

Inferences of dietary preferences of Miocene squirrels (Xerinae, Sciuridae) from the Iberian Peninsula and Namibia using microwear analyses and enamel thickness

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ABSTRACT

In this work, we compared microwear features and enamel thickness from upper molars (M1 and M2) of extinct Xerinae squirrels from the Miocene of Namibia (*Vulcanisciurus* sp) and the Iberian Peninsula (*Atlantoxerus* nov. sp. and *Heteroxerus rubricati*). We also examined the microwear from young and adult specimens of one extant squirrel, *Atlantoxerus getulus*, to compare it with the extinct species. Both, the microwear features and enamel thickness showed that the Miocene African species presented a more abrasive diet than the Iberian ones.

Keywords: Microwear, enamel thickness, Sciuridae, ground squirrels, dietary inference.

RESUMEN

En este trabajo comparamos las marcas de microdesgaste y el grosor de esmalte de molares superiores (M1 y M2) de ardillas de la subfamilia Xerinae del Mioceno de Namibia (*Vulcanisciurus* sp) y de la Península Ibérica (*Atlantoxerus* nov. sp. y *Heteroxerus rubricati*). Además, hemos examinado el microdesgaste de la especie actual *Atlantoxerus getulus*, tanto en individuos juveniles como en adultos, para compararlo con las especies extintas. Tanto el microdesgaste como el grosor del esmalte mostraron que la especie miocena africana presentaba una dieta más abrasiva que las ibéricas.

Palabras clave: Microdesgaste, grosor de esmalte, ardillas terrestres, inferencia de dieta.

1. INTRODUCTION

The subfamily Xerinae includes three major living groups of squirrels: the North American and Eurasian ground squirrels (tribe Marmotini), the African tree squirrels (tribe Protoxerini) and the African ground squirrels (tribe Xerini) (Thorington *et al.*, 2012). Nevertheless, the geographical distributions that we observe today for these groups are not the same than the ones they had in the past. The well-known fossil record of Xerini squirrels in Miocene European and Asian sites demonstrates that they were present in Eurasia (Mckenna & Bell, 1997). This evidence, along with molecular data, suggests that both Protoxerini and Xerini tribes come from two different Euroasiatic ancestors that moved into Africa at different times during the Miocene (Ge *et al.*, 2014). Nevertheless, fossils of protoxerines have only been found in Africa (Winkler *et al.*, 2010), including two extinct genera (*Vulcanisciurus* and *Kubwaxerus*) and two extant ones (*Paraxerus* and *Heliosciurus*, with a fossil record that goes back to the late Miocene of Namibia and the early Pliocene of Kenya, respectively).

The Neogene fossil record from Spain is particularly abundant in squirrels of the subfamily Xerinae. Previous works described species belonging to the tribes Marmotini, such as *Spermophilinus* and *Paleosciurus* (Cuenca Bescós, 1988; Cuenca Bescós & Canudo, 1992), and Xerini, which is very frequent in the Spanish fossil record (Prieto *et al.*, 2013), including genera as *Heteroxerus* and *Atlantoxerus* (Cuenca Bescós, 1988; Peláez-Campomanes, 2001). The latter has one extant representative, the species *Atlantoxerus getulus*, found in Western Sahara, Algeria and Morocco and recently introduced in the Canary Islands (Spain).

The fossil record of this group consists mostly of isolated teeth. This issue, linked to the extremely conservative tooth shape of squirrels (Emry & Thorington, 1984), makes the characterisation of feeding adaptations of extinct species based on morphological analyses particularly difficult. Therefore, other methodologies are considered more useful for this purpose. Dental microwear patterns have been previously used to explore feeding habits in rodents (Rensberger, 1978; Lewis *et al.*, 2000; Hopley *et al.*, 2006; Townsend & Croft, 2008; Gomes Rodrigues *et al.*, 2009; Firmat *et al.*, 2010; Kaya & Kaymakçi, 2013; Oliver *et al.*, 2014) but they have been seldom applied to squirrels (Nelson *et al.*, 2005; Gusovsky & Sinitsa, 2019). Additionally, the thickness of enamel has also been proposed as an important feature for reconstructing diets and environments of fossil mammals (van Dam *et al.*, 2011).

