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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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Abstract.

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

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

1. Introduction

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

The fossil record of the group so far extends back to the end of the Eocene (Antoine et al., 2012; Boivin et al., 2017, 2019a, 2022). Caviomorphs would thus testify to an at least 35 million year-long endemic evolutionary history on the South American continent, marked by several adaptive radiation events. However, any role of ecological factors in those phases of diversification remains poorly known (e.g., Boivin et al., 2019a). The Paleogene fossil record of caviomorphs consists mainly of isolated teeth, but very few well-preserved skulls or associated post-cranial remains allow for functional morphology approaches (Verzi, 2002; Candela and Picasso, 2008, Boivin et al., 2019b). Among the ecological factors that may have driven the radiations of caviomorphs, food preference is a factor that is known to be very important in modern niche partitioning (Bowers, 1982; Castro-Arellano and Lacher, 2009; Shiels et al., 2013).

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

If DMTA is a state-of-the-art approach of surface metrological characterization (Ungar and Evans, 2016; Arman et al., 2019), two factors challenge the robustness of dietary reconstructions based on microwear texture: the inherently low sample sizes of paleontological datasets and a tendency to overlook potential sources of intra-specific variation (Calandra and Merceron, 2016; Arman et al., 2019). Indeed, fossil data are often fragmentary and can suffer from post-mortem surface alterations during the fossilization process (Weber et al., this issue). They suffer also from a lack of information regarding many factors that can be a source of biological variations, such as sex, season of death, or characteristics of the habitat in which the individuals lived. Thus, paleoecological inferences are often made by analogy with extant taxa, at the specific or generic level, under the assumption that the chosen sample of extant specimens is sufficiently representative. As such, a majority of DMTA studies focus on inter-specific differences, accepting a presumably minor intra-specific variability without exploring it.

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

2. Materials and Methods

2.1. Locality

The locality of Cacao is situated in the north-eastern part of French Guiana, along the Comté River, 45 kilometers south of Cayenne. Specimens were sampled in five loci (LI-1, LI-2, LI-4, LI-5, and LI-8; Table 1, Fig. 1) following a clear gradient of anthropization and considering the known home range of the targeted species (see below). The vegetation cover across the loci varies from nearby cultivated areas (various fruits and vegetables) and highly disturbed areas around those fields (LI-4 and LI-5) to old secondary well-drained forests (LI-1, LI-2, and LI-8) with relatively middle-height closed canopy (around 28 m) and openings from small windfalls (Guitet et al., 2015). French Guiana is dominated by a warm and wet tropical rainforest climate. Precipitation at Cacao can range from 3,500 to 4,000 mm yearly, with more than 250 rainy days per year (Météo France). Two rainy and two dry seasons can be distinguished: a short rainy season from December to February, a short dry season from March to mid April, a long rainy season from April to July, and finally a long dry season between August and November (Catzeflis et al., 2018). The lowest monthly rainfall values are recorded in September and October (Catzeflis et al., 2018).

2.2. Materials

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

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

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

The studied specimens were not radio-tracked because the objective of the fieldwork was to collect (trap and kill) specimens. However, Guillotin (1982) studied in detail the home range (3,145 m^2 for females and 8,431 m^2 for males, with a maximum diameter of approximately 85 m for females and 131 m for males, Table 1; Guillotin, 1982), and the cumulated distance traveled per night (297 m for females and 586 m for males) of *P. cuvieri* in French Guiana. Everard and Tikasingh (1973) described the home range of *P. guyannensis* (14,000 m^2 for males and 1,500 m^2 for females). Those values indicate that both species stay in a relatively small area and do not tend to move over large distances.

2.3. Dental Microwear Textural Analysis (DMTA)

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

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

The SSFA (Scott et al., 2006) on the selected enamel surface was conducted with the Toothfrax and Sfrax software programs (Surfract Corporation, Norwich, Vermont, USA). We obtained the complexity (area scale of fractal complexity: Asfc), the anisotropy (exact proportion of length scale anisotropy of relief: epLsar), the heterogeneity of complexity (heterogeneity of the area scale of fractal complexity between sub-surfaces from a given surface: HAsfc), and the textural fill volume (Tfv; textural fill volume at 0.2 μm) of the studied surface. In this study, we calculated heterogeneity of complexity from four (HAsfc4), nine (HAsfc9) and 16 (HAsfc16) cells, respectively (Supplementary Data S1). Scott et al. (2006) have described each of these variables in detail.

