 that this possibility applies also to this group. Indeed, they show differences in dental
415 microwear between the two time periods (July and October), particularly highlighted in *P.*
416 *guyannensis*. The differences might be either driven by a drop or change in fruit composition
417 or the inclusion of fungi (AMF) and insects in diet. Among those fallback foods, the former
418 contains high concentration of spores covered by resistant and protective tissues likely acting
419 as abrasive agents on dental tissue, while insects display diverse mechanical properties from
420 soft caterpillars to hard and brittle beetles. These fallback foods might be responsible for the
421 seasonal differences in dental microwear textures (Ungar et al., 2008; Strani et al., 2019).

422 Several studies recently shed light on the intra-specific variability of dental microwear
423 textures depending on the composition of diet (for instance in ungulates, Ramdarshan et al.,
424 2016; Bignon-lau et al., 2017), or even the water content of the consumed items (i.e., dry
425 *versus* wet grass in guinea pigs; Winkler et al., 2019a). Other studies even aimed further and
426 looked into the variability at the individual level (Arman et al., 2019), often relying on
427 experimental controlled feeding settings in order to identify the factors involved in intra-
428 individual variability and quantify it (Ramdarshan et al., 2017; Winkler et al., 2021). The
429 intraspecific variability has to be explored from the individual level, comparing teeth and
430 wear facets from the same individual to improve data acquisition and reproducibility
431 (Ramdarshan et al., 2017; Arman et al., 2019; Winkler et al., 2021), to a larger scale,
432 comparing between- and within-population variations of the same taxa across different
433 ecoregions (Burgman et al., 2016; Arman et al., 2019). This work does not address the intra-
434 individual variability but focuses on factors of variability at the population level. Our results
435 show that the dental microwear textures reflect differences in habitat structure at a small
436 spatial scale (1.5 km transect) emphasizing the benefit of tooth wear analysis in general and
437 especially DMTA to track variations of food availability at the micro-habitat scale (Belmaker,
438 2018). Microwear textures from both species of *Proechimys* overlap when factors such as sex,

439 seasonality, and types of vegetation cover are considered, but interspecific differences are
440 detected when both species are compared regardless of the other factors. These results
441 illustrate particularly well the variability and flexibility of diets and feeding behaviors of
442 caviomorph rodents and their potential impact on diet estimations of fossil taxa (Robinet et
443 al., 2018). It also highlights the importance of having a well-known sample as detailed as
444 possible rather than numerous specimens with low traceability (i.e., geographic provenance
445 and date of capture). Indeed, one limiting factor in interpreting the DMTA results obtained for
446 caviomorphs is the critical lack of detailed published ethological reports and ecological data
447 for the majority of groups, as well as the little experimental data on dental microwear texture
448 among caviomorph taxa (but see Winkler et al., 2019a, 2020, 2021). Indeed, while *P. cuvieri*
449 is well studied and observations were made for both sexes, in both seasons (Guillotin, 1982;
450 Feer et al., 2001), this is not the case for *P. guyannensis*.

451 This underscores that exploring the variability characterizing extant species at various
452 scales is adding more layers of complexity to paleoecological interpretations (Catz et al.,
453 2020; Ungar et al., 2020). Indeed, questions such as seasonality, or depositional timing are
454 important issues in paleontology but also in archaeology (Milner and Bailey, 2005; Sánchez-
455 Hernández et al. 2014). Analysis of dental microwear and its intra-sample variation can
456 complement other approaches to assess these aspects at a site scale (Kohn et al. 1998; Berlioz
457 et al. 2017; Green et al. 2018; Blumenthal et al. 2019; Merceron et al. 2021).

458

459 **Conclusion**

460 This work, focused on two sympatric species of spiny rats (*Proechimys*) from French
461 Guiana, applying DMTA, is the first to explore intra- and inter-specific variations of wild
462 caviomorph rodents. In our case, DMTA detected differences of diet between the two species.
463 Seasonal variations in fruit and seeds availability, as well as distinct feeding strategies

464 between males and females might explain the differences detected by DMTA. Microwear
465 textures from both species overlap when factors such as sex, seasonality and types of
466 vegetation cover are considered, reflecting a dietary overlap between *P. guyannensis* and *P.*
467 *cuvieri*.

