

Variations in *Microtus arvalis* and *Microtus agrestis* (Arvicolinae, Rodentia) Dental Morphologies in an Archaeological Context: the Case of Teixoneres Cave (Late Pleistocene, North-Eastern Iberia)

Elisa Luzi^{1,2} · Juan Manuel López-García¹ · Ruth Blasco³ · Florent Rivals^{1,2,4} · Jordi Rosell^{1,2}

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Abstract Morphological and morphometric variations in the first lower molars of *Microtus arvalis* and *Microtus agrestis* from the late Pleistocene site of Teixoneres Cave (Barcelona, Spain) have been investigated in order to understand the modifications in dental patterns occurring in these two species in a peripheral region of their distribution area. It was possible to identify along the sequence differences in size and frequencies of morphotypes within the two populations, corresponding to environmental and climatic oscillations. Hypotheses to explain these intraspecific changes are discussed, and the variations are ascribed primarily to small-scale intraregional movements of these two rodent populations.

Keywords *Microtus arvalis* · *Microtus agrestis* · Morphology · Intraspecific Variation · Late Pleistocene

Introduction

Microtus arvalis (common vole) and *Microtus agrestis* (field vole) are arvicoline rodents with prismatic, ever-growing teeth. Their extant range covers a large part of continental Europe, from the Atlantic coast to central Russia. In the Iberian Peninsula, they are both present in the Pyrenean region. Isolated populations of *M. arvalis* have been reported in central Spain but its distribution area is widening due to the colonization of agricultural areas in the Castilla y León region (Luque-Larena et al. 2013). *Microtus agrestis* is present throughout northern Spain and in Portugal, where a cryptic lineage of this species has been detected (Paupério et al. 2012). Their remains, notably their molars, are present in the fossil record of late Pleistocene sites all across Europe, their habitat including most of the Mediterranean region (Kovalsky 2001). There are numerous studies describing their taxonomic, phylogenetic, and evolutionary position within the arvicolid tree (Haynes et al. 2003; Jaarola et al. 2004; Bužan et al. 2008; Jaarola and Searle 2008; Robovský et al. 2008), their biochronological, ecological, and environmental significance in the fossil record (Chaline 1972; Rekovets and Nadachowski 1995; Hernández Fernández and Peláez-Campomanes 2005; Sala and Masini 2007; Cuenca-Bescós et al. 2010), and the intraspecific phenotypic variation of the two species (Nadachowski 1982; Jaarola and Searle 2004; Kapischke et al. 2009; Markova et al. 2010).

Analyzing intraspecific morphological and morphometric differences in paleontological and archaeological contexts helps clarify processes and patterns of adaptation and evolution in rodents. It makes it possible to observe intraspecific variations over large time spans, and hence

✉ Elisa Luzi
elisa.luzi@urv.cat

¹ IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Marcel·lí Domingo s/n. Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

² Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya, 35, 43002 Tarragona, Spain

³ Centro Nacional de Investigación Sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain

⁴ ICREA, Institució Catalana de Recerca i Estudis Avançats, Barcelona, Spain

to recognize phenotypic changes and evolutionary trends in the history of species. In this study, we investigate the morphological and morphometric characters of the *M. arvalis* and *M. agrestis* populations of Teixoneres Cave, located in a peripheral region of their distribution area, in order to describe the modifications they underwent over time and, if possible, to determine the mechanisms of adaptation linked to changes in environmental conditions. *Microtus arvalis* and *M. agrestis* inhabited the region surrounding the site during the late Pleistocene but only the field vole is currently present in the area (IUCN 2015).

