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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**

Céline Robinet, Gildas Merceron, François Catzeflis, Adriana M Candela,  
Laurent Marivaux

► **To cite this version:**

Céline Robinet, Gildas Merceron, François Catzeflis, Adriana M Candela, Laurent Marivaux. 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. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2022, Understanding dental proxies of ancient diets, 591, pp.110880. 10.1016/j.palaeo.2022.110880 . hal-03579274

**HAL Id: hal-03579274**

**<https://hal.umontpellier.fr/hal-03579274>**

Submitted on 18 Feb 2022

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1 *Palaeogeography, Palaeoclimatology, Palaeoecology*

2 Doi: <https://doi.org/10.1016/j.palaeo.2022.110880>

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

8 Céline Robinet\*<sup>a</sup>, Gildas Merceron<sup>b</sup>, François Catzeflis<sup>c</sup> †, Adriana M. Candela<sup>a</sup>, Laurent  
9 Marivaux<sup>c</sup>

10

11 <sup>a</sup> División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, La Plata,  
12 B1900FWA, Argentina. [c.robinet@fcnym.unlp.edu.ar](mailto:c.robinet@fcnym.unlp.edu.ar), [acandela@fcnym.unlp.edu.ar](mailto:acandela@fcnym.unlp.edu.ar)

13 <sup>b</sup> Laboratoire PALEVOPRIM, UMR 7262 CNRS-INEE & Université de Poitiers, Bât. B35,  
14 TSA 51106, F-86073 Poitiers Cedex 9, France. [gildas.merceron@univ-poitiers.fr](mailto:gildas.merceron@univ-poitiers.fr)

15 <sup>c</sup> Institut des Sciences de l'Évolution de Montpellier (ISE-M), UMR 5554 CNRS, IRD, EPHE  
16 & Université de Montpellier, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France.  
17 [laurent.marivaux@umontpellier.fr](mailto:laurent.marivaux@umontpellier.fr)

18

19 \*Corresponding author: [c.robinet@fcnym.unlp.edu.ar](mailto:c.robinet@fcnym.unlp.edu.ar) or [cr.robinet@gmail.com](mailto:cr.robinet@gmail.com)

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 m<sup>2</sup> for females and 8,431 m<sup>2</sup> 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 m<sup>2</sup> for males and 1,500 m<sup>2</sup> 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  $1360 \times 1024$  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  $50 \times 50$   
183  $\mu\text{m}$  area was extracted, from which the 2<sup>nd</sup> 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  $\mu\text{m}$ ) 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  $\mu\text{m}$ ; 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

### 483 **Acknowledgements**

484 The authors thank Manuel Ruedi, curator of the mammal collection at the *Museum d'Histoire*  
485 *Naturelle de Genève*, for permitting access to the studied rodent specimens under his care. We  
486 wish to thank Anusha Ramdarshan (Rekki) and Julien Claude (ISE-M) for their help in the  
487 use of the software R, Manon Hullot (ISE-M) for our helpful conversations, and Léanie  
488 Alloing-Séguier (Toulouse) for her courtesy in proofreading this manuscript. We thank

489 Frederic Delsuc (ISE-M) for access to the field documentation of our late colleague François  
490 Catzefflis. We also wish to thank Thomas Tütken, from the Institute of Geosciences at the  
491 Johannes Gutenberg University, and two anonymous reviewers for their helpful comments on  
492 this work. FC acknowledges the technical expertise of Michel Gillioz and Laurent Vallotton  
493 at the Geneva Natural History Museum for curating specimens with care. The efficient help in  
494 the field of Fidel Botero, Aline Catzefflis, Gilles Peroz, Gilbert Pistre, and Manuel Ruedi was  
495 very much appreciated, as well as the kind collaboration with Benoit de Thoisy and Anne  
496 Lavergne from the *Institut Pasteur* at Cayenne (French Guiana). This article is dedicated to  
497 the memory of François Catzefflis, who passed away on November 25, 2021. A long-time  
498 colleague and friend, he was a key figure in the gathering of osteological mammal collections,  
499 particularly in French Guiana. This work could not have been accomplished without his long-  
500 standing field efforts and research in Cacao. This is ISEM publication 202X-0XX SUD.