468 Our results highlight that several points should be considered when applying DMTA
469 to interpret diet of fossil taxa. The primary component of a diet does not always have the
470 strongest impact on dental microwear texture. Indeed, microwear texture reflects the physical
471 properties of food rather than its proportions in the diet. Given our results, it can be expected
472 that the secondary components of the diet are dominant in the dental microwear texture
473 formation in some cases. Our observations on living species also highlight how different
474 factors might result in overlapping values of microwear texture parameters for species with
475 different diets. While these results do not call into question the power of the DMTA to
476 explore the paleoecology of extinct taxa in terms of diet, they do emphasize the necessity to
477 recognize the high sensitivity and limitations of the method. DMTA reflects mechanical wear
478 properties of diet but not all components of its full spectrum equally. The fragmentary nature
479 of fossil samples only allows for a limited estimation of the diet variation of extinct taxa.
480 However, this same intra-sample variability can be used to better identify the modalities of
481 deposition events through non-destructive sampling.

482

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513

514 **Supplementary Data**

515 **Supplementary Data SD1.** - Detailed list of studied specimens and individual microwear
516 textural parameters. The file name indicates the fact that the scan was realized on a mold
517 (Zinv for inverted), the species (Pc for *P. cuvieri*; Pg for *P. guyannensis*), the collection
518 number of the specimen, the scanned tooth (UM1 for first upper molar; l for left, r for
519 right), the scanned area (pct for protocone; ml for the mesio-lingual portion of the
520 protocone). The suffix -bis appears when a scan was retaken after a first failed attempt.
521 The vegetation cover factor modalities are old secondary forest (corresponding to 1) and
522 disturbed forest (corresponding to 2). The microwear texture parameters are the complexity
523 (Asfc), the anisotropy (epLsar), the heterogeneity of complexity (HASfc4, 9 and 16), and
524 the textural fill volume (Tfv).

525

526 **Supplementary Data SD2.** - Detailed stepwise model selection by AIC criterion for each
527 microwear textural parameters. The factors included into the starting model are: "species"
528 with the modalities *Proechimys cuvieri* and *Proechimys guyannensis*, "sex" with the
529 modalities males and females, "vegetation cover" with the modalities old secondary forest
530 (corresponding to loci 1, 2 and 8) and disturbed forest (corresponding to loci 4 and 5),
531 "month of capture" with the modalities July and October, and all the interactions between
532 those factors.

533

534 **Supplementary Data SD3.** - Detailed description, structure of the distribution, and
535 potential effect of the factor "year of capture".

536

537 **Supplementary Data SD4.** - Complete analyses of variances (ANOVA) results for the
538 best selected model for each microwear textural parameters following a Box-Cox

539 transformation. The modalities are *Proechimys cuvieri* and *Proechimys guyannensis* for the
540 factor "species", males and females for "sex", old secondary forest (corresponding to loci
541 1, 2 and 8) and disturbed forest (corresponding to loci 4 and 5) for "vegetation cover", July
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543

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892 **Figure captions**

893

894 **Figure 1.** Geographic map of the region of interest. A: Geographical location of French
895 Guiana in South America (left) and of the little village of Cacao (red cross), south of Cayenne
896 on the Comté River (right). B: Aerial photograph (Geoportail; www.geoportail.gouv.fr) of the
897 Cacao area with the location of the five sites of capture from the anthropized region (left)
898 toward old secondary forest (right). The numbered (1, 2, 4, 5, 8) white circles correspond to
899 the five loci of capture (respectively LI-1, LI-2, LI-4, LI-5, and LI-8). See Table 1 for exact
900 GPS coordinates. [2 columns width]

901

902 **Figure 2.** Graphical representation of the acquisition process of dental microwear parameters
903 from the studied specimens (A) to the studied areas of molar microwear (B). A, (left) position
904 of the studied left first upper molar (M1) on the cranium of *Proechimys cuvieri*
905 (MHNG1975.046) in occlusal view (scale bar = 1 cm) and (right) measurement position of
906 the chewing facet on the same tooth (scale bar = 1 mm). The light gray filling indicates the
907 enamel layer. The black rectangle indicates the 175 x 132 μm 3D scan acquired on the
908 LeicaDCM "Trident". The surface generated was treated using the LeicaMap software
909 (Mountain technology, Leica Microsystems). An area of study of 50 x 50 μm was cut out
910 manually. Arrow indicates mesio-lingual direction. B, (left) topographic representations and
911 (right) photosimulations of the 50 \times 50 μm studied surface of *Proechimys cuvieri*
912 (MHNG1975.046, top) and *Proechimys guyannensis* (MHNG1984.001, bottom) with the
913 values of their associated Asfc (no unit) and Tfv (in μm^3) parameters. [1.5 column width]

914

915 **Figure 3.** Boxplots of significant microwear texture variables. A, by species; B, by species
916 and sex. Females are in black, and males are in light gray. Pc, *Proechimys cuvieri*; Pg,

917 *Proechimys guyannensis*; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume.