The Site

Teixoneres Cave belongs to the karst system of Coves del Toll. It is located at 760 m a.s.l., near the village of Moia (41°48'25" N, 2°09'02" E, Barcelona, Spain). The site has been known since the 1940s and has been excavated at various times by different research teams (Rosell et al. 2008). Current systematic excavations started in 2003 and are still ongoing. Teixoneres is a U-shaped cave and it presents three differentiated chambers (called X, Y, and Z), with a total length of 30 m. Five formations can be distinguished in the stratigraphy of the site, divided into ten archaeo-paleontological levels and 15 sub-units (Rosell et al. 2016; Talamo et al. 2016). So far, a portion of the upper sequence 160 cm thick has been excavated and divided into six lithostratigraphic units (I to IV, top to bottom). Units I and IV correspond to speleothems that cover a large part of the surface of the cave (Tissoux et al. 2006). Units II and III, with their respective subdivisions IIa-IIb and IIIa-IIIb, yielded lithic industries ascribed to the Mousterian and faunal remains of macromammals and

small vertebrates (Tissoux et al. 2006; Rosell et al. 2010, 2016; López-García et al. 2012; Sánchez-Hernández et al. 2014; Talamo et al. 2016). Recent ¹⁴C dating yields a chronological range of 33,060 cal BP at 68.2 % confidence at the top of unit II and >51,000 to 40,610 cal BP at 68.2 % confidence for unit IIIb (Talamo et al. 2016).

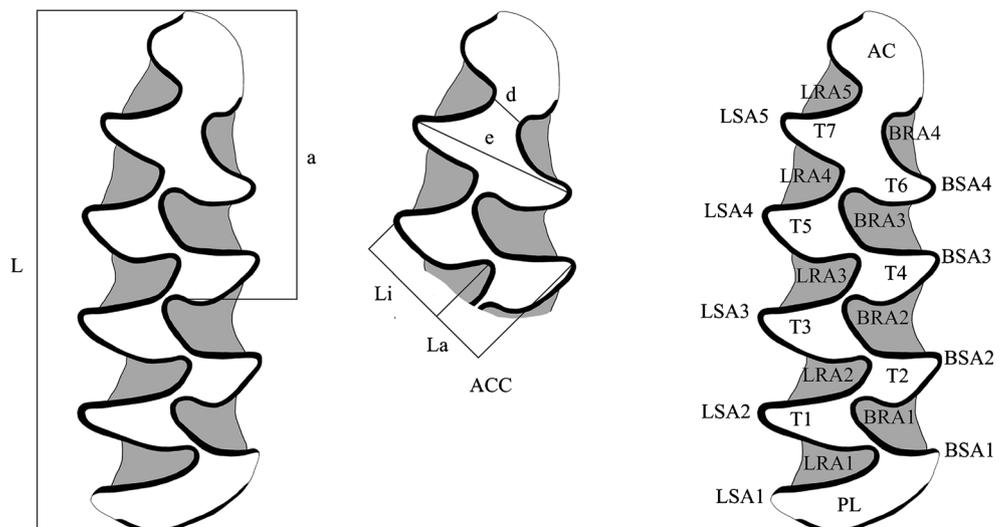
Material and Methods

The material analyzed in this study comes from levels IIb, IIIa, and IIIb of Teixoneres Cave and includes both published and unpublished findings from the most recent field seasons.

The morphology of 80 first lower molars (m1) from *M. agrestis* and 137 m1 from *M. arvalis* (both right and left) has been studied following the criteria given by Chaline (1972), Nadachowski (1982), Rekovets and Nadachowski (1995), and Markova (2013). In order to describe the elements of the occlusal surface of the m1, we applied the nomenclature proposed by Van der Meulen (1973): **LRA**, **LSA**, **BRA**, and **BSA** represent, respectively, lingual reentrant and salient angles and buccal reentrant and salient angles; **T** refers to triangles, and all are numbered consecutively from the posterior lobe (**LP**) to the anterior cap (**AC**). The morphotypes have been distinguished on the basis of the different degrees of development of reentrant and salient angles in the anterior part of the m1 and different degrees of separation between the elements of ACC, i.e., T6-T7-AC (Fig. 1).