501

## 502 **Funding**

503 This work was supported by the CoopIntEER CNRS/CONICET (252540; PIs: A. Candela  
504 and L. Marivaux) and the ECOS-SUD/FONCyT (A14-U01; PIs: P.-O. Antoine [ISE-M] and  
505 F. Pujos [IANIGLA, Mendoza]) international collaboration programs, and by the *Laboratoire*  
506 *de Paléontologie* (ISE-M; PI: L. Marivaux). Dental microwear textural analyses were  
507 supported by the French *Agence Nationale de la Recherche* (ANR) “TRIDENT” project  
508 (ANR-13-JSV7-0008-01; PI: G. Merceron). Field work, including trapping and killing of wild  
509 rodents, at Cacao was also funded by the ANR (ANR-2006-SEST-20-01; PI: Th. De Meeus,  
510 IRD-Montpellier). This work was further supported by the *Investissements d’Avenir* grant  
511 managed by the ANR (Labex CEBA [*Centre d’Etude de la Biodiversité Amazonienne*], ANR-  
512 10-LABX-25-01).

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  
542 and October for "month of capture".

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](http://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  $\mu\text{m}$  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  $\mu\text{m}$  was cut out  
910 manually. Arrow indicates mesio-lingual direction. B, (left) topographic representations and  
911 (right) photosimulations of the 50  $\times$  50  $\mu\text{m}$  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  $\mu\text{m}^3$ ) 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 <sup>a</sup>
<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 <sup>a</sup>References: 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<sup>a</sup> 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 <sup>3</sup>			HAsfc4			HAsfc9			HAsfc16			Tfv		
		m	med	sd	m	med	sd	m	med	sd	m	med	sd	m	med	sd	m	med	sd
<b>By species</b>																			
<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
<b>By month of capture</b>																			
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

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937 <sup>a</sup> 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<sup>a</sup>.

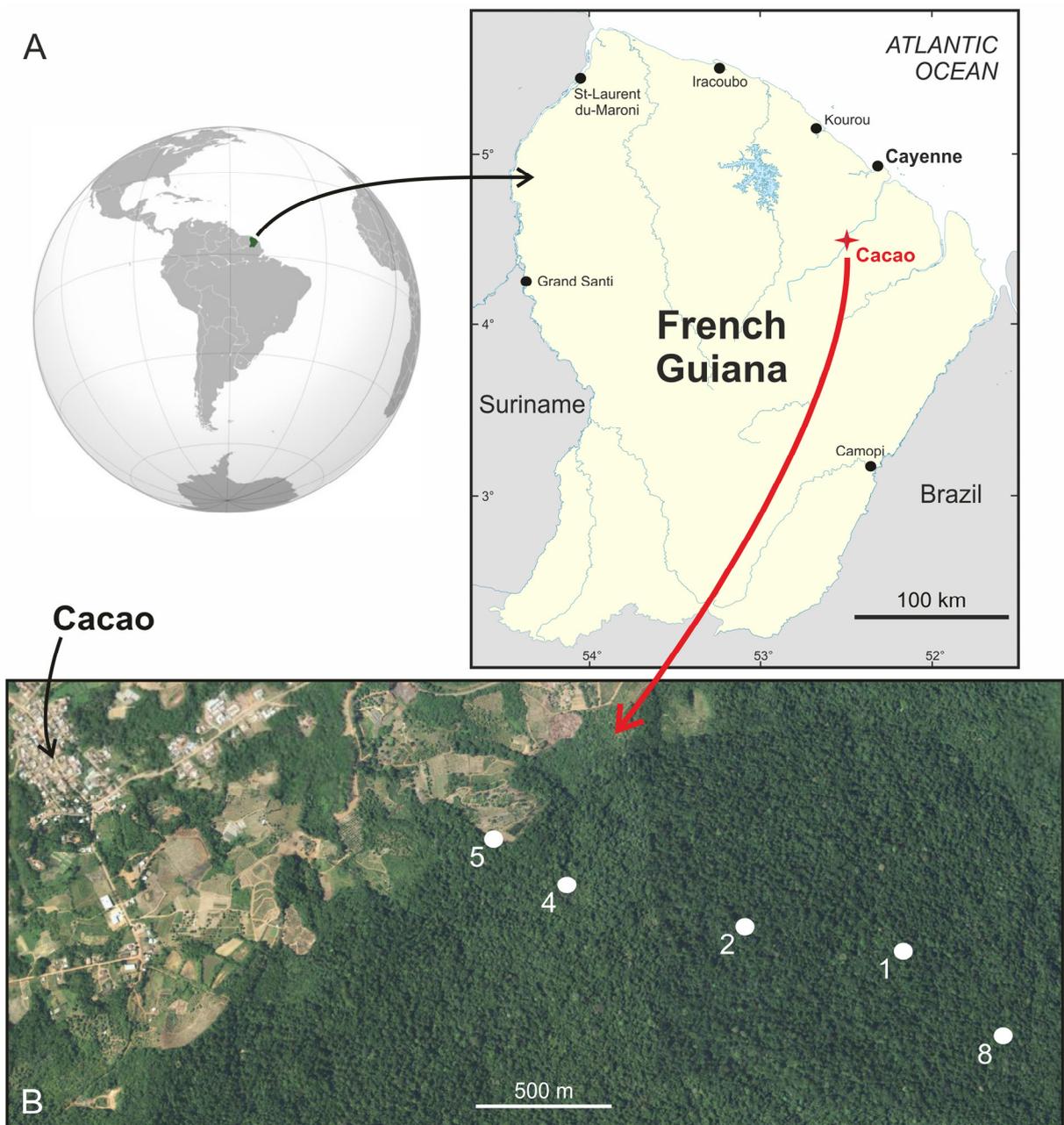
Parameter	Treatment	<i>F</i> value	<i>p</i> value
Asfc	species	24.06	<0.001
	sex	8.79	0.005
	month of capture	8.42	0.007
	species x month of capture	8.07	0.008
	vegetation cover x month of capture	4.96	0.033
epLsar	species x month of capture	5.47	0.026
	species x sex x vegetation cover	4.73	0.037
Tfv	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 <sup>a</sup> 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.