The aim of this work is to characterise the dietary adaptations of extinct squirrels from the middle Miocene of the Iberian Peninsula and Africa based on microwear analyses and enamel thickness of isolated teeth. We also

included one extant species from the Canary Islands, with known dietary preferences, to compare with the results of the Miocene fossils.

2. MATERIAL AND METHODS

We explored the feeding preferences of two middle-Miocene extinct species of squirrels from two fossil sites of the Iberian Peninsula (nine specimens *Atlantoxerus* n. sp. from La Col-C and 11 specimens of *Heteroxerus rubricati* from San Roque 4A) and one from an African fossil site of the same age (seven specimens *Vulcanisciurus* sp., Berg Aukas, Namibia). We also included one extant species (three specimens *Atlantoxerus getulus*) from the Canary Islands (Spain), to compare the results with the extinct species from the same genus present in the Iberian Peninsula. Of the three specimens of *Atlantoxerus getulus*, two were juvenile (MNCN-5526 and MNCN-5529) and one was adult (MNCN-5525). The Spanish specimens analysed in this work are stored in the collections of the Museo Nacional de Ciencias Naturales-CSIC (MNCN) in Madrid. The Namibian material is stored in the National Museum of Namibia.

Microwear was measured between the protocone and hypocone of upper first and second molars (M1 and M2) (Fig. 1), except for the African *Vulcanisciurus*, for which we also included lower molars (p4, m2 and m3) (Fig. 2). We selected specimens with good preservation of the occlusal surface, avoiding the ones with advanced wear as well as unworn molars. Following Oliver *et al.* (2014), a square area of 0.01 mm² was examined using ObjectJ (software Fiji-ImageJ 1.04s). We quantified four microwear features: number of fine scratches (Nfs), number of wide scratches (Nws), number of large pits (Nlp) and number of small pits (Nsp) (Table 1). Pits were differentiated from scratches on the basis of a width/length ratio higher than 1/4 (Grine, 1986). Distinction between wide and fine features was settled at a maximum width of 5 µm (Gomes Rodrigues *et al.*, 2009). To avoid inter-observer errors only one observer examined the photographs (AO). All the measurements were taken from photographs from an Environmental Scanning Electron Microscope (ESEM) Fei, model Quanta 200, with backscattered electron detector at 500x magnification. Overall, we measured the microwear features of the occlusal surface of 37 cheek teeth. We included both right and left molars and, for the extant species, we used the mean of the values obtained for the different teeth of the same specimen to conduct the analyses (Table 1). Finally, we explored the differences in microwear features among species through a Principal Component Analysis (PCA), which allowed us to identify the features explaining most of the variance. To

Table 1. Microwear data for 27 fossil and 3 extant specimens. For the extant species both left and right M1 and M2 were measured. R: right specimen; L: left specimen. Nfs: number of fine scratches; Nws: number of wide scratches; Nlp: number of large pits; Nsp: number of small pits.