The m1 of arvicolids presents diagnostic morphological features that allow the taxonomic identification of fossil and extant forms. Even though the morphological and morphometric characters in the m1 of the two species may overlap, *M. arvalis* and *M. agrestis* can be identified

Fig. 1 Nomenclature and measurement methods used for m1 in the description of arvicolines. **L**: total length; **a**: length of the anteroconid complex; **e**: width of the anteroconid complex; **d**: degree of closure of AC; **La**: width of T4; **Li**: width of T5; **PL**: posterior lobe; **ACC**: anteroconid complex; **AC**: anterior cap; **BRA**: buccal reentrant angle; **BSA**: buccal salient angle; **LRA**: lingual reentrant angle; **LSA**: lingual salient angle; **T1-T7**: triangles 1–7



and separated (Nadachowski 1982, 1984). *Microtus arvalis* presents a more symmetric and parallel disposition of both triangles and re-entrant angles, especially at the level of T6 and T7 and a more rounded ACC. On the other hand, *M. agrestis* shows a marked asymmetry between T4 and T5 and a stronger alternation of re-entrant

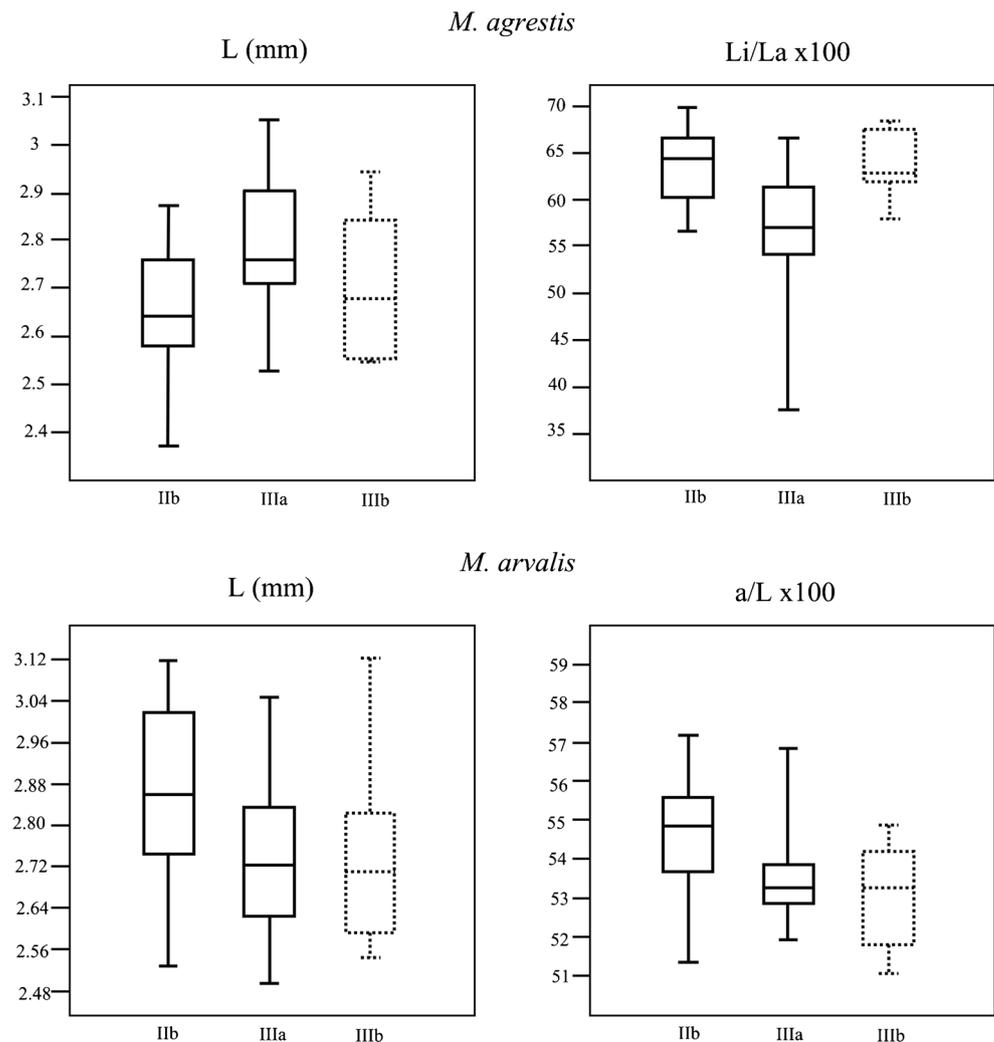
angle, which reduces the confluence between T6 and T7, giving a more angular shape to the ACC.