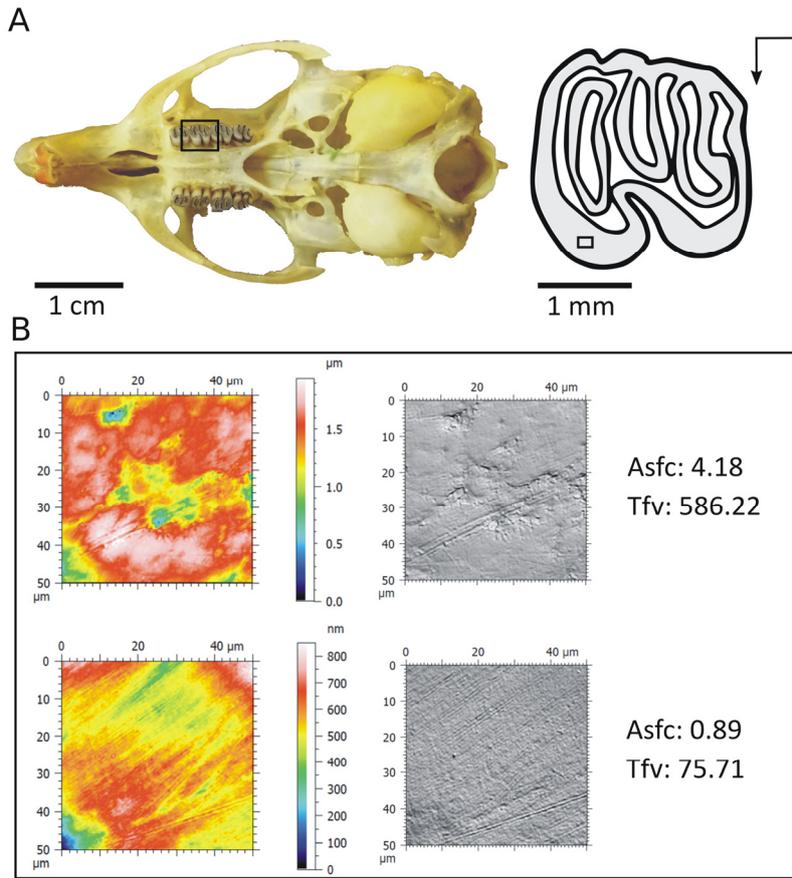
A	<i>P. guyannensis</i> F	<i>P. guyannensis</i> M	<i>P. cuvieri</i> F
<i>P. guyannensis</i> M			
<i>P. cuvieri</i> F	<b>Asfc, Tfv</b>		
<i>P. cuvieri</i> M	<b>Asfc, Tfv</b>	<b>Asfc, Tfv</b>	Asfc, Tfv
B	<i>P. guyannensis</i> Oct	<i>P. guyannensis</i> Jul	<i>P. cuvieri</i> Oct
<i>P. guyannensis</i> Jul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