Species	Specimen number	Dental element	Side	Nfs	Nws	Nlp	Nsp
	BA-94-52-4	M1/2	L	16	3	31	7
	BERG-92-55-2	M1/2	L	24	9	13	10
	BERG-92-553-1	M1/2	R	15	7	22	6
<i>Vulcanisciurus</i>	BA-51-92-4	M1/2	R	17	6	15	12
	BA-94-52-6	p4	L	5	7	13	19
	BA-94-52-8	m2	L	11	7	20	7
	BA-94-52-10	m3	R	10	3	10	5
	SR4A-65	M1/2	R	18	5	7	33
	SR4A-67	M1/2	R	33	1	8	40
	SR4A-73	M1/2	R	17	1	5	31
	SR4A-80	M1/2	R	30	3	4	33
	SR4A-81	M1/2		26	1	5	61
<i>Heteroxerus rubricati</i>	SR4A-82	M1/2	L	26	2	4	40
	SR4A-83	M1/2	L	33	0	4	36
	SR4A-86	M1/2	L	51	2	3	59
	SR4A-93	M1/2	R	29	1	1	17
	SR4A-101	M1/2	R	44	2	2	46
	SR4A-103	M1/2	L	45	3	17	32
	COL-C-160	M1/2	R	26	4	6	25
	COL-C-178	M1/2	R	39	7	5	31
	COL-C-183	M1/2	R	27	3	4	18
	COL-C-191	M1/2	L	24	2	5	31
<i>Atlantoxerus nov. sp.</i>	COL-C-198	M1/2	R	28	0	6	19
	COL-C-203	M1/2	L	18	6	9	32
	COL-C-207	M1/2	L	42	3	12	28
	COL-C-248	M1/2	L	36	5	14	31
	COL-C-251	M1/2	R	29	0	2	22
	MNCN-5526	M1	R	15	5	22	7
	MNCN-5526	M2	R	17	1	23	14
	MNCN-5529	M1	R	17	6	13	4
	MNCN-5529	M2	R	12	2	14	16
<i>Atlantoxerus getulus</i>	MNCN-5529	M1	L	11	6	6	11
	MNCN-5529	M2	L	7	3	4	12
	MNCN-5525	M1	L	30	3	3	30
	MNCN-5525	M2	L	26	5	5	18
	MNCN-5525	M1	R	21	7	11	26
	MNCN-5525	M1	R	30	0	8	23

test differences among species we used a non-parametric Kruskal-Wallis test for independent variables, since we could not assume normality or equal variance. In order to identify the differences, we performed a pairwise comparison (Wilcoxon test) with Bonferroni correction for the p-values. All the statistical analyses were carried out in the R environment (R Development Core team, 2008) with a significance level of $\alpha = 0.05$.

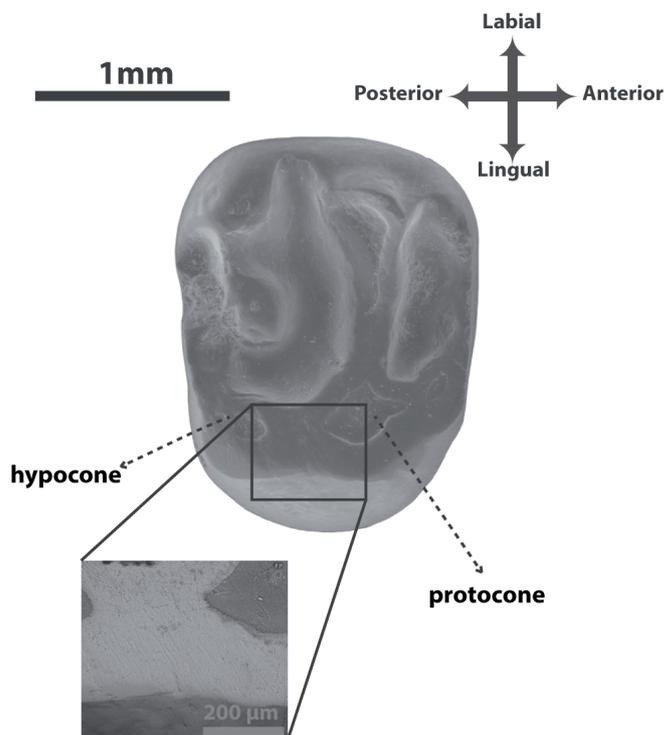


Figure 1. Location of the protocone and hypocone (following the nomenclature of Cuenca Bescós, 1988) in a right upper molar from La Col-C (COL-C-178). The zoomed square area shows the surface where microwear features were measured.