The nomenclature and measurement parameters used to analyze the first lower molars of the *M. arvalis* and *M. agrestis* of Teixoneres Cave follow those proposed by Van der Meulen (1973), Nadachowski (1984), and

Table 1 Measurements of m1 of *M. arvalis* and *M. agrestis*. n: number of specimens; mean: mean value of the sample; max: maximum value of the sample; min: minimum value of the sample; SD: standard deviation. All measures are in mm. For abbreviations of measurements taken see Fig. 1

	<i>Microtus arvalis</i> of Teixoneres					<i>Microtus agrestis</i> of Teixoneres				
	n	mean	max	min	SD	n	mean	max	min	SD
L	60	2.778	3.125	2.494	0.17	35	2.713	3.053	2.369	0.14
a	60	1.496	1.725	1.3	0.11	35	1.456	1.635	1.225	0.08
e	60	0.772	0.925	0.64	0.05	35	0.784	0.916	0.656	0.06
d	60	0.232	0.368	0.145	0.05	35	0.227	0.404	0.137	0.05
La	60	0.395	0.474	0.349	0.02	35	0.39	0.408	0.278	0.02
Li	60	0.57	0.626	0.474	0.03	35	0.592	0.74	0.516	0.04
a/L x100	60	53.81	57.17	51.03	1.46	35	53.69	56.94	51.47	1.4
La/Li x100	60	69.31	80.59	61.53	3.99	35	61.13	69.81	37.56	6.83
<i>Microtus arvalis</i> - IIb						<i>Microtus agrestis</i> - IIb				
	n	mean	max	min	SD	n	mean	max	min	SD
L	22	2.855	1.725	2.528	0.17	17	2.662	2.871	2.369	0.12
a	22	1.56	1.725	1.361	0.1	17	1.436	1.566	1.225	0.08
e	22	0.787	0.925	0.704	0.05	17	0.775	0.869	0.656	0.06
d	22	0.222	0.368	0.147	0.05	17	0.219	0.32	0.137	0.05
La	22	0.393	0.451	0.349	0.02	17	0.364	0.384	0.337	0.01
Li	22	0.571	0.625	0.512	0.03	17	0.569	0.606	0.52	0.02
a/L x100	22	54.63	57.17	51.32	1.47	17	53.94	56.94	51.69	1.64
La/Li x100	22	68.93	78.57	61.53	4.03	17	64.06	69.81	56.64	3.58
<i>Microtus arvalis</i> - IIIa						<i>Microtus agrestis</i> - IIIa				
	n	mean	max	min	SD	n	mean	max	min	SD
L	23	2.729	3.049	2.494	0.15	13	2.787	3.053	2.527	0.14
a	23	1.461	1.68	1.308	0.09	13	1.481	1.611	1.355	0.07
e	23	0.752	0.847	0.64	0.04	13	0.804	0.916	0.671	0.07
d	23	0.226	0.348	0.145	0.04	13	0.229	0.285	0.159	0.04
La	23	0.39	0.43	0.352	0.02	13	0.347	0.408	0.278	0.03
Li	23	0.566	0.626	0.474	0.03	13	0.623	0.74	0.516	0.06
a/L x100	23	53.55	56.86	51.19	1.17	13	53.15	54.73	51.68	0.8
La/Li x100	23	69.06	80.59	63.53	4.54	13	56.31	66.55	37.56	8.28
<i>Microtus arvalis</i> - IIIb						<i>Microtus agrestis</i> - IIIb				
	n	mean	max	min	SD	n	mean	max	min	SD
L	15	2.74	3.125	2.545	0.17	5	2.693	2.944	2.546	0.16
a	15	1.454	1.675	1.3	0.11	5	1.46	1.635	1.39	0.1
e	15	0.782	0.882	0.718	0.04	5	0.763	0.817	0.723	0.03
d	15	0.256	0.35	0.17	0.04	5	0.247	0.404	0.173	0.09
La	15	0.405	0.474	0.36	0.02	5	0.372	0.399	0.324	0.03
Li	15	0.576	0.622	0.537	0.02	5	0.584	0.61	0.56	0.01
a/L x100	15	53.03	54.87	51.03	1.32	5	54.21	55.53	51.47	1.6
La/Li x100	15	70.26	78.34	67.03	3.03	5	63.71	68.43	57.85	4.35