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

2.4. Statistics

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

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

For each parameter, in order to consider all the factors and their interactions, we started with a model that can be described as: DMT parameter ~ Species x Sex x Vegetation cover x Month of capture, where the factor "species" has the modalities *Proechimys cuvieri* and *P. guyannensis*, the factor "sex" has the modalities males and females, the factor "vegetation cover" has the modalities old secondary forest (corresponding to loci 1, 2 and 8) and disturbed forest (corresponding to loci 4 and 5), and the factor "month of capture" has the modalities July and October. We then conducted a stepwise model selection based on Akaike’s Information Criterion (AIC) values using the stepAIC function incorporated in the MASS package (detailed in Supplementary Data SD2) and retained the best model (lowest AIC's values).

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

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

3. Results

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

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

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

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

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

4. Discussion

4.1. Ecological interpretations

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

Although fruit pulp is the primary component of the diet of both species of *Proechimys*, our results show that this "soft" (Vogel et al. 2014) item is most likely not the diet component having the largest impact on the enamel surfaces, as differences in dental microwear textures are noticed between the two species (Table 4; Fig. 3). On one hand, the inclusion of seeds and insects (Guillotin, 1982; Feer et al., 2001), many of them being hard and brittle, in the diet of *P. cuvieri* may generate more variable and more complex (Asfc) microwear textures, associated with more deeply scarred textures as highlighted by the higher textural fill volume (Tfv) values (Table 2; Fig. 3A). On the other hand, the diet of *P. guyannensis* is supplemented by leaves but also AMF (Arbuscular Mycorrhizal Fungi, Janos et al., 1995; Mangan and Adler, 1999). These AMF contain chitin-bearing spores protected by compact aggregations of spores called sporocarps (Giovannetti and Gianinazzi-Pearson, 1994). One may guess that those micrometric (between 30 to 160 µm; Janos et al., 1995) spores might lead to less complex (Asfc) microwear textures and lower values of textural fill volume (Tfv) (Tables 3 and 4; Fig. 3), having a similar effect as siliceous phytoliths and other small abrasives in grazer species (Scott, 2012).

Overall, textural fill volume (Tfv) and complexity (Asfc) of females are lower than those of males (Tables 3 and 5), which may reflect differences in diet between sexes in *Proechimys*. Dietary differences between males and females are known among different species of mammals reflecting differences in energetic requirements and physiology (e.g., Cransac et al., 2001; Kamilar and Pokemper, 2008). Such differences in diet being reflected in dental microwear patterns has previously been recorded in other species (see Merceron et al., 2010; Percher et al., 2018). The ecology of *P. guyannensis* is not known in details, but males of *P. cuvieri* seem to be more frugivorous than females, and consume fewer insects (Henry, 1997). As males have a home range twice larger than females (Guillotin, 1982), they might resort to secondary components of their diet less often than females. Furthermore, insects might fulfill the increased protein requirements of gestation and lactation periods in female rodents (Zambrano et al., 2005). Thus, the slight differences in textural fill volume (Tfv) and complexity (Asfc) observed between males and females of *P. cuvieri* might reflect a slightly higher proportion of seeds in the diet of males compared to females. Lower values of textural fill volume (Tfv) indicate a less deeply scarred texture. Insects (preferentially consumed by females) and seeds (preferentially consumed by males) are both hard items, but the former are more diverse mechanically speaking (e.g., beetles vs. caterpillars) and might offer less resistance to mastication than dense seeds (Strait, 1993).