In order to measure enamel thickness, we used a Micro-CT scanner Nikon XTH 160, which produced 3D images of the teeth analysed. We selected unworn specimens with good preservation of the occlusal surface. The measurement of the enamel was made with the software VGStudio MAX 3.0.5 (2019), after orienting the different dental elements using the methodology of van Dam *et al.* (2011) to define the reference occlusal plane. Parallel to the latter we defined the plane that contains the maximum width of the tooth (Fig. 3a). From that plane we calculated the maximum protocone height (Fig.3a). The enamel thickness of the protocone was measured in all specimens at the plane situated at the medium height of the protocone and at the level of the line connecting paracone and protocone, as shown in Figure 3b.

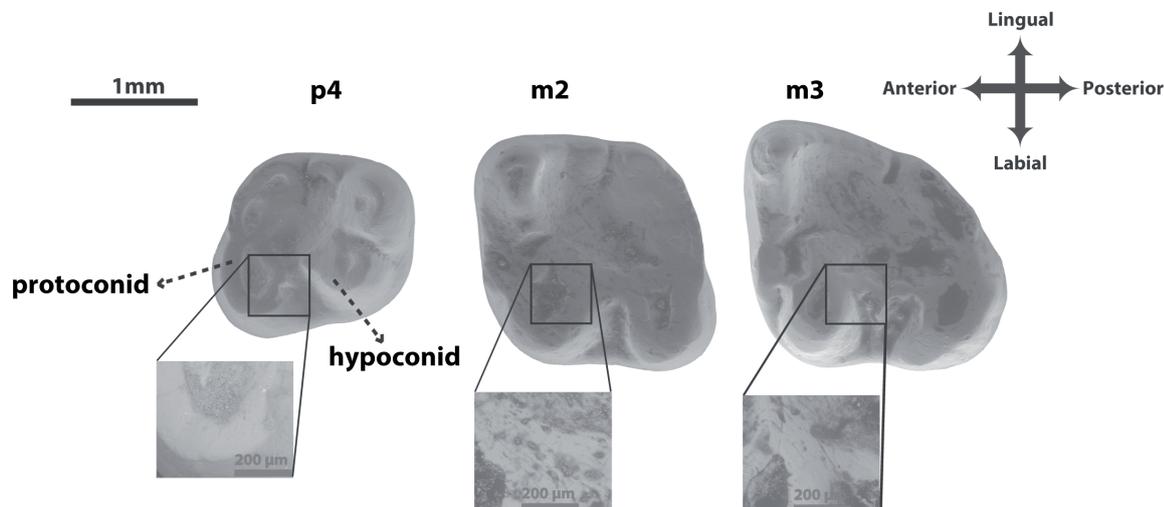


Figure 2. Location of the protoconid and hypoconid for the lower teeth of *Vulcanisciurus*. Left fourth premolar (BA-94-52-6), middle second molar (BA-94-52-8) and right third molar (BA-94-52-10). The zoomed square areas show the surfaces where microwear features were measured.