Fig. 2 Box plot showing significant measurements of *M. agrestis* (L and Li/La) and *M. arvalis* (L and a/L). Black lines: levels IIb and IIIa. Dotted: level IIIb (not statistically significant)



Cuenca-Bescós and Laplana (1995). **L** represents the total length of the tooth, **a** the length of the anteroconid, **d** the degree of closure of the anterior cap, **e** the width of the anteroconid complex (ACC), **La** the width of T4, and **Li** the width of T5. **La/Li** is the ratio between the values La and Li and quantifies the degree of buccal-lingual asymmetry of the m1; **a/L** is the ratio between the values of a and L and quantifies the development of the anterior part of the tooth. Only complete specimens have been measured. Juvenile specimens have been excluded from the study. Photographs of the teeth have been taken using a Dino-lite USB microscope at 90× and measurements taken using ImageJ software. All measurements are given in millimeters.

In order to assess the statistical significance of the intraspecific differences between different levels, a t-test has been performed on the data using PAST 3 software with the null hypothesis being of the two samples having equal mean and significance achieved for values of $p < 0.05$ (Hammer and Harper 2006).

Results

Morphometrics

The *M. arvalis* and *M. agrestis* populations undergo several changes through the sequence of Teixoneres Cave (Table 1).

The L in the m1 from *M. arvalis* is significantly higher in level IIb than in level IIIa ($p = 0.012$). This increase is due to an elongation of the anteroconid, as shown by the modification of the a/L index ($p = 0.009$), while the ratio between the labial and lingual triangles stays constant ($p > 0.5$). On the other hand, L in the m1 from *M. agrestis* decreases from level IIIa to level IIb ($p = 0.016$), with stable a/L values ($p > 0.12$) and a more marked asymmetry between T4 and T5 ($p = 0.001$) (Fig. 2).

Level IIIb has not yet yielded enough remains of *M. arvalis* and *M. agrestis* to be statistically significant per se ($n = 15$ for *M. arvalis* and $n = 5$ for *M. agrestis* with $p > 0.05$ for all

values) but data from this level are included in order to achieve a better understanding of the two populations as a whole.

Morphology

Different morphologies can be recognized within the two populations (Fig. 3).

For *M. arvalis*:

- type A: opposed T6–7, broad confluence with AC, and BRA4 more developed than LRA5;
- type B: T6 and T7 slightly alternating, broad confluence with AC;
- type C: T6–7 and AC confluent, with small incipient BSA5 and LSA6;
- type D: reduced confluence between T6–7 and AC, with developed BSA5 and LSA6.

All morphotypes are present in the three levels, type B always being dominant and type C very rare.

For *M. agrestis*:

- type 1: BRA4 and LRA5 visible but poorly developed;
- type 2: BRA4 well developed;
- type 3: well-developed LRA5 and visible LSA6;
- type 4: with small incipient BSA5 and LSA6;
- type 5: T6 completely separated from T7;
- type 6: T6 completely separated from T7, with LSA6 and LRA6 more developed than type 5 and a pronounced asymmetry between the lingual and the buccal side of the tooth.

The morphotypes change in frequency within the sequence. Type 6 is present only in level IIIa, where type 1 is absent (Table 2).