918 Solid lines indicate when Tukey's HSD tests were significant ($p < 0.05$). [single column

919 width]

920

921 **Figure 4.** Boxplots of significant microwear texture variables. A, by species and month of

922 capture; B, by species and vegetation cover. Specimen captured in July are in black, and in

923 October in light gray. The old secondary forest vegetation cover (1) is in light blue filling, and

924 the disturbed forest vegetation cover (2) is in blue filling. Pc, *Proechimys cuvieri*; Pg,

925 *Proechimys guyannensis*; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume.

926 Solid lines indicate when Tukey's HSD tests were significant ($p < 0.05$). [single column

927 width]

928 **Tables**

929

930 **Table 1.** GPS coordinates and elevation of the five loci of capture in French Guiana.

Locus	Latitude	Longitude	Elevation
LI-1	N 4°33.935'	W52°26.640'	165 m
LI-2	N 4°34.010'	W52°26.940'	140 m
LI-4	N 4°33.950'	W52°27.130'	82 m
LI-5	N 4°34.150'	W52°27.315'	103 m
LI-8	N 4°33.708'	W52°26.590'	197 m

931 **Table 2.** Ecological data of species considered in this study. Body masses following Alvarez et al. (2017; supplementary data).

Species	N	Mean mass	Activity patterns	Breeding pattern	Diet	References ^a
<i>Proechimys cuvieri</i>	27	323 g	terrestrial nocturnal	year-round (in French Guiana)	fruit pulp (53%) and seeds (13%), insect (32%), leaves and fiber (2%)	1; 2; 5; 6; 8
<i>Proechimys guyannensis</i>	15	263 g	terrestrial nocturnal	seasonal (reportedly)	mainly frugivorous (pulp) but also seeds and arbuscular mycorrhizal fungi	2; 3; 4; 7; 8

932 ^aReferences: 1) Guillotin, 1982; 2) Emmons and Feer, 1997; 3) Eisenberg and Redford, 1999; 4) Mangan and Adler, 1999; 5) Feer et al., 2001;

933 6) Catzeflis and Patton, 2016a; 7) Catzeflis and Patton, 2016b; 8) Fabre et al., 2016.

934

935 **Table 3.** Descriptive statistics of dental microwear texture parameters^a for each species by sex, by month of capture, and by type of vegetation
 936 cover. Abbreviations: m, mean; med, median; sd, standard deviation.

	N	Asfc			epLsar x10 ³			HAsfc4			HAsfc9			HAsfc16			Tfv		
		m	med	sd	m	med	sd	m	med	sd	m	med	sd	m	med	sd	m	med	sd
By species																			
<i>P. cuvieri</i>	27	1.98	1.09	2.06	3.68	3.68	1.35	0.36	0.31	0.20	0.49	0.39	0.37	0.51	0.39	0.30	330.27	137.97	438.74
M	10	2.48	1.83	1.97	3.51	3.27	1.32	0.31	0.25	0.18	0.39	0.29	0.24	0.47	0.32	0.30	500.30	256.25	564.74
F	17	1.68	0.98	2.12	3.77	3.76	1.39	0.39	0.37	0.21	0.55	0.40	0.42	0.53	0.45	0.31	230.25	50.81	323.57
<i>P. guyannensis</i>	15	0.64	0.45	0.49	4.54	4.64	2.14	0.39	0.36	0.13	0.44	0.39	0.19	0.48	0.44	0.16	188.60	1.00	418.70
M	10	0.73	0.51	0.55	3.90	4.48	1.82	0.42	0.38	0.14	0.45	0.39	0.20	0.49	0.44	0.16	274.52	13.45	497.60
F	5	0.44	0.28	0.29	5.82	6.34	2.34	0.34	0.32	0.11	0.41	0.39	0.16	0.44	0.44	0.17	16.77	1.00	33.00
By month of capture																			
July	20																		
<i>P. cuvieri</i>	16	2.23	0.92	2.54	3.83	3.65	1.34	0.35	0.27	0.22	0.54	0.39	0.44	0.52	0.39	0.33	219.42	61.18	302.57
<i>P. guyannensis</i>	4	1.16	0.99	0.66	3.37	2.54	2.69	0.31	0.29	0.09	0.34	0.33	0.11	0.36	0.36	0.11	378.69	125.51	590.74
October	22																		
<i>P. cuvieri</i>	11	1.61	1.10	1.07	3.46	4.11	1.39	0.37	0.34	0.17	0.43	0.38	0.22	0.49	0.39	0.28	491.51	287.38	561.15
<i>P. guyannensis</i>	11	0.45	0.36	0.22	4.96	4.87	1.87	0.42	0.37	0.13	0.47	0.40	0.20	0.52	0.45	0.16	119.48	1.00	347.89