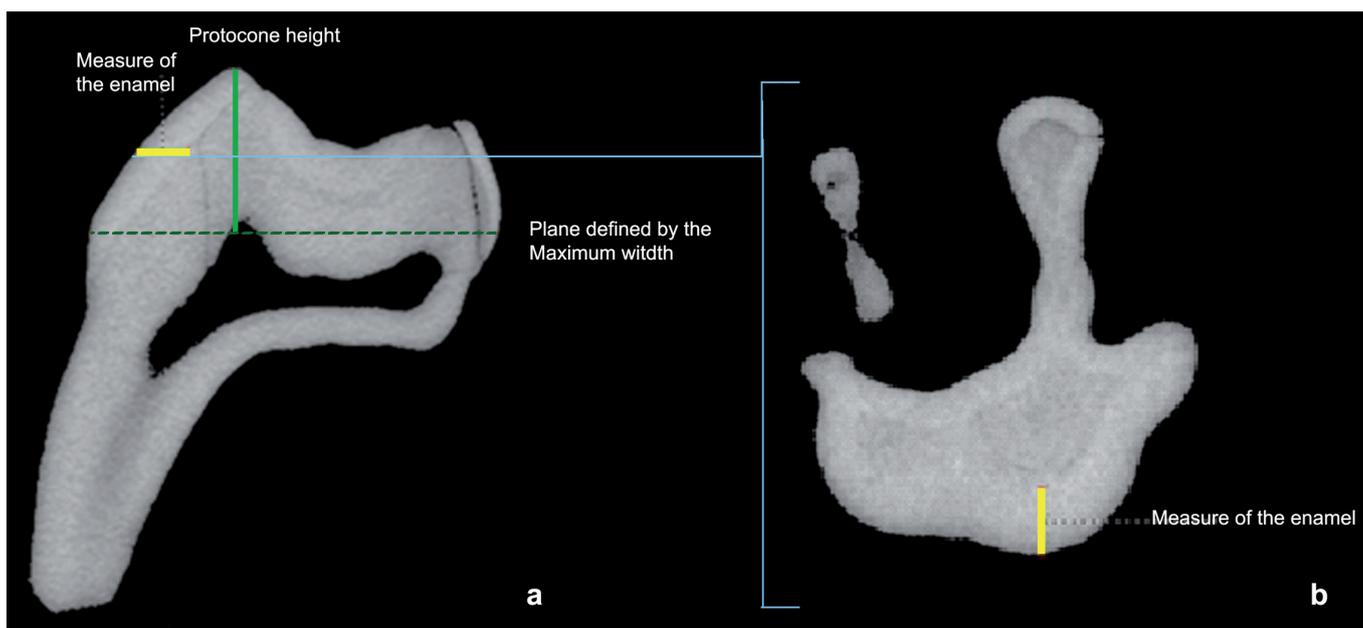


Figure 3. 3D model of M1/M2 of *Heteroxerus rubricati* from SR4 (SR4-71). **a)** Cross-section perpendicular to the occlusal plane. The line connecting the paracone and the protocone is showed in blue. The dashed line indicates the maximum width of the tooth. The vertical green line indicates the protocone height. **b)** Cross-section parallel to the occlusal plane at the medium height of the protocone.

3. RESULTS

3.1. Microwear

The results of the microwear analyses for the four species included are presented in Table 1. As stated in the methods section, we quantified the number of fine and wide wear marks and their morphology, causing four types of

structures (Nfs, Nws, Nlp, Nsp). In general, the shallow structures (Nfs and Nsp) are more frequent than more conspicuous marks (Nws and Nlp). Nevertheless, this pattern is not the same in the specimens of *Vulcanisciurus*, where we found more deep marks than shallow. The specimens of *Atlantoxerus getulus* used in this study show a high variability in the amount of microwear structures. This seem to correspond to the age of the individual, as the juveniles (MNCN-5526 and MNCN-5529), with decidual

dentition still present, show a higher frequency of deep marks, similar to the pattern found in *Vulcanisciurus*.

The Kruskal-Wallis test showed highly significant differences among species for all the variables (Table 2). The pairwise comparisons (Table 3) showed that *Vulcanisciurus* is significantly different from *Heteroxerus rubricati* for all the variables (Nfs, Nws, Nlp and Nsp), while its differences with *Atlantoxerus* n. sp. are restricted to some of the variables (Nfs, Nlp and Nsp) and it is not different from *Atlantoxerus getulus* for any variable. In fact, *Atlantoxerus getulus* is not significantly different from any species for any variables. The PCA (Fig. 4) illustrates the differences among species. The first three components of the PCA explained 92.6% of our sample's variance (Table 4). The first component (59% of the variance) is mostly represented by the number of fine scratches and small pits in the positive values and wide scratches and large pits in the negative values (Table 4). The second

Table 2. Results of Kruskal-Wallis tests (KW) for the microwear variables (see Table 1).

	df	KW chi-squared	p-value
Nfs	3	15.826	0.001
Nws	3	11.898	0.008
Nlp	3	14.673	0.002
Nsp	3	21.421	<0.01

Table 3. Non-parametric pairwise comparisons (Wilcoxon Rank Sum Tests) between species, with Bonferroni correction. Significant results ($p < 0.05$) shown in bold.