Discussion

Quantitative variations in small-mammal fossil assemblages linked to changes in climatic conditions have been studied extensively in the recent years (e.g., López-García et al. 2015; Rofes et al. 2015; Berto et al. 2016; Royer et al. 2016). In the specific case of Teixoneres Cave, López-García et al. (2012) were able to detect at least two different environmental and climatic oscillations: dry and cooler conditions in sub-unit IIb and humid and temperate conditions in level IIIa. Even though the study of new material from sub-unit IIIb is still in progress, it seems to indicate that Mediterranean conditions persist, as in IIIa, but with an increased presence of *Iberomys cabreræ* and *Microtus (T.) duodecimcostatus*. The presence of *Capreolus capreolus* and *Equus hydruntinus* among the large mammals record (Talamo et al. 2016) confirms the stronger Mediterranean climate setting. Therefore, a low occurrence of *M. arvalis* and *M. agrestis*, more adapted to mid-European conditions, characterizes, to-date, level IIIb.

Sub-units IIb and IIIa yielded a sufficient number of specimens (a total of 108 *M. arvalis* and 68 *M. agrestis*) to attempt some interpretations. A first connection can be made between the environmental and climatic changes recognized along the sequence and the modifications occurring within the two

Fig. 3 Morphotypes of *M. arvalis* (a: left m1, from level IIb) and *M. agrestis* (1 and 4: right m1, from level IIb; 2, 3, 5 and 6: left m1, from level IIIa). Occlusal view. Scale: 1 mm

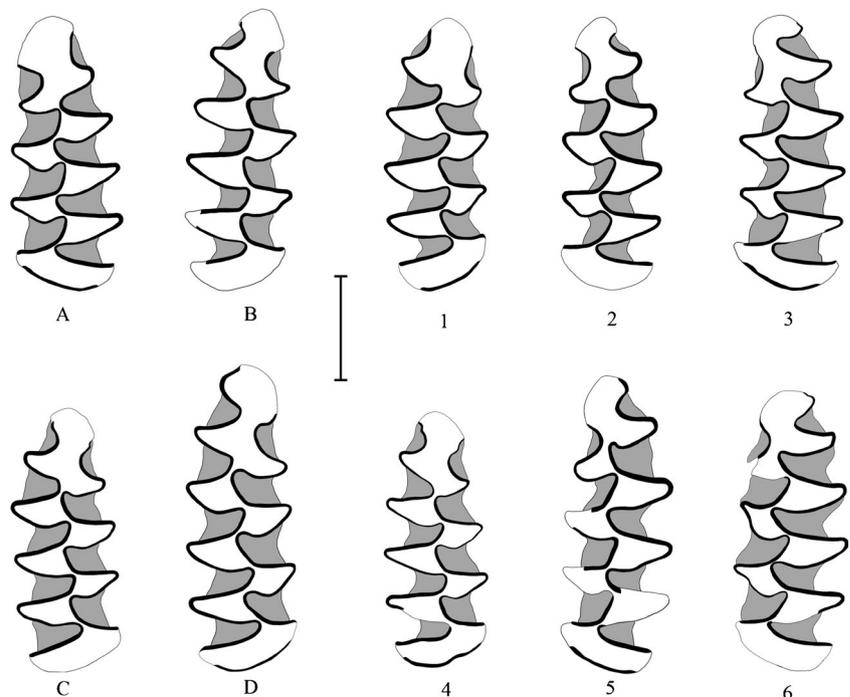


Table 2 Frequencies of morphotypes of *M. agrestis*. -: absent; *: present (<15 %); **: abundant (15–35 %); ***: dominant (>40 %). n: number of m1 analysed

Morphotype	IIb	IIIa	IIIb
1	*	-	**
2	***	**	***
3	*	***	*
4	*	*	*
5	*	*	-
6	-	*	-
n	49	19	8