By vegetation cover

Old secondary forest 28

P. cuvieri 16 1.68 1.10 1.35 3.54 3.27 1.14 0.34 0.29 0.21 0.52 0.37 0.44 0.49 0.35 0.31 190.62 54.96 300.02

P. guyannensis 12 0.58 0.41 0.53 4.67 4.57 2.29 0.42 0.38 0.13 0.47 0.41 0.19 0.50 0.46 0.16 122.75 1.00 361.15

Disturbed forest 14

P. cuvieri 11 2.41 1.04 2.83 3.87 4.24 1.64 0.38 0.37 0.20 0.46 0.40 0.24 0.53 0.45 0.30 533.39 333.04 537.47

P. guyannensis 3 0.86 0.87 0.04 4.01 4.87 1.57 0.30 0.29 0.07 0.29 0.26 0.10 0.36 0.40 0.10 452.02 117.21 616.19

937 ^a Asfc: complexity; epLsar: anisotropy; HAsfc: heterogeneity of complexity calculated from 4, 9 and 16 cells, respectively; Tfv: textural fill

938 volume.

939 **Table 4.** Significant analyses of variance (ANOVA) on Box-Cox transformed data for
 940 species, sex, type of vegetation cover, and month of capture on all dental microwear texture
 941 parameters^a.