	<i>Atlantoxerus getulus</i>	<i>Atlantoxerus nov. sp.</i>	<i>Heteroxerus rubricati</i>
<i>Atlantoxerus nov. sp.</i>	0.382		
Nfs <i>Heteroxerus rubricati</i>	0.367	1.000	
<i>Vulcanisciurus</i>	1.000	0.011	0.008
<i>Atlantoxerus nov. sp.</i>	1.000		
Nws <i>Heteroxerus rubricati</i>	0.340	0.995	
<i>Vulcanisciurus</i>	1.000	0.317	0.011
<i>Atlantoxerus nov. sp.</i>	0.826		
Nlp <i>Heteroxerus rubricati</i>	0.362	1.000	
<i>Vulcanisciurus</i>	1.000	0.025	0.012
<i>Atlantoxerus nov. sp.</i>	0.376		
Nsp <i>Heteroxerus rubricati</i>	0.116	0.028	
<i>Vulcanisciurus</i>	1.000	0.010	0.005

component explains 18% of the variance, mostly weighted by the Nws, but also positively correlated with all the variables. The third component (15.5% of the variance) is explained by the number of large pits in the positive values and the number of large scratches in the negative values (Table 4).

Table 4. Results of the PCA including the dental microwear variables. The component matrix shows the correlations between the variables and each of the PCA factors.

	Component			
	1	2	3	4
Eigenvalues	2.45	0.7	0.54	0.3
% of variance	61.4	17.6	13.4	7.6
Nfs	0.78	0.48	0.28	-0.29
Nws	-0.7	0.6	-0.4	-0.02
Nlp	-0.78	0.23	0.54	0.2
Nsp	0.86	0.26	-0.08	0.42

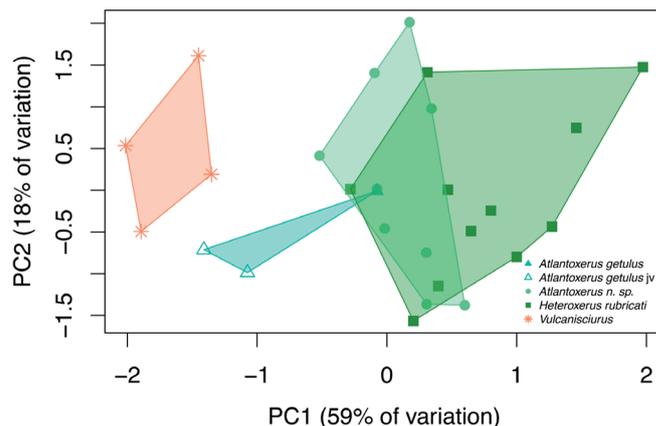


Figure 4. PCA plot of microwear variables (PC1 × PC2). Species from the tribe Xerini are represented in green colours, while the species from the tribe Protoxerini is represented in orange. The juvenile specimens of *Atlantoxerus getulus* are represented with empty triangles.

3.2. Enamel thickness

The results obtained for the enamel thickness measurement (Table 5) show that all the specimens measured have relatively thick enamel in the lingual area of the protocone, with values above 10% of the molar width. The two specimens of *Vulcanisciurus* examined showed an enamel thickness of 0.33 mm, which represented 13.69% and 14.10% of the tooth width, respectively (Table 5). This species shows the widest enamel thickness of all the

Table 5. Results for the enamel thickness measurement. Max: maximum.