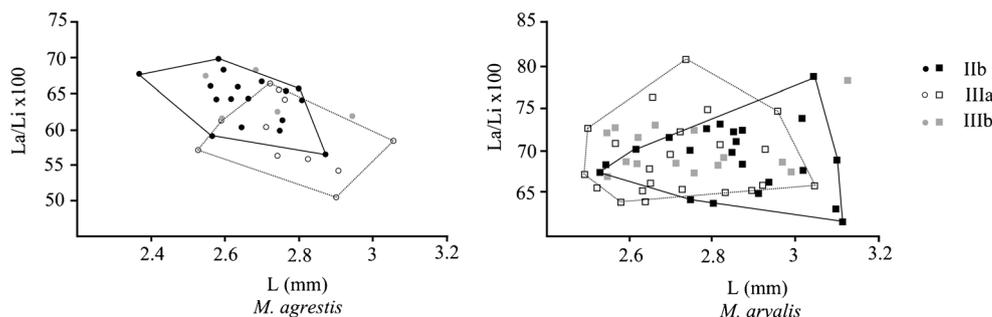
populations. The population of *M. arvalis* maintains the same morphotypes with the same distribution in both levels. The differences lie in the size of m1 and in particular in the elongation of the anteroconid with respect to the total length of the tooth. Assuming that, within a particular species, bigger tooth size corresponds to a larger body size (Gould 1975; Ungar 2010), the increase in the values from sub-unit IIIa to IIb could represent a local adaptation to a climatic change in precipitations and temperature. Larger common voles exhibit better management of water and heat dispersion than smaller individuals, who tend to drink more (Dienske 1979; De Jonge 1983), thus spending more time in zones without cover and increasing their vulnerability to predation. Furthermore, a larger m1 entails the obvious advantage of a larger grinding surface, and the teeth can thus support higher abrasion and consequently wear at a slower rate. So, given the decrease in both precipitation and temperature in the passage from sub-unit IIIa to IIb, that part of the population with a larger m1 would have found itself in a favorable position to proliferate and thus raise the mean L and a/L values of the fossil record.

The two sub-populations of *M. agrestis* present distinct characteristics in terms of measurements and morphotype distribution. In sub-unit IIIa, the m1s are large and asymmetrical, whereas in IIb they are smaller and more symmetrical (Fig. 4). The most complex morphotype 6, present in IIIa, is absent in IIb, where the more simplified morphotype 1 is present.

Despite the low number of specimens in sub-unit IIIb, we can observe that the more complicated morphotypes – 5 and 6 – are absent while the most simple one is present. In *M. agrestis*, water consumption increases with body size, especially at higher temperatures (Dienske 1979). The presence of large-sized field voles in sub-unit IIIa is in agreement with the humid conditions detected for this level in previous studies (López-García et al. 2012), as is the decrease in size in level IIb, which is connected to lower precipitation and a drier climate. The reduced asymmetry and the loss of a morphotype with the occurrence of a new one can also be related to the same climatic changes.

In arvicolids, the anterior part of the first lower molar (ACC) and the posterior part of the third upper molar (M3; called the posterocon complex) are the most susceptible to morphological changes and these differences have been used in paleontology to identify species and to draw evolutionary lines and patterns (Heller 1936; Chaline 1972; Nadachowski 1982; Rekovets and Nadachowski 1995; Markova 2013; Borodin and Markova 2015). Recent studies also highlight the role of developmental pathways and environmental factors in shaping the morphology of teeth in rodents (Jernvall 2000; Kassai et al. 2005; Laffont et al. 2009; Renaud et al. 2009; Jernvall and Thesleff 2012). In particular, a study of the M3 of *Clethrionomys* (= *Myodes*) *glareolus* (Ledevine et al. 2010b) suggests that changes in morphology could be triggered by size variations in teeth linked not to the developmental cascade along the molar row but rather to epigenetic factors. Because of the tooth being larger, the extra space available at the end of it (at the posterocon in the case of M3) would allow a complication of the morphotype and the addition of a further triangle. A viable hypothesis for the shift in the *M. agrestis* population might thus ascribe the change to epigenetic causes: the modification of environmental conditions could be affecting, directly or as a side effect, the shape of teeth in single individuals. In Teixoneres Cave, we observe that the changes in morphology occur in m1 from *M. agrestis* with the same relative space available at the anterior end of the tooth, as shown by the relative stability of a/L index, while in *M. arvalis* morphologies remain stable despite the increase in length due to an elongation of the anteroconid.