Specimens captured in October have less complex (Asfc) microwear textures associated with lower values of textural fill volume (Tfv) than specimens captured in July (Tables 3-5; Fig. 4). These differences are mainly apparent in individuals of *P. guyannensis* captured in October, which also have lower values in complexity (Asfc) and textural fill volumes (Tfv) as well as slightly higher values of anisotropy than those of *P. cuvieri* captured the very same month (Table 5, Fig. 4). Besides, *P. guyannensis* individuals captured in October also have slightly higher values of anisotropy than individuals of the same species captured in July (Table 5). It is known that fruit availability is highly seasonal even in tropical rainforests (Leigh, 1999; Forget et al., 2002; Jansen et al., 2002), even if the amplitude of fructification seasonality is lessened in secondary forests compared to primary forests in French Guiana (Sabatier, 1985). The peak of fructification generally coincides with the start of the wet season, between March and May. Neither July nor October can be considered as high fructification seasons, however, overall availability of fruit seems higher in July than in October (Charles-Dominique et al., 1981; Guillotin, 1982). It then seems that a drop-in food availability occurring during the dry season (October) has a significant impact on the diet, particularly that of *P. guyannensis*. As observed for other mycophageous species of *Proechimys*, AMF may become especially critical when competition for primary resources (fruit) is elevated due to scarcity of fruit (Mangan and Adler, 1999). No difference of microwear texture is detected between individuals of *P. cuvieri* captured in both months, which could indicate either that *P. cuvieri* does not modify its diet much across the months or that their potential fallback food –mostly consumed in October– either have similar material properties as their preferred food resources, or have few effects on enamel surface. On the contrary, the seasonal differences in dental microwear texture in *P. guyannensis* support that in October when fruit are less abundant, the new component in diet, mostly leaves and fungi (AMF), have different properties than the primary dietary components (fruit and seeds). Our results also confirm that when fruit are abundant, during the wet season in July, both species seem to have more similar diets.

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

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

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

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

4.3. Implications for paleoecology

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

An important point to keep in mind, when estimating the diet of extinct species, is that similar dental microwear textures can be the result of different ingested dietary items sharing similar material properties (Calandra and Merceron, 2016). Conversely, significant differences in dental microwear textures on homologous dental facets of different species are indeed evidence for difference in dietary habits. The primary component of diet does not always have the strongest impact on dental microwear texture. Marshall and Wrangham (2007) suggested that dental adaptations might reflect fallback foods (such as fungi, leaves, and insects) rather than preferred foods (such as fruit). For many species, preferred foods require little specialization and can be processed relatively easily, whereas fallback foods are less easily processed, and require more specialization (Robinson and Wilson, 1998). Experimental settings (Merceron et al., 2016b; Ramdarshan et al., 2016; Teaford et al., 2018; Winkler et al., 2019a) and applied studies (Merceron et al., 2010; Berlioz et al., 2018) have shown that fallback foods and secondary components of the diet may considerably affect dental microwear textures. Our results on a wild population of caviomorph rodents confirm that this possibility applies also to this group. Indeed, they show differences in dental microwear between the two time periods (July and October), particularly highlighted in *P. guyannensis*. The differences might be either driven by a drop or change in fruit composition or the inclusion of fungi (AMF) and insects in diet. Among those fallback foods, the former contains high concentration of spores covered by resistant and protective tissues likely acting as abrasive agents on dental tissue, while insects display diverse mechanical properties from soft caterpillars to hard and brittle beetles. These fallback foods might be responsible for the seasonal differences in dental microwear textures (Ungar et al., 2008; Strani et al., 2019).