946



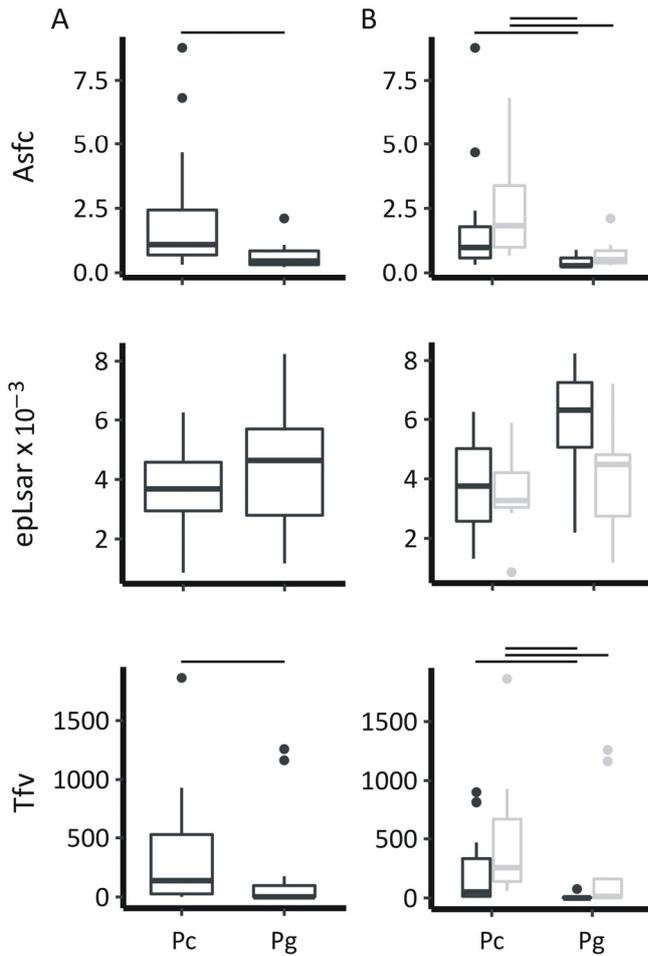
947

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](http://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]



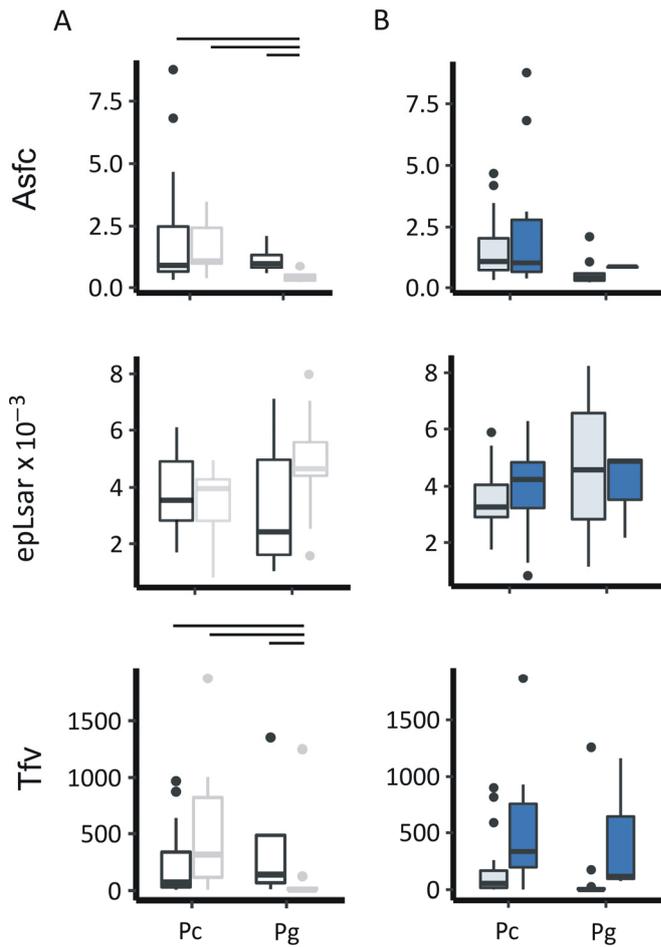
955

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 μm<sup>3</sup>) 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]