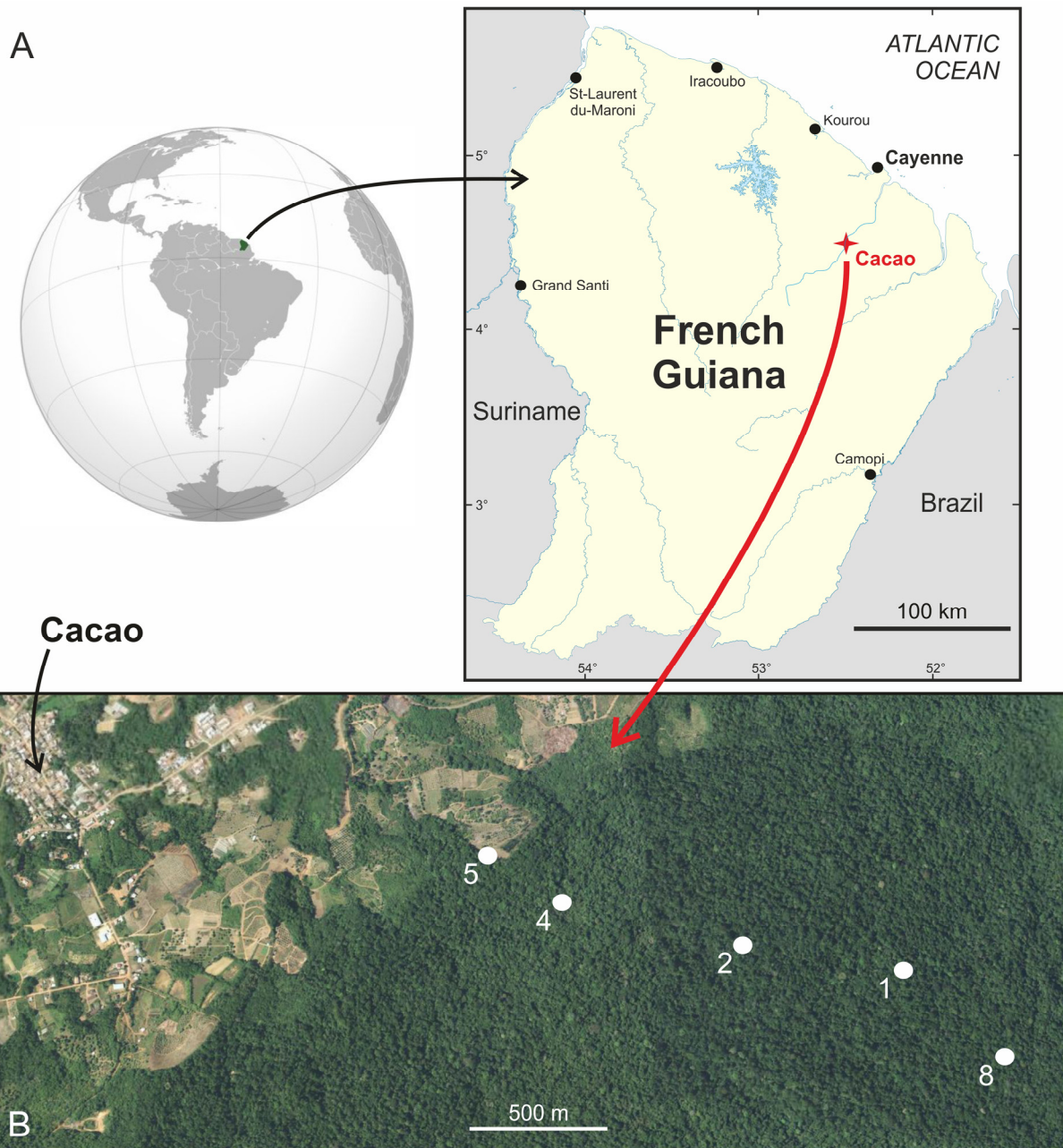
Parameter	Treatment	<i>F</i> value	<i>p</i> value
Asfc	species	24.06	<0.001
	sex	8.79	0.005
	month of capture	8.42	0.007
	species x month of capture	8.07	0.008
	vegetation cover x month of capture	4.96	0.033
epLsar	species x month of capture	5.47	0.026
	species x sex x vegetation cover	4.73	0.037
Tfv	species	14.26	<0.001
	sex	9.34	0.004
	vegetation cover	12.28	0.001
	month of capture	6.42	0.016
	species x month of capture	5.08	0.031

942 ^a Asfc: complexity; epLsar: anisotropy; Tfv: textural fill volume.

943 **Table 5.** Posthoc pairwise comparisons A, between sexes (F, females; M, males); B, between
 944 month of capture (Oct, October; Jul, July). Significance at $p < 0.05$ is indicated in regular font
 945 for Fischer's LSD tests (marginal), and in bold for both Tukey's HSD and Fisher's LSD tests.