Several studies recently shed light on the intra-specific variability of dental microwear textures depending on the composition of diet (for instance in ungulates, Ramdarshan et al., 2016; Bignon-lau et al., 2017), or even the water content of the consumed items (i.e., dry *versus* wet grass in guinea pigs; Winkler et al., 2019a). Other studies even aimed further and looked into the variability at the individual level (Arman et al., 2019), often relying on experimental controlled feeding settings in order to identify the factors involved in intra-individual variability and quantify it (Ramdarshan et al., 2017; Winkler et al., 2021). The intraspecific variability has to be explored from the individual level, comparing teeth and wear facets from the same individual to improve data acquisition and reproducibility (Ramdarshan et al., 2017; Arman et al., 2019; Winkler et al., 2021), to a larger scale, comparing between- and within-population variations of the same taxa across different ecoregions (Burgman et al., 2016; Arman et al., 2019). This work does not address the intra-individual variability but focuses on factors of variability at the population level. Our results show that the dental microwear textures reflect differences in habitat structure at a small spatial scale (1.5 km transect) emphasizing the benefit of tooth wear analysis in general and especially DMTA to track variations of food availability at the micro-habitat scale (Belmaker, 2018). Microwear textures from both species of *Proechimys* overlap when factors such as sex, seasonality, and types of vegetation cover are considered, but interspecific differences are detected when both species are compared regardless of the other factors. These results illustrate particularly well the variability and flexibility of diets and feeding behaviors of caviomorph rodents and their potential impact on diet estimations of fossil taxa (Robinet et al., 2018). It also highlights the importance of having a well-known sample as detailed as possible rather than numerous specimens with low traceability (i.e., geographic provenance and date of capture). Indeed, one limiting factor in interpreting the DMTA results obtained for caviomorphs is the critical lack of detailed published ethological reports and ecological data for the majority of groups, as well as the little experimental data on dental microwear texture among caviomorph taxa (but see Winkler et al., 2019a, 2020, 2021). Indeed, while *P. cuvieri* is well studied and observations were made for both sexes, in both seasons (Guillotin, 1982; Feer et al., 2001), this is not the case for *P. guyannensis*.

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

Conclusion

This work, focused on two sympatric species of spiny rats (*Proechimys*) from French Guiana, applying DMTA, is the first to explore intra- and inter-specific variations of wild caviomorph rodents. In our case, DMTA detected differences of diet between the two species. Seasonal variations in fruit and seeds availability, as well as distinct feeding strategies between males and females might explain the differences detected by DMTA. Microwear textures from both species overlap when factors such as sex, seasonality and types of vegetation cover are considered, reflecting a dietary overlap between *P. guyannensis* and *P. cuvieri*.

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

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Supplementary Data

Supplementary Data SD1. - Detailed list of studied specimens and individual microwear textural parameters. The file name indicates the fact that the scan was realized on a mold (Zinv for inverted), the species (Pc for *P. cuvieri*; Pg for *P. guyannensis*), the collection number of the specimen, the scanned tooth (UM1 for first upper molar; l for left, r for right), the scanned area (pct for protocone; ml for the mesio-lingual portion of the protocone). The suffix -bis appears when a scan was retaken after a first failed attempt. The vegetation cover factor modalities are old secondary forest (corresponding to 1) and disturbed forest (corresponding to 2). The microwear texture parameters are the complexity (Asfc), the anisotropy (epLsar), the heterogeneity of complexity (HAsfc4, 9 and 16), and the textural fill volume (Tfv).

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

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

Supplementary Data SD4. - Complete analyses of variances (ANOVA) results for the best selected model for each microwear textural parameters following a Box-Cox transformation. The modalities are *Proechimys cuvieri* and *Proechimys guyannensis* for the factor "species", males and females for "sex", old secondary forest (corresponding to loci 1, 2 and 8) and disturbed forest (corresponding to loci 4 and 5) for "vegetation cover", July and October for "month of capture".

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Figure captions

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

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

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

Proechimys guyannensis; Asfc, complexity; epLsar, anisotropy; Tfv, textural fill volume. Solid lines indicate when Tukey's HSD tests were significant ($p < 0.05$). **[single column width]**

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Tables

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

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]
Proechimys cuvieri	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
Proechimys guyannensis	15	263 g	terrestrial nocturnal	seasonal (reportedly)	mainly frugivorous (pulp) but also seeds and arbuscular mycorrhizal fungi	2; 3; 4; 7; 8

[a] References: 1) Guillotin, 1982; 2) Emmons and Feer, 1997; 3) Eisenberg and Redford, 1999; 4) Mangan and Adler, 1999; 5) Feer et al., 2001; 6) Catzeflis and Patton, 2016a; 7) Catzeflis and Patton, 2016b; 8) Fabre et al., 2016.