Species	Specimen number	Max. width (mm)	Absolute enamel thickness (mm)	Relative enamel thickness (%)
<i>Vulcanisciurus</i>	BA-94-52-5	2.34	0.33	14.10
	BA-94-52	2.41	0.33	13.69
<i>Heteroxerus rubricati</i>	SR4A-71	2.07	0.26	12.56
	SR4A-94	2.14	0.25	11.68
<i>Atlantoxerus</i> nov. sp.	COL-C-218	2.10	0.24	11.43
<i>Atlantoxerus getulus</i>	ATL-5519	2.89	0.35	12.11

samples studied. The fossil specimens of *Heteroxerus* and *Atlantoxerus* have very similar values in maximum width, enamel thickness and percentage of enamel (see Table 5). The specimen of the extant *Atlantoxerus getulus* was the widest tooth analysed (maximum width of 2.89 mm). However, the enamel thickness is proportioned, and the percentage of enamel (12.11%) is very similar to *Heteroxerus rubricati* and *Atlantoxerus* n. sp. (11.68-12.56% and 11.43%, respectively).

4. DISCUSSION

Aside from the clear relationship between microwear features and dietary preferences, there are several factors that can be influencing the wear patterns and their interpretation. One same structure can be interpreted in several ways. For instance, large pits and wide scratches are the result of a hard diet, possibly caused by seed processing (Solounias & Semprebon, 2002), insects (Gomes Rodrigues *et al.*, 2009), or the ingestion of dust and grit with the food (Townsend & Croft, 2008). Likewise, course scratches have been related to the ingestion of grass (Solounias & Semprebon, 2002; Gomes Rodrigues *et al.*, 2009) or fruits (Gusovsky & Sinitsa, 2019). Therefore, we need to be careful in the inferences of diet based only on microwear data, and it is important to include other sources of data as we did here with the enamel thickness.

The first component of the PCA, which separates specimens with more frequent deep microwear features from specimens with higher number of shallower marks, can be interpreted as an ordination of the specimens along the hardness of their diet. Therefore, the first component of the PCA shows that *Vulcanisciurus* presents a harder diet than *Atlantoxerus getulus*, suggesting a diet based on hard nuts and seeds or insects. As shown by Solounias & Semprebon (2002), this could also be due to an arid environment that favours the ingestion of dust and grit, which would be consistent with the increasing aridity in

Namibia in the early Miocene (Mein & Pickford, 2008). These microwear results are consistent with the enamel thickness measurements, where *Vulcanisciurus* presented the thickest enamel, suggesting also a more abrasive or a harder diet.

The differences found between the juvenile and the adult specimens of *Atlantoxerus getulus* could be related to a change in their diet during the ontogenetic development. The similar microwear pattern found in the extinct *Atlantoxerus* from La Col-C and the adults of the extant *Atlantoxerus getulus* suggests similar dietary preferences, while the juvenile specimens of *Atlantoxerus getulus* present similar microwear features to *Vulcanisciurus*, with a higher amount of wide scratches and large pits. The extant species *Atlantoxerus getulus* from the Canary Islands eats seeds and fruit flesh when seasonally available (López-Darias & Nogales, 2008), which is consistent with the number of small pits and fine scratches found in the adult specimen. Therefore, the differences between adults and juveniles found here could be due to a higher ingestion of grit and dust during their period in the nest, as juveniles spend more time than adults in the burrows (Murie & Harris, 1982), or to the scarcity of fruits during the breeding season, forcing the juveniles to eat more seeds than fleshy fruits (López-Darias & Nogales, 2008). Finally, *Heteroxerus rubricati* from San Roque 4A shows microwear features that could be associated with grass eaters (Solounias & Semprebon, 2002; Gomes Rodrigues *et al.*, 2009).

The results of the microwear analyses were congruent with the enamel thickness. They showed similar diets between the Iberian species of squirrels, which could be related to a softer diet or with less dust in the Iberian environment than in the African one. Nevertheless, these results should be taken carefully until a more detailed work with more specimens and species allows us to establish the presence of statistical differences between populations.

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