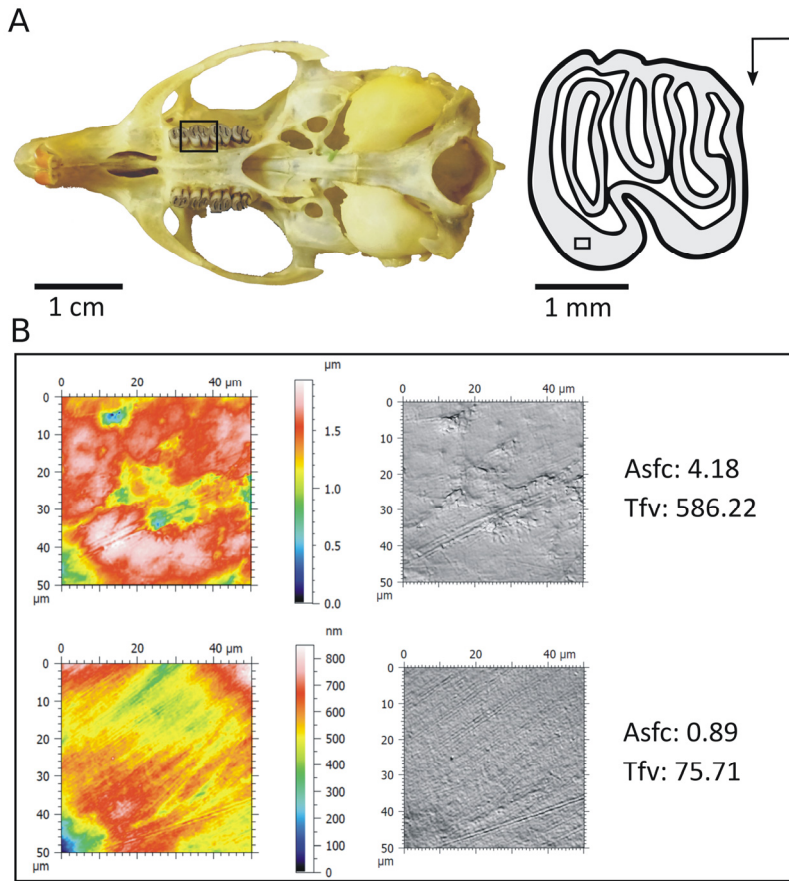
A	<i>P. guyannensis</i> F	<i>P. guyannensis</i> M	<i>P. cuvieri</i> F
<i>P. guyannensis</i> M			
<i>P. cuvieri</i> F	Asfc, Tfv		
<i>P. cuvieri</i> M	Asfc, Tfv	Asfc, Tfv	Asfc, Tfv
B	<i>P. guyannensis</i> Oct	<i>P. guyannensis</i> Jul	<i>P. cuvieri</i> Oct
<i>P. guyannensis</i> Jul	Asfc, Tfv, epLsar		
<i>P. cuvieri</i> Oct	Asfc, Tfv, epLsar		
<i>P. cuvieri</i> Jul	Asfc, Tfv		

946



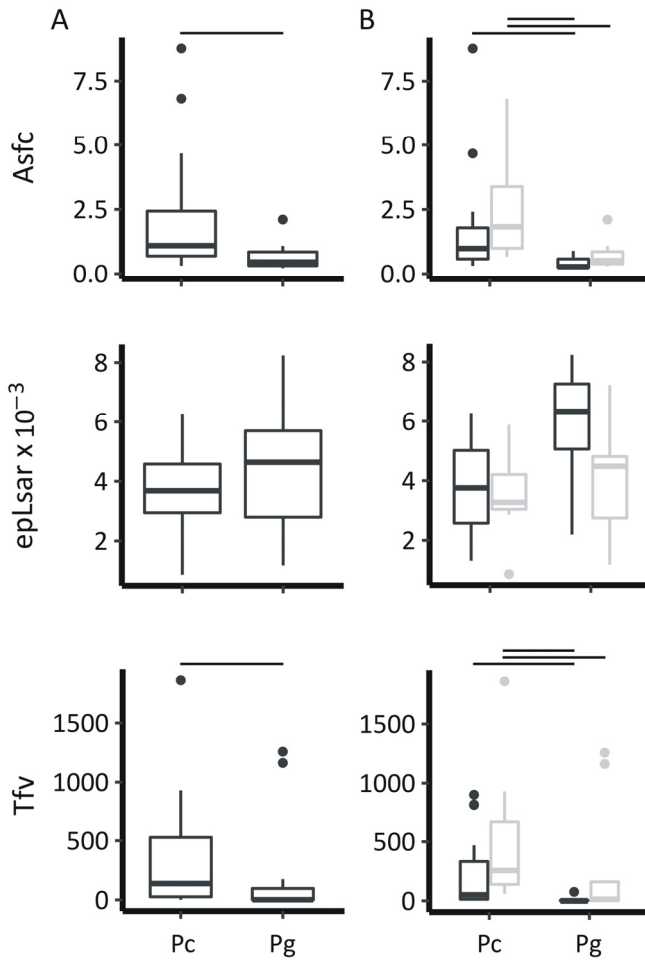
947

948 **Figure 1.** Geographic map of the region of interest. A: Geographical location of French
 949 Guiana in South America (left) and of the little village of Cacao (red cross), south of Cayenne
 950 on the Comté River (right). B: Aerial photograph (Geoportail; www.geoportail.gouv.fr) of the
 951 Cacao area with the location of the five sites of capture from the anthropized region (left)
 952 toward old secondary forest (right). The numbered (1, 2, 4, 5, 8) white circles correspond to
 953 the five loci of capture (respectively LI-1, LI-2, LI-4, LI-5, and LI-8). See Table 1 for exact
 954 GPS coordinates. [2 columns width]