Table 3. Descriptive statistics of dental microwear texture parameters[a] for each species by sex, by month of capture, and by type of vegetation 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																			
P. cuvieri	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
P. guyannensis	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																		
P. cuvieri	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
P. guyannensis	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																		
P. cuvieri	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
P. guyannensis	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

[a] Asfc: complexity; epLsar: anisotropy; HAsfc: heterogeneity of complexity calculated from 4, 9 and 16 cells, respectively; Tfv: textural fill volume.

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

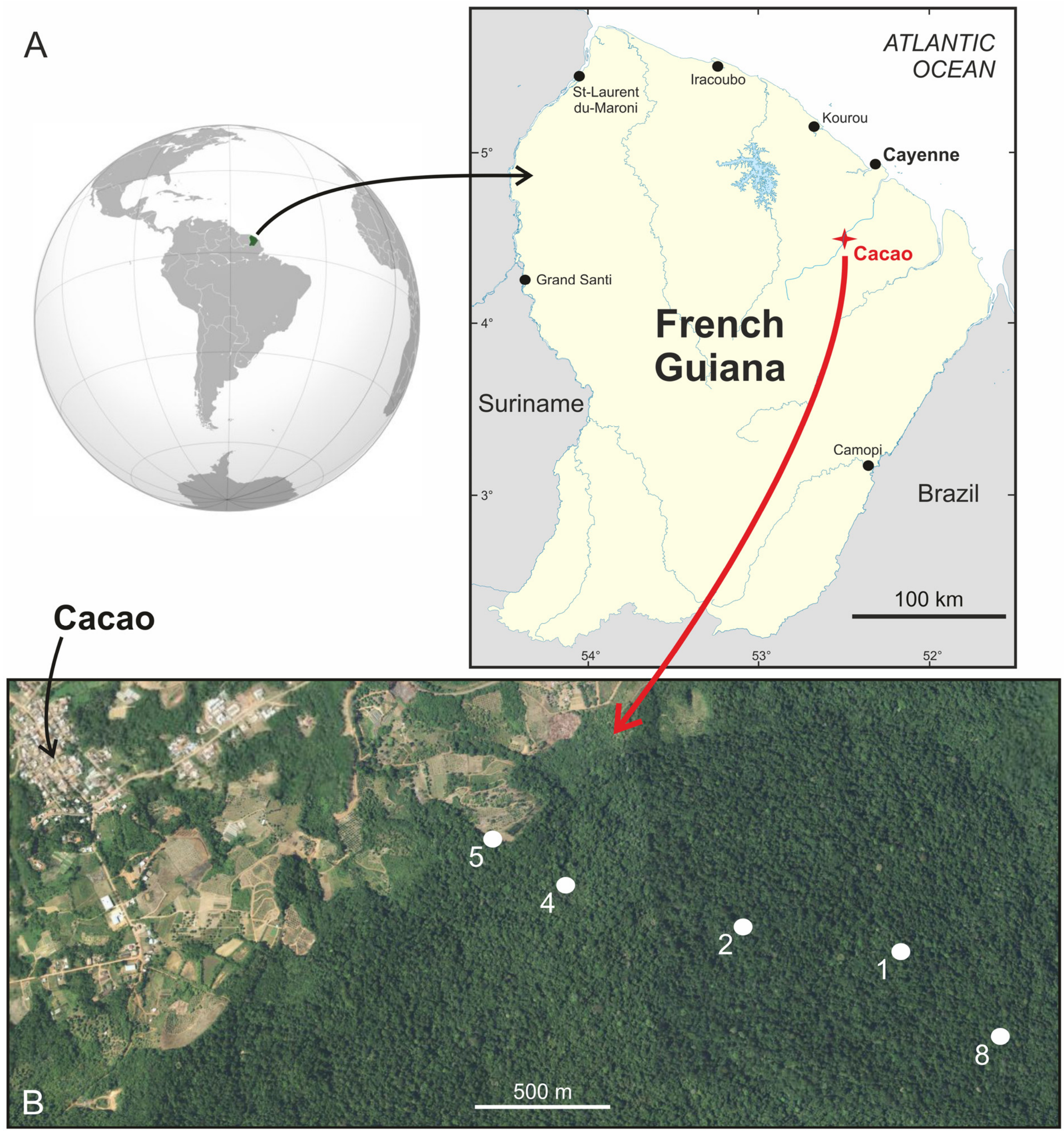
Parameter	Treatment	*F* value	*p* value
Asfc	species	24.06	<0.001
	sex	8.79	0.005
	month of capture	8.42	0.007
	species x month of capture	8.07	0.008
	vegetation cover x month of capture	4.96	0.033
epLsar	species x month of capture	5.47	0.026
	species x sex x vegetation cover	4.73	0.037
Tfv	species	14.26	<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