Fig. 4 Graphic representation of the variations in the *M. agrestis* and *M. arvalis* populations



Variations in the overall size of m1 and in the a/L index do not seem to affect the shape of ACC. So, in this case, even though epigenetic factors cannot be completely excluded, other factors have to be considered.

Dental patterns have proved to be strongly related to genetic factors in arvicolines (Stohl 1984; Polly et al. 2011; Markova et al. 2013a), and heritability, especially from the maternal line, plays a fundamental role in determining molar morphology. Furthermore, differences in molar shape and the frequencies of morphotypes have been described for several species, and the geographic distribution related to the history of the species (i.e., isolation, dispersal, contact with nearby populations) accounts for most of the variations observed (Tougaard et al. 2008; Ledevin et al. 2010a; Markova et al. 2010, 2013b; Paupério 2012; Renvoisé et al. 2012; Tiunov et al. 2013; Cucchi et al. 2014). While it is impossible to test directly the hypothesis of heritability in the context of Teixoneres Cave, the geographical setting of the site suggests the hypothesis that there was contact between different groups. Teixoneres Cave is located at the southern boundary of the distribution areas of both species in north-eastern Iberia, so the periodic isolation of groups and the arrival of new ones are easier to observe. Furthermore, being located at the intersection between the coastal and central part of north-eastern Iberia, at 760 m a.s.l. and surrounded by creeks, the site is set in a transitional zone that can allow intra-regional movements of small mammals to and from the littoral, from lower to higher altitudes, and along the water streams. Therefore, the morphological variations in *M. agrestis* could be due to a displacement of populations moving to colonize new territories made available by favorable environmental conditions. Contact between the newcomers and the local individuals could have increased the variability of the morphotypes. On the other hand, the lack of changes in the *M. arvalis* phenotypes can be interpreted as indicating a geographically distinct and stable population. This may have been a consequence of the high territoriality and high reproductive capacity of the common vole (Dienske 1979; De Jonge 1983).

It is not usual to observe such variations in the late Pleistocene fossil record (Nadachowski 1982; Rekovets and Nadachowski 1995) and in a relatively short period such as those represented in the sequence of Teixoneres Cave. However, the present case proves that it is possible in an archaeological context to notice significant intraspecific differences linked to local environmental conditions and intraregional population movements.

Conclusions

The populations of *M. arvalis* and *M. agrestis* from Teixoneres Cave provide an example of quantitative and qualitative intraspecific differences induced by environmental

factors observable in an archaeological context. The data presented support the previous climatic and environmental reconstructions inferred from the study of the small mammal fossil assemblages. They also describe the dynamics of adaptation of the two populations in a peripheral region of their area of distribution.

The variations in length of the m1 can be directly related to climatic changes, acting on both populations in favor of appropriately sized individuals. Bigger *M. arvalis* are favored by drier conditions. In contrast, *M. agrestis* tends to get smaller when precipitation diminishes.

On the other hand, the morphological modifications appear as a secondary result of the environmental changes. While the population of *M. arvalis* proved to be geographically stable, retaining the same morphotypes at the same frequencies throughout the sequence, *M. agrestis* underwent several modifications, providing evidence of local dispersals of sub-populations from nearby territories triggered by the increase in suitable areas available. Although epigenetic mechanisms regulating tooth development certainly have a role in shaping dental variability, small-scale regional movements and the local history of populations, especially in peripheral areas of the species range, play a major part in the definition of the morphological traits of molars. Additional study will be necessary to assess and highlight variation patterns on wider regional context and larger temporal scale.

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