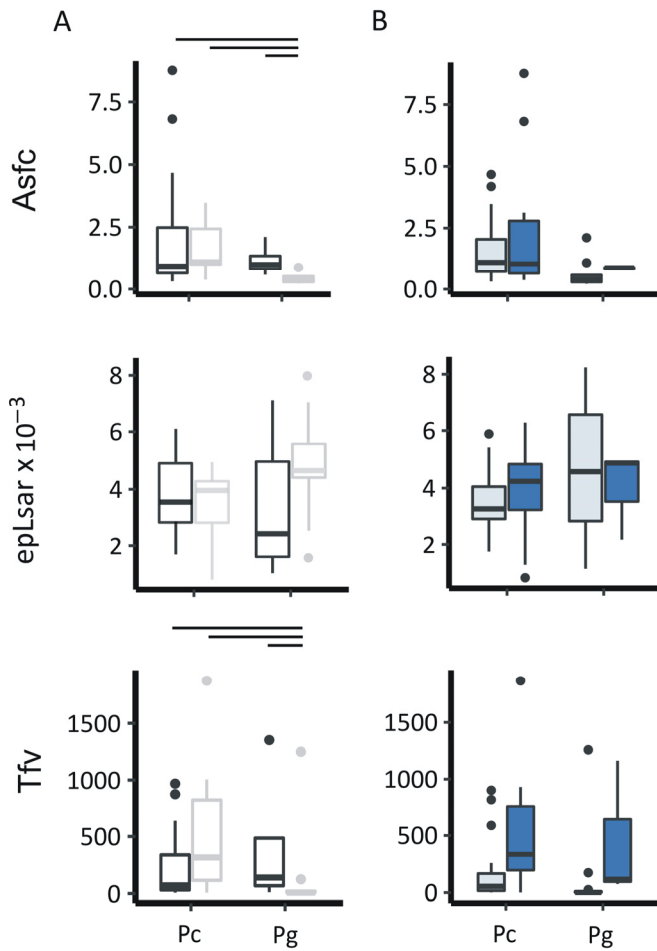
955

956 **Figure 2.** Graphical representation of the acquisition process of dental microwear parameters
 957 from the studied specimens (A) to the studied areas of molar microwear (B). A, (left) position
 958 of the studied left first upper molar (M1) on the cranium of *Proechimys cuvieri*
 959 (MHNG1975.046) in occlusal view (scale bar = 1 cm) and (right) measurement position of
 960 the chewing facet on the same tooth (scale bar = 1 mm). The light gray filling indicates the
 961 enamel layer. The black rectangle indicates the 175 x 132 μm 3D scan acquired on the
 962 LeicaDCM "Trident". The surface generated was treated using the LeicaMap software
 963 (Mountain technology, Leica Microsystems). An area of study of 50 x 50 μm was cut out
 964 manually. Arrow indicates mesio-lingual direction. B, (left) topographic representations and
 965 (right) photosimulations of the 50 × 50 μm studied surface of *Proechimys cuvieri*
 966 (MHNG1975.046, top) and *Proechimys guyannensis* (MHNG1984.001, bottom) with the
 967 values of their associated Asfc (no unit) and Tfv (in μm³) parameters. [1.5 column width]



968

969 **Figure 3.** Boxplots of significant microwear texture variables. A, by species; B, by species
 970 and sex. Females are in black, and males are in light gray. Pc, *Proechimys cuvieri*; Pg,
 971 *Proechimys guyannensis*; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume.
 972 Solid lines indicate when Tukey's HSD tests were significant ($p < 0.05$). [single column
 973 width]



974

975 **Figure 4.** Boxplots of significant microwear texture variables. A, by species and month of
 976 capture; B, by species and vegetation cover. Specimen captured in July are in black, and in
 977 October in light gray. The old secondary forest vegetation cover (1) is in light blue filling, and
 978 the disturbed forest vegetation cover (2) is in blue filling. Pc, *Proechimys cuvieri*; Pg,
 979 *Proechimys guyannensis*; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume.

980 Solid lines indicate when Tukey's HSD tests were significant ($p < 0.05$). [single column

981 width]