[a] Asfc: complexity; epLsar: anisotropy; Tfv: textural fill volume.

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

A	*P. guyannensis* F	*P. guyannensis* M	*P. cuvieri* F
P. guyannensis M			
P. cuvieri F	**Asfc**, **Tfv**		
P. cuvieri M	**Asfc**, **Tfv**	**Asfc**, **Tfv**	Asfc, Tfv

B	*P. guyannensis* Oct	*P. guyannensis* Jul	*P. cuvieri* Oct
P. guyannensis Jul	**Asfc**, **Tfv,** epLsar		
P. cuvieri Oct	**Asfc**, **Tfv,** epLsar		
P. cuvieri Jul	**Asfc**, **Tfv**		



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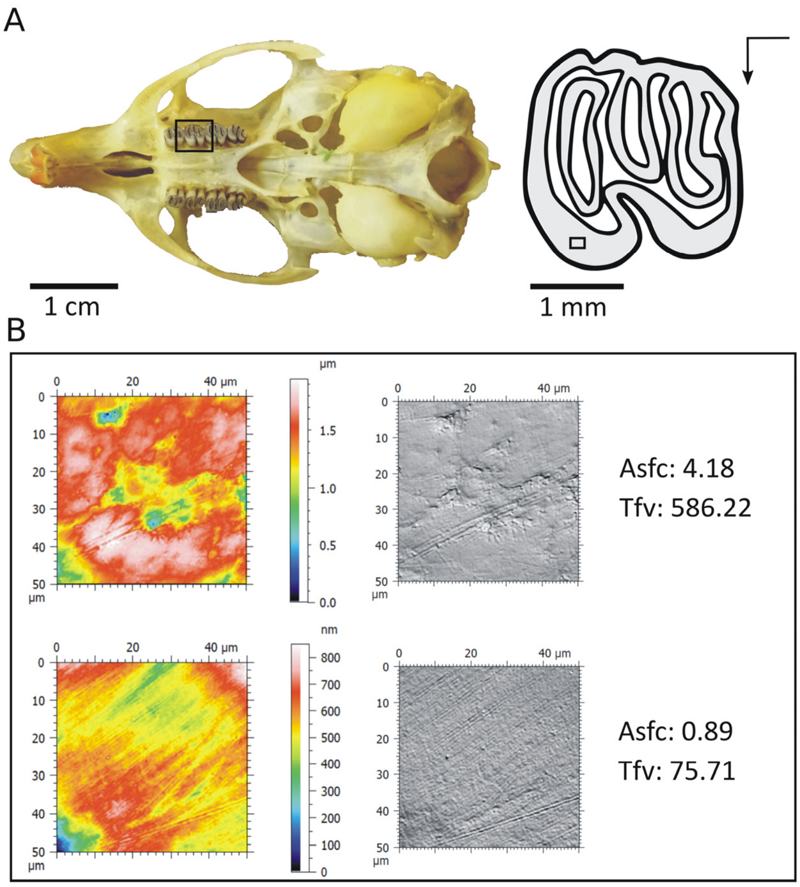

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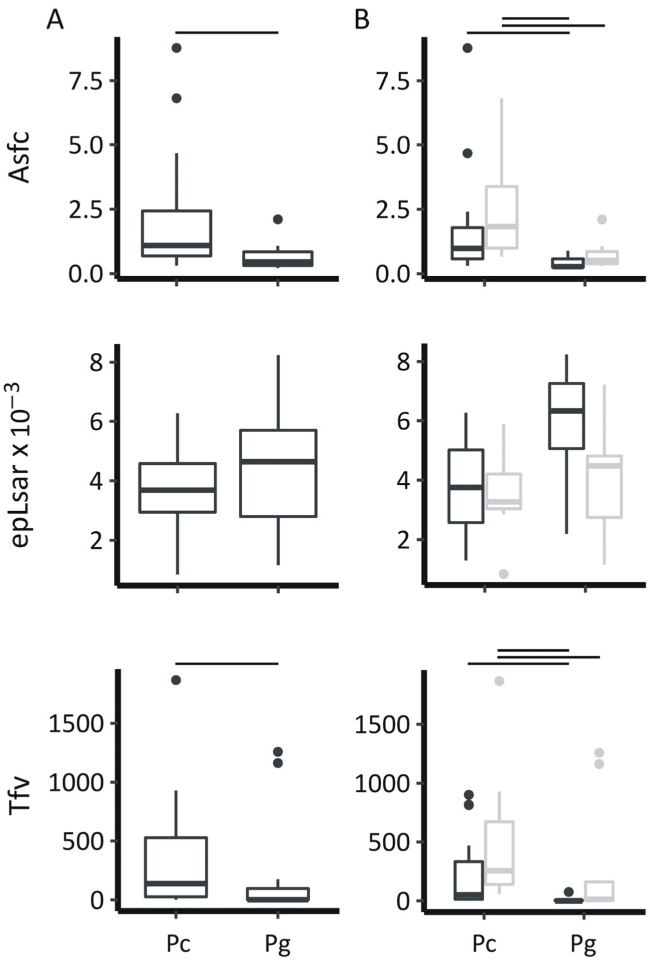

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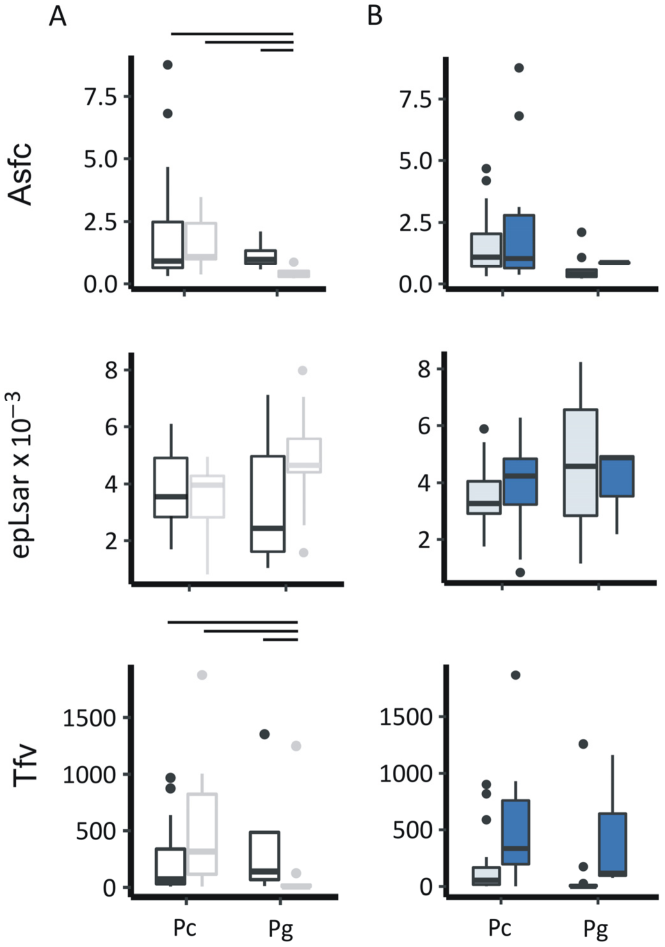

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